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Investigating Changes in Pacific Herring Spawn Density (layers)

Étude des changements de la densité du frai du hareng du Pacifique (couches)

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ABSTRACT

This report examines biological, ecological and methodological factors that affect estimates of egg density, or egg 'layers' in spawning areas of the British Columbia coast. Recent literature indicates that the density of spawning herring depends on intrinsic behavioural mechanisms that apply to all pelagic schooling fish, including herring. If so, egg density may not vary directly with the spawning stock biomass (SSB). This report examines the relationship between egg density and SSB by analysis of the metrics (i.e. measurements) of individual spawning *events*, of which there are several hundred per year in BC. The important metrics are spawn length, spawn width and number of egg layers. Spawn metrics were assessed and compared with abundance trends in the five main herring populations in BC. In general, the metrics do not decrease or increase in unison with the abundance of populations. Even as all BC populations were in a period of contraction for the last 5 years, the dimensions of individual spawn events remained relatively consistent, although there were fewer spawn events. An exception to the apparent consistency of spawn metrics was egg density or egg layers. In BC the mean number of egg layers declined significantly in all coastal areas over the last two decades but the decline was especially sharp during the last 5 years. Mean egg layers declined in some regions even as the total spawning area increased. This decline in layers might have biological or methodological explanations that are examined in this paper. There is no obvious biological explanation and analysis in this paper shows that survey effort has remained relatively consistent. An unexpected observation was that in the last decade there has been an increase in the incidence of 'trace' observation – recorded arbitrarily and unrealistically as 0.01 layers. The incidence of the trace category was relatively rare in the early years of diver surveys but it has increased and now accounts for more than 40 percent of all observations in most regions in recent years. It seems probable that this change in estimated egg layers is associated with a subtle and unintentional change in dive survey protocols. A recommendation is that the rationale for using the trace category as true estimate of layers should be re-examined. Other recommendations refer to potentially important details about the computational procedures used to derive the herring spawn index used in support of the assessment model.

RÉSUMÉ

Le présent rapport examine les facteurs biologiques, écologiques et méthodologiques qui influent sur les estimations de la densité des œufs ou des « couches » d'œufs dans les aires de ponte de la côte de la Colombie-Britannique. La documentation récente indique que la densité du hareng frayant dépend de mécanismes comportementaux intrinsèques qui s'appliquent à toutes les espèces pélagiques rassemblées en bancs, y compris au hareng. Si c'est le cas, il se peut que la densité des œufs ne varie pas directement en fonction de la biomasse du stock reproducteur (BSR). Le présent rapport étudie le lien entre la densité des œufs et la BSR en analysant les paramètres (c.-à-d. les mesures) des divers *événements* de ponte qui se produisent par centaines chaque année en C.-B. Les paramètres importants sont la longueur du frai, la largeur du frai et le nombre de couches d'œufs. On a évalué les paramètres du frai et on les a comparés aux tendances de l'abondance dans les cinq principales populations de hareng de Colombie-Britannique. De façon générale, les paramètres n'ont pas tendance à diminuer ou à augmenter en fonction de l'abondance des populations. Les dimensions des différents événements de ponte sont restées relativement stables même si toutes les populations de C.-B ont connu une période de contraction au cours des cinq dernières années et s'il y a eu moins d'événements de ponte. La densité des œufs ou les couches d'œufs ont toutefois constitué une exception à l'uniformité apparente des paramètres relatifs au frai. Pendant les deux dernières décennies, le nombre moyen de couches d'œufs a diminué de façon notable dans toutes les zones côtières de la C.-B., mais la diminution a été particulièrement marquée au cours des cinq dernières années. Dans certaines régions, les couches moyennes d'œufs ont diminué même si l'aire totale de ponte a augmenté. Cette diminution des couches pourrait s'expliquer par des facteurs biologiques ou méthodologiques examinés dans le présent document. Il n'existe pas d'explication biologique évidente et l'analyse exécutée dans le présent document montre que les efforts déployés pour les relevés sont restés relativement uniformes. De façon inattendue, on a toutefois constaté au cours de la dernière décennie une augmentation de la fréquence des observations de frai « à l'état de traces », notées de façon arbitraire et irréaliste comme des couches 0,01. Relativement rare les premières années où les relevés ont été effectués en plongée, cette catégorie de frai « à l'état de traces » a augmenté et représente maintenant plus de 40 % des observations effectuées dans la plupart des régions aux cours des dernières années. Il semble probable que ce changement des couches estimatives d'œufs soit associé à une modification subtile et non intentionnelle des protocoles de relevé en plongée. Une recommandation demande de réexaminer les raisons qui justifient le recours à la catégorie de frai à l'état de traces comme estimation exacte des couches. Les autres recommandations se rapportent à des détails potentiellement importants concernant les méthodes de calcul employées pour déterminer l'indice du frai du hareng dans le modèle d'évaluation.

INTRODUCTION

A fundamental question about herring reproductive biology is how the spatial distribution of spawning herring and the distribution of their eggs changes with varying levels of abundance, or spawning stock abundance (SSB). Throughout the northeast Pacific each major herring population spawns in many different places within a region (Hay et al. 2000, Haegele and Schweigert 1985, Schweigert and Haegele 2001). Along the coast of British Columbia there are several hundred records of spawning each year. Each of these records may be a separate event that requires the mutual reproductive readiness of many individuals, usually many millions. This paper addresses the following questions: Do the characteristics of spawning events change as herring population abundance varies? Are individual spawning events orchestrated by the population abundance as a whole, or by the abundance and density of the participants in each spawning event? Although simple, these questions have implications for basic biological understanding of fish behaviour as well as fisheries management. Specifically, do density-dependent interactions among spawning individuals vary during periods of high or low population abundance? If so, we might expect high egg density (or high egg layers or high eggs/m^2) when SSB was high and vice versa. If density-dependent interactions do not change, egg density (eggs/m^2) would be relatively consistent among years, even as SSB changes. Further, the consequence of low spawning biomass would be a reduction in the total area of spawning, but not necessarily in the density of eggs within spawning areas. The annual spawn survey provides an essential fisheries-independent index of abundance that is used for annual herring assessments. As much as possible it is essential to understand the factors affecting estimates of egg density.

In the North Pacific herring spawn in inter-tidal and shallow sub-tidal areas (Haegele and Schweigert 1985). Spawn deposition is usually assessed by measuring two main spatial dimensions: length and width plus a separate measure of spawn density that would reflect the number of eggs in a square metre of a spawning bed. In recent years, SCUBA divers have quantified egg density as the number of egg layers. Usually there are fewer than 3-4 layers, and rarely more than 10. The number of spawn layers, when combined with estimates of the proportion and type of surface areas of the seabed that is covered with vegetation, can be converted to estimates of eggs/m^2 (Schweigert 1993). When summed over a spawning bed the total egg number can be converted to an estimate of spawning biomass based on a relative fecundity estimate of about 200 eggs/g for females (Hay 1985) or about 100 eggs/g (or 10^8 eggs/t) when weights of both sexes of a spawning group are included.

Annual quantitative assessments of spawn deposition are used as a fisheries-independent index for all eastern-Pacific herring populations that are fished commercially. The form of the spawn assessment varies among different jurisdictions, but all have the fundamental assumption that, for the assessment area, the cumulative measure of spawn is proportional to the spawning stock biomass (SSB) that deposited the eggs. Recent herring assessments in British Columbia indicate a decline in most herring stocks, to the extent that most commercial herring roe fisheries were closed in 2009 and 2010. In 2010 independent comments from a number of fishery managers, fishers and processors noted that the apparent spawning biomass in several assessment areas appeared to be higher than recent assessments indicate (e.g. Cleary et al. 2010, Schweigert et al. 2009). The recent contrast between field observations. which indicated relatively abundant herring stocks and the more conservative assessments was part of the rationale for examination of egg layers in this report.

Different perspectives between fishers and assessment scientists about relative and absolute abundance of commercially fished populations are not unexpected and are well known in many fisheries (Hilborn and Walters 1992). When fishers argue that there is more fish present than are estimated by formal scientific assessments, there could be an appearance of self-interest so it is prudent for scientists to be cautious and sceptical. On the other hand, as Hilborn and Walters (1992) point out, scientists must not automatically dismiss the possibility that the field observations are incorrect. This advice may be appropriate at the present time relative to BC herring abundance because some DFO fishery managers, on the basis of field observations, also felt that some herring stocks were more abundant than were indicated by recent assessments.

If field observations were valid then the assessments could be too conservative, perhaps as a consequence of some subtle change in spawning biology that has affected the spawn data input to the assessment model or perhaps as a computational error. Alternately, the assessments may be correct but field observations may be flawed as a consequence of some change in the biology of herring. For instance, it is clear that conventional estimates of CPUE (catch per unit effort) can be misleading for many small pelagic species that tend to condense their geographical distributions as SSB declines, with a consequence that CPUE in some areas may increase – opposite to the trend in biomass (Parish 1999). Perhaps similar processes occur in Pacific herring where a concentration of herring into smaller areas renders them more conspicuous. If so, the appearance of high abundance in one area would not necessarily be a valid indication of the abundance of the population as a whole.

Spawn surveys represent a significant component of assessment methods and this report examines the possibility of systematic change in the estimates of herring spawning deposition, either as a natural biological change or a problem in the spawn data collection or analysis. The main focus of this paper is on factors that might affect the herring spawn index, especially the potential for change in the estimate of the ‘layers’ of spawn.

1.1 INDICES OF SPAWN AND BASIC ASSUMPTIONS

Spawn assessments are similar to other fisheries-independent indices, such as acoustic assessments, but spawn assessments have the advantage of providing an index that is directly related to the sexually mature component of a population because relative fecundity, or the number of eggs produced by females per unit body weight, is nearly constant at about 200 eggs/g (Hay 1985) or 100 eggs/g (or 10^8eggs/t) for both sexes. Further, estimation of a spawn index does not encounter problems related to species identification or other issues related to acoustic surveys.

Depending on the location or management jurisdiction, spawn indices may be used to estimate the spawning biomass directly, or used as a key element (or tuner) in some form of virtual population analysis or age-structured analysis. The impact of the spawn index on the estimated spawning biomass will depend on how much weight is given to the index, within the assessment model (Cleary et al. 2010). In British Columbia, herring spawn indices are used as tuners for age-structure analysis in the main stock assessment areas (Fig. 1) where there are sufficient population data to support age-structure analyses. In other ‘minor areas’ (Fig. 1) the spawn index is used more directly: an estimate of the spawning biomass is derived directly from the spawn index.

Herring spawn assessments are conceptually simple but there is a basic assumption that all spawning is located and estimated. In practice, however, it is understood that sometimes some is missed, but in general such omissions are not believed to have significant impacts on the outcome of assessments. One aspect not usually measured, but could be, is the *effort* made to find spawn. For instance, the task of searching for spawn requires considerable effort. Additional effort is required for the logistical deployment of people to measure spawn. Although these topics are discussed every year at assessment meetings, the search effort for spawn is not directly incorporated in the assessment models. Instead the models usually assume that all spawn is found and all is measured consistently over time. For such an assumption to be fully met, the resources (or ‘effort’) to conduct the spawn surveys must be available and equal to the task. For instance, the survey logistics require that the survey resources (support vessels, divers, and sometimes spawn-spotting aircraft) be available sufficiently early, to assess early spawns, and sufficiently late, to cover late spawns. Complete spawn assessments also require sufficient resources to examine multiple spawns that may occur concurrently in widely separate locations. Further, inoperable weather conditions can confound spawn assessment resources.

A mismatch between survey resources could diminish the search effort to find spawn and perhaps the required effort to evaluate spawn. If this effort were diminished to the point where significant spawn is missed, then there could be a corresponding decrease in the cumulative measure of spawn deposition. This aspect is considered briefly in the present report.

1.2 SPAWN METRICS: REGION-BASED OR EVENT-BASED

The term ‘metric’ is used to describe various measurements of herring spawn, such as length and width, where the fundamental unit is a metre (m). It also is used here to describe the quantification of herring spawn in ‘layers’. Metrics of herring spawn data can be examined at different geographical units. Analysis in this report distinguishes between two types. One is region-based where the metric describes spawn according to each of the five assessment areas in BC (Fig. 1). The other is event-based where the metric describes the characteristics of individual spawn events. This distinction may be biologically important because density-dependent processes that operate during spawning are best examined according to event-based data configurations. Spawn events, or spawn records, have unique spatial dimensions such as unique mean lengths, mean widths, mean depths and unique egg densities such as the mean number of egg layers.

The distinction between region-based and event-based analyses is relevant to the main issues addressed in this paper: do spawn layers change in relation to changes in herring abundance? If egg density is controlled mainly by density-dependent processes operating within spawn events, there may not necessarily be any relationship between total abundance (SSB) and the unique properties of spawn events, especially egg layers.

1.3 OBJECTIVES FOR THIS PAPER

There are two basic objectives of this paper: (1) to review information that is known, or assumed, or hypothesized about physiological, ecological and behavioural controls that affect Pacific herring spawning behaviour, as factors that can affect the number of egg layers in spawning sites; (2) to review information about factors that affect the estimation of egg layers and the variability of those estimates. The second objective is mainly concerned with aspects of the resources, effort and methodology of spawn surveys.

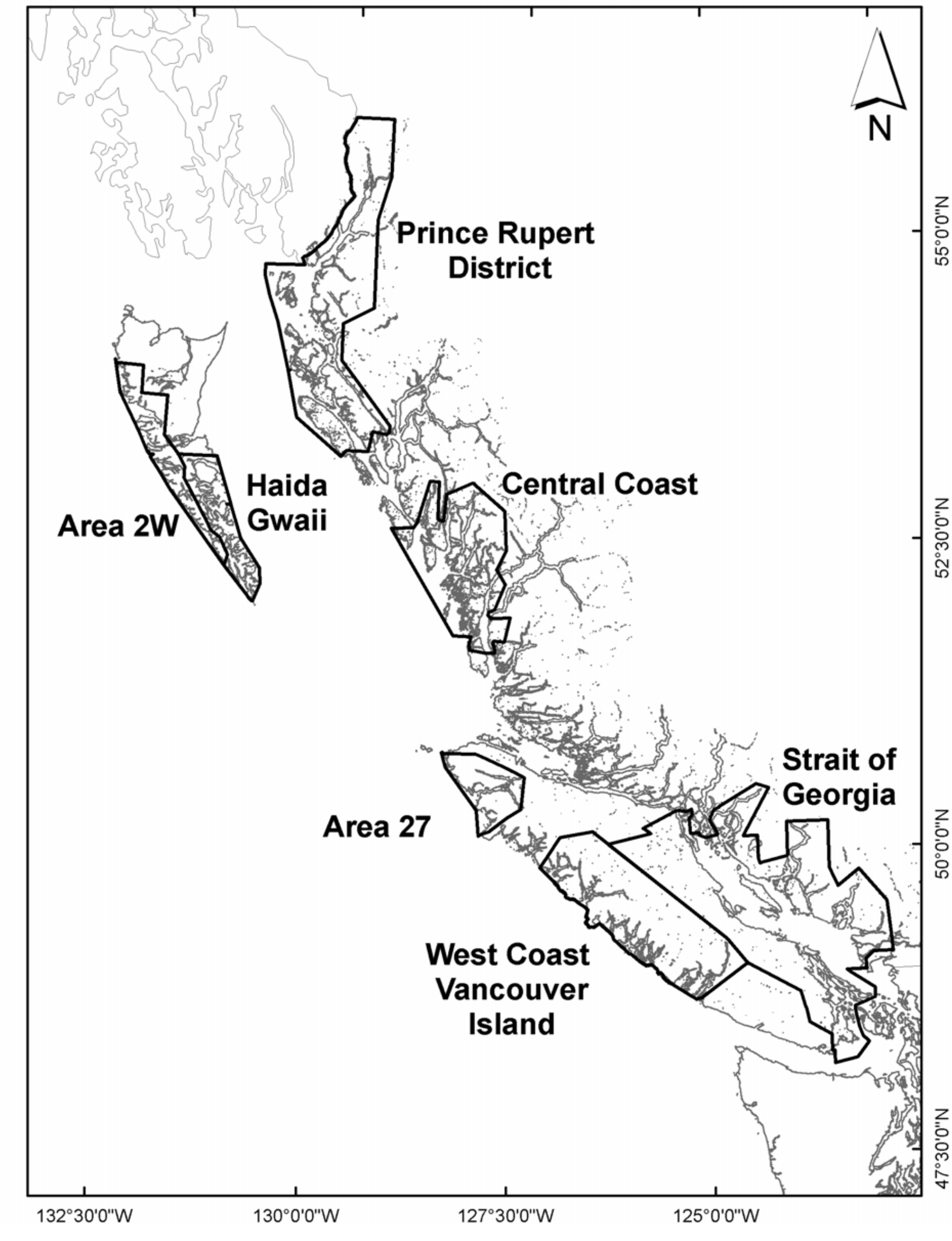

Figure 1. Map of B.C. herring stock areas. The five major stock are Haida Gwaii (HG or QCI 2E), Prince Rupert District (PRD), Central Coast (CC), Strait of Georgia (SOG), West Coast Vancouver Island (WCVI), and the minor stock areas are Area 2W and Area 27.

METHODS

2.1 THE HERRING SPAWN DATABASE AND ANALYSIS

The herring spawn data base in Access© is maintained by the Pacific Biological Station, Fisheries and Oceans Canada. For nearly 30,000 records of herring spawning collected since 1928, there is information on the date (year, month, day), location and approximate size of each spawn event, including an estimate of the length along the shore, width and egg density.

This paper relies mainly on herring spawn data collected since 1984, when coast-wide diver surveys were implemented. Beginning at that time most estimates of spawn length, width and number of egg layers were made by SCUBA divers. The protocols for diver surveys are provided by Fort et al. (2009) and available on a Fisheries and Oceans Canada website (http://www.pac.dfo-mpo.gc.ca/science/species-especes/pelagic-pelagique/herring-hareng/hertags/pdf/SurveyManual.pdf). Relevant details about the structure and content of the herring spawn database are presented in Appendix 1a.

This report includes information on estimated spawning biomass from each herring assessment region in BC (Fig. 1) provided in Appendix Tables 2.1 to 2.5, for each herring assessment region, in the annual herring assessment report (Cleary et al. 2010). The assessment report includes detailed information about the methodology for estimating the herring spawn index. A key part of that methodology is reproduced in Appendix 1b.

All analyses in this paper were made using Microsoft Access© and Excel©. Statistical tests were made using Minitab© (version 14). All statistical analyses were confined to simple comparisons using correlations, linear regression analysis or ANOVAs. Significance levels, when applicable, were reported as NS (non-significant) for probability values > 0.05.

2.2 QUANTIFYING SPAWN SURVEY EFFORT IN SPACE AND TIME

Between 1984 and 1987 surveys of spawn by SCUBA diver teams began as research surveys in various parts of the BC coast. By 1988 diver surveys were used for most areas of the BC coast. Detailed protocols for the survey methodology are presented in Fort et al. (2009). Divers assess spawn along *transects* (Fig. 2-3) by first determining the approximate margins of spawn and then placing a leadline across a spawn, perpendicular to the shore. Then starting at the deepest end divers proceed shoreward. At selected points, called *stations*, the divers stop and estimate the spawn density, in terms of a visual estimate of spawn layers (Fig. 4). This is done within a 0.5 m^2 *quadrat* that also is used to estimate the proportion of the seabed, within the quadrat, that is covered by vegetation. Divers also assess the numbers of layers on the bottom and the dominant bottom substrate (rocks, mud, sand, etc). In most instances, if herring spawn occurs, it is one or more vegetative species (macrophytes) used as spawn substrate. Spawn layers are assessed for each macrophyte present (usually there is only one) and also on the bottom substrate, if eggs are present there. The spawn width is the distance between the outermost (usually the deepest) margin of spawn and the point closest to the shore. On the field sheets this is noted as the *distance*.

Spawn widths are estimated as the mean of all transect distances within the spawning bed. Estimates of mean egg density are based on a two-stage sampling design (Schweigert et al. 1985, 1990). Average egg density for each spawning bed is estimated as the weighted mean of the means of a series of quadrats located along each transect, where the weighting is based on the length of each transect. *(The preceding sentence is underlined because it is important and* *discussed later).* Schweigert 1993 provides a detailed description of the methods used to estimate egg numbers (a condensed version is shown in Appendix 1b). It is done according to equations that relate the observed estimate of egg layers on each vegetation type.

For each quadrat, observations are made on several variables:

- type of algal substrate;
- proportion of the quadrat covered by each algal type;
- number of layers of eggs on each algal type;
- proportion of the bottom substrate covered by eggs;
- number of egg layers on the bottom substrate.
-

Egg deposition for each sampling quadrat is estimated from the predictive equation described in the 1989 assessment (Haist and Schweigert 1990, Schweigert 1993). A single spawn event (or a spawn record) may be evaluated by a series of transects, each consisting of a number of stations (Fig. 4).

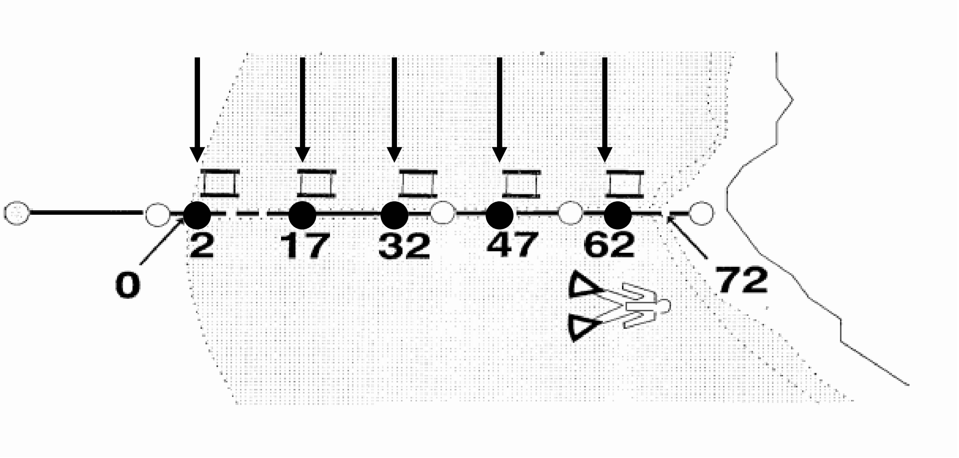

Figure 2. Diagram of a spawn transect. The transect is the dark horizontal line with 5 stations (dark circles under the vertical arrow), separated by a distance of 15 m (adapted from Fig. 4, Fort et al. 2009). The stippled area represents spawn. The open circles represent transect markers for divers. The transect 'distance' (the term used in the herring spawn database) representing the spawn width is 72 m.

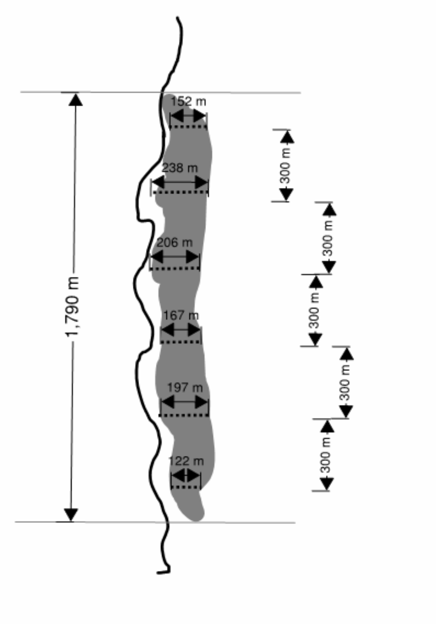

Figure 3. Diagram of a herring spawning record. This is a spawn event measured by showing six transect lines (short, dashed horizontal lines) each of which has five or more sampling stations. The transects are situated about 300m apart.

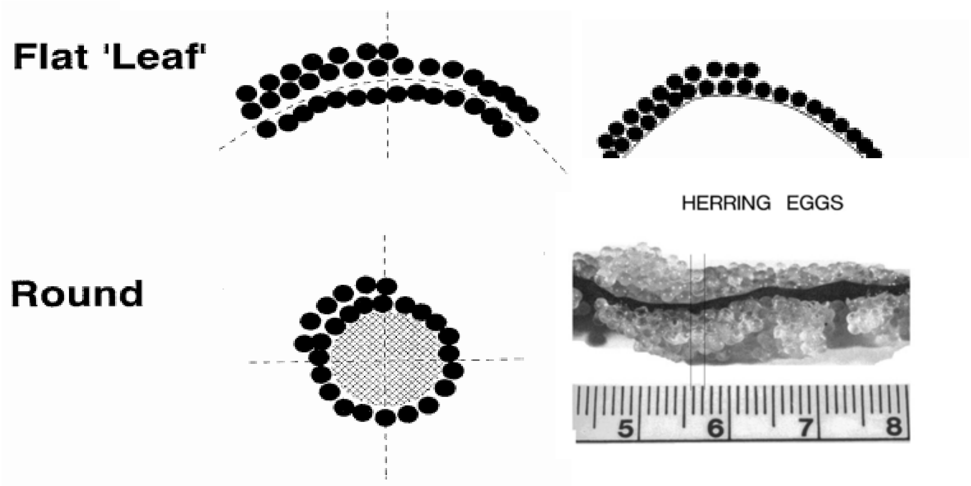

Figure 4. Diagram of layers (adapted from Fort et al. 2009). The two drawings on the left show a diagrammatic image of 2.5 layers on flat and round vegetation. The upper right drawing shows 1.5 layers. The lower right photograph shows multiple herring layers on eelgrass.

2.3 OTHER DATA AND INFORMATION SOURCES

Oceanographic data on sea surface temperature (SST) and salinity are from the DFO website: (1) http://www.pac.dfo-mpo.gc.ca/science/oceans/data-donnees/lighthouses-phares/index-eng.htm.

These data were provided by P.B. McCarter in the DFO herring website (above) and incorporated into statistical software (Minitab©).
(2) http://www.pac.dfo-mpo.gc.ca/science/species-especes/pelagic-pelagique/herring-hareng/herspawn/pages/project-eng.htm

2.3.1 Data on abundance: region-based versus event-based metrics

Estimates of cumulative spawn length (km), spawn area (km^2) and number of spawn records were extracted as individual records that were then pooled by year and assessment region. The cumulative spawn length was simply the sum of the length of each record. The cumulative area was based on the mean spawn width for each spawn record, multiplied by the spawn length. These metrics of herring abundance, plus the estimated SSB from the most recent assessment report (Cleary et al. 2010) were examined for each of the five assessment regions (Fig. 1) for the period of 1984-2010.

Event-based analyses use estimates of mean length, width and egg layer number pooled for each spawn event. Within the herring spawn database, event-based data are summarized mainly in the 'ALLSPAWN' table (see Appendix 1a).

2.3.2 Data on variation of layers in time and space

All analyses of egg layers were derived from the 'VEGETATION TABLE' or the 'VEGTRANS' table. Depending on the analyses other data were linked to these to determine information of date, transect position, depth, etc. Analyses of these data examined the differences and similarities in temporal and spatial trends.

2.3.3 Frequency of trace layers

For some analyses egg layer categories were used by pooling egg layer estimates into discrete layer bins. When such pooling was required, egg layer estimates between 0.01 and 0.49 layers were combined as '0+' layers. Frequency changes in the category of 'trace' layers, usually recorded arbitrarily as '0.01' layers, were examined for all regions using linear regression and correlation analyses.

2.3.4 Quantifying spawn survey effort

Data on recent survey effort, based on the number of days that vessels were charted as dive platforms, was provided by Lorena Hamer, HCRS. Variation in diver survey effort was examined in multiple ways including: (i) the duration of charter vessels that support diver survey; (ii) the duration of the interval between the spawning date and the subsequent survey date; (iii) the duration of time (in minutes) that divers spend recording egg layers for each station on quadrats; (iv) the number of transects made each year, within each region; (v) the starting dates of spawn surveys. These latter analyses do not measure 'effort' *per se*, but instead provide a perspective about whether the surveys might have been early or late, and thereby missing some spawning activity. For temporal comparisons of dates, calendar dates were first converted to a 'day-of-the-year' (DOY) after adjusting for leap years.

2.3.5 Data on the spawning environment

Variation in seven types of vegetation (sea grasses, flat kelp, standing kelp, leafy algae, rockweed, *Sargassum*, and string algae) used as substrate for incubating was compared by depth and regions. A further category called 'grunge', used by divers when eggs occur on non-descript bottom debris, was also included. Temporal variation in the percent vegetation cover and the proportion of bottom covered by eggs, noted by divers at each sampling quadrat, also was examined. Temporal variation in sea surface temperature and salinity, estimated for the day of spawning for each spawn record for each region was examined.

2.3.6 Potential causes of egg loss – literature review

The final section of this report is a brief discussion on factors affecting egg survival and egg loss. The purpose of the review is to determine if there are any precedents or obvious explanations for temporal changes in the frequency of 'trace' observations. The summary is based on a review of the literature (> 70 papers and reports) concerned with predation of herring eggs and related factors. The subject matter of the literature is described in terms of the types of mortality that can impact eggs including the types of predators and the approximate geographic locations of the studies. The literature review is presented in an appendix, in the form of an annotated bibliography.

RESULTS AND DISCUSSION

3.1 TEMPORAL VARIATION: REGION METRICS VERSUS EVENT METRICS

Estimates for SSB from the 2010 herring assessment report (Cleary et al. 2010) show a decline in all regions (Table 1) from 1984 to 2010. The trends in Table 1 are described simply as arrows, pointing up or down, and are based on simple plots of the data by year for each region (shown in Appendix Table 2). In most instances the trends are obvious and unequivocal. In a few instances where the 26-year trend is not clear, the trend (arrow direction) is based on recent years.

The spawn index and mean egg layers decreased with time in all regions. The cumulative spawn length in the Strait of Georgia increased as the SSB and spawn index decreased. In general, if estimated as the proportion of boxes in Table 1, more of the event-metrics increased (~30%) compared to region-metrics (~7%).

Trends in the spatial dimensions of spawn events (lower part of Table 1) showed little coherence with changes in SSB or other event metrics. The dimensions of spawn events, especially spawn length and width, vary independently from changes in SSB. This tentative conclusion however, does not apply to the estimation of mean egg layers. Egg layers declined in all regions and the trend appears consistent with changes in SSB. If the analyses ended at this stage the implication would be that two of the dimensions of spawn events (length and width) are independent of the SSB, but egg density is not.

<u>Table 1. Metrics of spawn – description and analysis</u>. The upper panel shows temporal trends in each region. Each metric (left box of table) is based on trends shown in Appendices identified by the appendix number and figure as A2F1 (meaning 'Appendix 2, Figure 1, etc). The direction of the arrows indicates increasing (up) or decreasing (down) trends with intermediate or uncertain trends shown as arrows pointing slightly in either direction. The solid grey arrows describe regional metrics. The lower open arrows describe event metrics. The filled boxes indicate comparisons that are inconsistent with general trends – such as an increase in the spawning area of the Prince Rupert District, when the SSB has declined.

	Metric/region	**Haida Gwaii**	**Prince Rupert District**	**Central coast**	**Strait of Georgia**	**West Coast Vancouver Island**
Region metrics	**SSB** (A2F1)	↓	↓	↓	↓	↓
	Spawn index (A2F2)	↓	↓	↓	↓	↓
	Sum length (A2F3)	→	→	↘	↗	↓
	Area (A2F4)	→	↗	↘	↘	↓
	Spawn records (A2F5)	→	→	↘	↓	↓
	Mean layers (*by region*) (A2F6)	↓	↓	↓	↓	↓
Event metrics	**Mean length** (A2F7)	→	↘	↗	↗	↓
	Mean width (A2F8)	↘	↑	↑	→	↘
	Mean area (A2F9)	→	↑	↑	→	↓
	Mean layers (*by event*) (A2F10)	↓	↓	↓	↓	↓

Table 2 shows a summary of correlation analyses between region metrics and Table 3 shows the same for event metrics. Temporal trends in most of the regional metrics vary coherently but few of the event metrics do the same. The results summarized in Tables 2 and 3 corroborate the implication observed in Table 1, that the metrics of spawn events (mean spawn width and mean length) are mainly independent of changes in SSB.

It is not surprising that the herring spawn index and cumulative spawn lengths and areas are correlated with the SSB (Table 2) because they are not independent: the SSB is based partially on input of data that rely on spawn measurements. The number of spawn records is not used as input for SSB estimation and is independent of other spawn metrics but it changes in accordance with the SSB (bottom row of Table 2). If two metrics of spawn events (mean length and width) are determined by the biological interactions within the specific event (i.e., maximal densities limits of spawning adults), it is odd that mean egg layers appear to be under the influence of the SSB.

Table 2. Correlation matrices for regional metrics for five stock assessment regions. Temporal trends in the herring spawn index, cumulative spawn length, cumulative spawn area and total number of records (of spawn events) are compared by correlation analysis to the annual estimate of spawning stock biomass (SSB). In each box the upper number is the correlation coefficient and the lower number is the probability of significance. Appendices showing data plots corresponding to each row can be identified by the appendix number and Figure as A3F1 (meaning 'Appendix 3, Figure 1, etc).

	SSB Haida Gwaii	**SSB Prince Rupert District**	**SSB Central Coast**	**SSB Strait of Georgia**	**SSB West Coast Vancouver Island**
Herring spawn index (A3F1)	0.700	0.685	0.550	0.818	0.777
p	0.00	0.00	0.00	0.00	0.00
Sum of length (A3F2)	0.591	***0.331***	0.664	0.604	0.781
p	0.00	***0.09***	0.00	0.00	0.00
Spawn area (A3F3)	***0.254***	***-0.321***	***0.257***	0.787	0.542
P	***0.20***	***0.10***	***0.20***	0.00	0.00
Number records (A3F4)	0.727	0.640	0.700	***0.271***	0.801
p	0.00	0.00	0.00	***0.17***	0.00

Table 3. Correlation matrices for event metrics. Temporal trends in the dimensions of spawn events (mean length, width, and area) are compared to the estimated spawning stock biomass (SSB) for each region. In each box the upper number is the correlation coefficient and the lower number is the probability of significance. Most of the spawn event metrics are either insignificant or have a negative correlation (shown in bold Italics) when compared to the annual estimate of the SSB. This table is a condensation of a correlation matrix shown in Appendix 3. Appendices showing data plots corresponding to each row can be identified by the appendix number and figure as A3F5 (meaning 'Appendix 3, Figure 5, etc).

	SSB Haida Gwaii	**SSB Prince Rupert District**	**SSB Central Coast**	**SSB Strait of Georgia**	**SSB West Coast Vancouver Island**
Mean spawn area (A3F5) p	***0.254*** ***0.20***	***-0.321*** ***0.10***	***0.257*** ***0.20***	0.787 0.00	0.542 0.00
Mean spawn length (A3F6) p	***-0.164*** ***0.41***	***-0.321*** ***0.10***	***-0.448*** ***0.02***	***0.312*** ***0.11***	***-0.471*** ***0.01***
Mean spawn width (A3F7) p	***-0.382*** ***0.05***	***-0.647*** ***0.00***	***-0.44*** ***0.02***	0.505 0.01	***-0.406*** ***0.04***

3.2 VARIATION OF LAYERS IN TIME AND SPACE

Mean egg layers declined in all regions between 1984 and 2010. The decline is apparent when examined both at the region and event levels. The approximate levels of the decline are described in Table 4 (with detailed plots provided in Appendix 2 and 4). The decline in mean egg layers in all regions, examined by linear regression (Fig. 5), is significant in all regions.

A potential explanation for the decline in egg layers is a change in the frequency distribution of layer categories. **This was an unexpected observation made at the beginning of these analyses.** Specifically it was clear that since the time when diver surveys began, there has been a gradual increase in the frequency of the ‘trace’ category used to classify low levels of spawn by divers (Table 4, row 3).

Trace layers refer to situations where “the density of eggs is very low or the percent cover by vegetation is low” (Fort et al. 2009). A trace category is entered into the spawn database as 0.01 layers. This is an arbitrary number and not meant to really reflect a real estimate of layers. Nevertheless it is incorporated into the computation of the herring spawn index as if it were a real number and a real observation. If trace observation were rare, the effect on the computation of the herring spawn index used in the assessments probably would be small. However, the frequency of trace observations has increased sharply in recent years in all regions.

Although the ‘trace’ category is entered as ‘0.01’ layers, there are a relatively small number of other data entries between 0.1 and 0.5. There also are a wide range of fractions of layer numbers, some to two decimal places. Therefore for convenience of analyses in this report, egg layer data were rounded to the nearest digit. The effect is that all layers estimates between 0.01 and 0.49 were rounded to zero and called ‘0+’ layers.

Decreases in mean layers could occur either by (a) an increase in the relative frequency of low-density spawn observations, such as ‘trace’ layers or (b) a decrease in the relative frequency of observations of high spawn layers. The distinction between these two potential causes can be examined by excluding observations of ‘trace layers’ from the analyses. This is examined in Appendix 4, Figures 2b-g that show, for each region: (i) an increase in the relative frequency of 1-layer and some 2-layer observations; (ii) little or no change in the relative frequency of observations of 3- and 4-layer observations; (iii) slight decreases in the relative frequency of some 5- and 6-layer observations. If the cause(s) of the changes in the estimation of egg layers were solely biological, the increase in the relative frequency of 1-layer and 2-layer observations (Appendix 4, Figures 2c-d) would not be expected. However, the apparent decreases in the relative frequency of the 5-layer and 6-layer observations could reflect both methodological and biological causes.

Table 4 (next page) shows temporal trends in egg layer data. Rows 3-4 show the changes in frequency of layer classes in each region. Row 5 shows that the frequency of the 0+ layer category is inversely proportional to the SSB estimates in each Region (See also Appendix 4, Figure 3). The frequency of the 0+ layer category has increased sharply in the last decade, especially during the last 5 years.

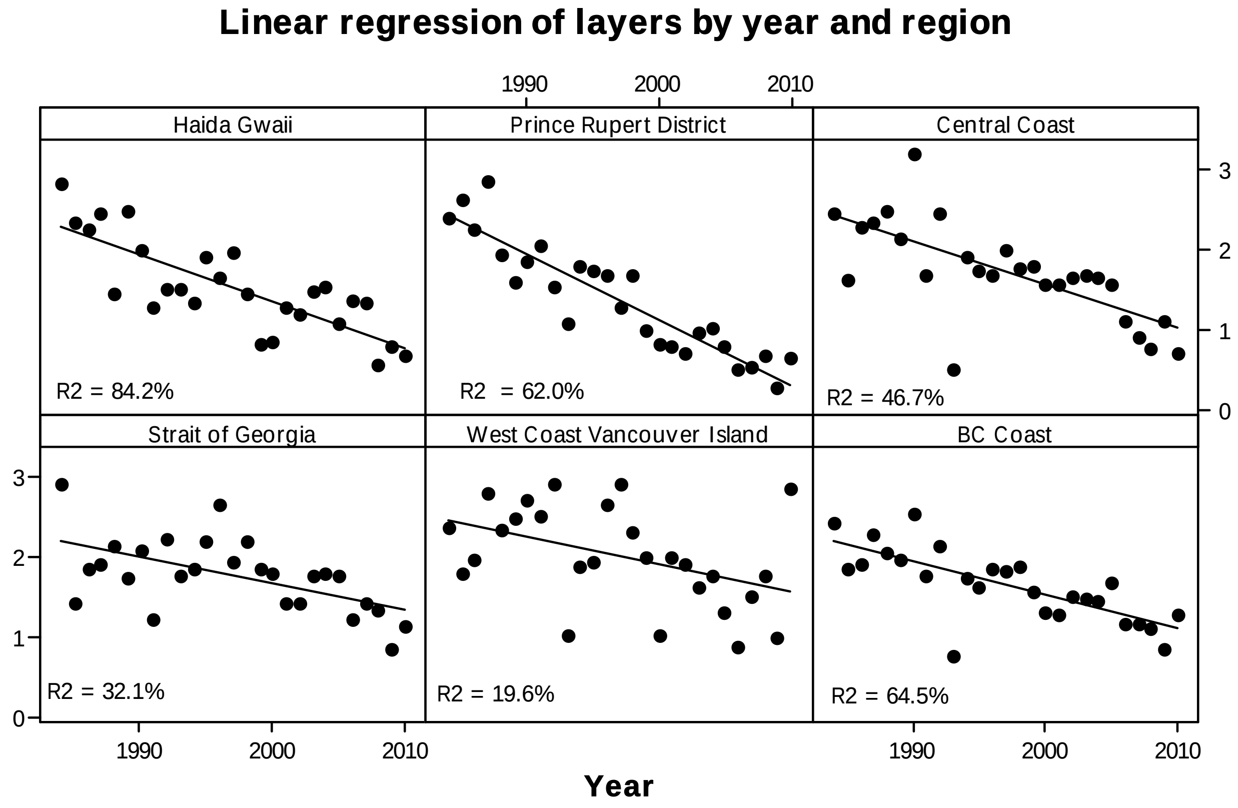

Figure 5. Regression of mean egg layers and time. Each regression is significant (p<<0.01).

Table 4. Temporal analysis of egg layers by region. Each metric (left box of table) is based on trends shown in Appendices identified by the appendix number and figure as A5F1 (meaning 'Appendix 5, Figure 1, etc). Trends in Lines 1-2 show that estimates of mean layers are decreasing in all regions (already referred to in Table 1) and the trends, when examined by linear regression, are significant. Some of the data are not necessarily linear with time so the use of linear regression here is only to examine the trend in the data. In line 1 the regression coefficients are shown for analysis of all data with the sample size (n) shown in parentheses as well as the annual total s (n = 27). In line 2 the regression coefficients are estimated for annual means for the last 20 years 1991-2010. Line 3 shows that the frequency of 'trace' layers (see text for definition) has increased in all regions but the frequency of thicker spawn layers (has decreased in all areas (line 4). The increase in the frequency of trace layers decreases inversely to estimates of SSB (line 5).

Temporal trend in egg layers/region	**Haida Gwaii**	**Prince Rupert District**	**Central coast**	**Strait of Georgia**	**West Coast Vancouver Island**
1. Mean layers estimated from regions - (A2F6). Reg. coeff. (n for all data): Reg. coeff.(annual Means from 1991-2010):	decreasing from ~2.5 to <1 p<0.01 (10247) p=0.427 NS (20)	decreasing from ~2.5 to <2 p<0.01 (21601) p<0.001** (20)	decreasing from ~2.5 to <3 p<0.01 (29118) p<0.015* (20)	decreasing from ~2.0 to ~1.0 p<0.01 (50907) p<0.001** (20)	decreasing from ~2.0 to ~1.0 p<0.01 (17225) p<0.001** (20)
2. Mean layers estimated from spawn events - (A2F10) and Figure 5. Regression coefficient:	decreasing from ~2.0 to <1.0 p<0.01	decreasing from ~2.0 to ~1.0 p<0.01	decreasing from ~2.0 to ~0.5 p<0.01	decreasing from ~2.5 to ~1.5 p<0.01	decreasing from ~2.0 to <1.0 p<0.01
3. Frequency of 0+ layers and SSB by year (0+ layers represent all observations between 0.01 and 0.49 layers) (A4F1)	increasing from ~ 25% to ~45%	increasing from ~ 20% to ~60%	increasing from ~ 20% to ~50%	increasing from ~ 20% to ~40%	increasing from ~ 20% to ~50%
4. Changes in frequency of 1-2 and 2-3+ layer classes (1-2 layer = '2L', 2-3+ layer = '3L") (A4F2)	2L slight decline, 3L sharp decline	2L slight decline, 3L moderate decline	2L slight decline, 3L moderate decline	2L slight decline, 3L moderate decline	2L slight decline, 3L sharp decline
5. Frequency of 0+ layers versus SSB (0+ layers represent all observations between 0.01 and 0.49 layers) (A4F3)	inverse - SSB high when '0+' is low	inverse - SSB high when '0+' is low	inverse - SSB high when '0+' is low	inverse - SSB high when '0+' is low	inverse - SSB high when '0+' is low

3.3 VARIATION IN SURVEY EFFORT

There are no exceptional changes in any of the measures of survey effort. There may have been slight decreases in recent vessel support (Table 5, Row 1) but not substantial. The temporal duration, from the beginning of surveys to the end, showed no evidence of a decrease that could account for any temporal change in spawn metrics (Table 5, Row 2). Probably the most important observation is that there was no apparent change in time in the interval between the spawning time and the dates of diver surveys (Table 5, Row 3). This is important because any systematic increase in the duration of the interval could have resulted in an increased loss of eggs by predation. Such a loss could have led to a reduction in egg layers, but this is not supported by the data. Another speculative explanation for a change in egg layer metrics was the possibility that divers were rushing through the work and perhaps spending less time on enumerating spawn and vegetation on quadrats. However there is no evidence of this from the data (Table 5, Row 3). Although slightly variable among regions, there is no evidence of a reduction in the time that divers spend on individual stations. Further, there is no evidence of any temporal reduction in the total survey effort, in terms of the numbers of transects examined in each region (Table 5, Rows 5).

Table 5. Temporal analysis of survey effort by region. Each metric (left box of table is based on trends shown in Appendices identified by the appendix number and figure as A5F1 (meaning 'Appendix 5, Figure 1, etc).

Survey metrics	**Haida Gwaii**	**Prince Rupert District**	**Central coast**	**Strait of Georgia**	**West Coast Vancouver Island**
1. Vessel survey duration (A5F1) Reg. coeff. (n=27):	possible trend - slight decrease in recent years 0.178 NS	possible trend - slight decrease in recent years 0.167 NS	possible trend - slight decrease in recent years 0.086 NS	possible trend - slight decrease in recent years 0.033*	possible trend - slight decrease in recent years 0.032 NS
2. Diver spawn survey duration (A5F2a, b) Reg. coeff. (n=27)	variable p =.256 ns	increase in time p=.076 ns	increase in time p=.371 ns	increase in time p<.012 *	increase in time p<.003 **
3. Diver observation time – minutes per quadrat (A5F3)	increasing	no change since mid-1990's	no change	no change since mid-1990's	decreasing
4. Number of transects per year (A5F4)	consistent ~100/y	slight recent decrease but still high ~150/y	decreasing by about 50% from ~400/y to ~200/y	possible recent decrease down to ~450/y	consistent but low ~25/y

3.4 SPAWNING ENVIRONMENT

The main vegetation types used as substrate for spawning occur in all regions but there are some minor differences (noted in the shaded grey boxes of Table 6, rows 1-8). The most exceptional difference is the prominence of *Sargassum* as a spawning substrate in the Strait of Georgia, but not elsewhere on the coast. Plots of egg layers by depth and vegetation type for each Region (see Appendix Figures A6F1) show that most eggs occur in the depth zone close to chart datum, or the low water mark.

There are substantial regional differences in the proportions of bottom areas that are covered with vegetation (Table 6, Rows 9-10 called 'vegetation/bottom trends'). There are unexplained but varying trends in the estimates of percent cover that are increasing in Haida Gwaii and the Strait of Georgia but decreasing in the Prince Rupert District. Estimates of the use of bottom substrates vary substantially among regions (probably reflecting different bottom substrates) but are mainly consistent over time within regions. Therefore these small changes in percent cover and use of bottom substrates would not explain the temporal variation in egg layers described above.

There are interesting trends in the mean temperature and salinity at spawning times (Table 6, Rows 11-12). All regions except the Strait of Georgia show a decline in temperature and most show variation in salinity. These oceanographic data are estimated for the day of spawning by the prevailing conditions at the nearest lighthouse. It seems probable that such changes must affect herring because it is established that the temperature at spawning time seems to be important (Alderdice and Velsen 1971, Hay and McCarter 2009). Regardless, the trends in temperature vary in opposite directions among regions, so such changes would not explain the unidirectional decrease in the numbers of egg layers.

Table 6. Summary of the spawning environment in each region. Each vegetation type is summarized briefly based on figures presented in Appendix 6, Figures 1-3). The shaded boxes indicate potential region-specific differences.

Vegetation types (A6F1)	**Haida Gwaii**	**Prince Rupert District**	**Central coast**	**Strait of Georgia**	**West Coast Vancouver Island**
1. Grasses	extensive, inter- and subtidal	extensive, inter- and subtidal	extensive, inter- and subtidal	extensive, inter- and subtidal	extensive, inter- and subtidal
2. Grunge	negligible	negligible	moderate	negligible	negligible
3. Flat kelp	extensive, to deep subtidal	moderate in subtidal	extensive, to deep subtidal	moderate, deepest vegetation used	moderate, to deep subtidal
4. Standing kelp	light	light	light	negligible	negligible
5. Leafy algae	moderate, mainly inter- and shallow sub-tidal	moderate, mainly inter- and shallow sub-tidal	moderate, mainly inter- and shallow sub-tidal	extensive, inter- and subtidal	moderate, but extending deep into subtidal
6. Rockweed	moderate, high intertidal	moderate in intertidal	extensive in intertidal	extensive in intertidal	moderate, high intertidal
7. Sargassum	negligible	negligible	light	**extensive in most inter- and shallow subtidal**	light
8. String algae	extensive, to moderate subtidal	extensive, inter- and subtidal	extensive, inter- and subtidal	extensive, inter- and subtidal	extensive, inter- and extending to deep subtidal

Vegetation/bottom trends (A6F2)	**Haida Gwaii**	**Prince Rupert District**	**Central coast**	**Strait of Georgia**	**West Coast Vancouver Island**
9. Percent vegetation cover	increasing to >60% in 2007	decreasing from ~60% to ~40% in 2008, higher since	variable among years but little trend with time	slight increase in time, from ~30% to ~40%	little apparent change with time
10. Percent bottom with eggs	gradual increase to ~40%	consistent at about ~25%	high (~60%) decreasing recently to < 50%	consistent at about ~30%	high ~40% in 2000, declined to ~25% in 2010

Temperature and salinity (A6F3)	**Haida Gwaii**	**Prince Rupert District**	**Central coast**	**Strait of Georgia**	**West Coast Vancouver Island**
11. Sea surface temperature	decline ~1 C^{o} to ~7C^{o}	decline ~1 C^{o} to ~7C^{o}	decline ~0.5 C^{o} to ~7.5C^{o}	**increase ~1 C^{o} to ~9C^{o}**	decline ~1.5 C^{o} to ~7.5C^{o}
12. Salinity	decline to ~27ppt from ~31.5ppt	unchanged at ~ 31ppt	decline to 28ppt from ~30ppt	variable at ~28ppt, but no time trend	**recent decline to ~26ppt**

3.5 DENSITY OF SPAWNING HERRING IN BC

Hay (1985) suggested that some behavioural or physiological mechanism must limit overall density of herring eggs because the instances of excessive egg number (>> ten million/m^2) are rare, both for Pacific and Atlantic herring. Along the BC coast egg densities usually are between 10^5/m^2 and 10^6/m^2 (Haegele et al. 1979, Schweigert et al. 1990). Herring produce about 200 eggs/g per spawning female or about 100 eggs/g of the combined male and female weights. Therefore, as a rough approximation, the biomass of herring required to produce egg densities from 10^5/m^2 -10^6/m^2 should be from 1000-10,000 g or between 1-10 kg/m^2.

Densities of spawning herring can be estimated using SSB data from assessment reports (Cleary et al. 2010) and the estimated spawn area from the spawn database. Total spawning area for each region and each year is the cumulative sum of the area for each spawn record (event). Dividing the total annual SSB (in kg) for each region by the total spawn area (in m^2) provides an estimate of the density of spawning herring in kg/m^2 (Fig. 6). Remarkably in each region there is a clear downward trend in the estimated density of spawning herring. Such a downward trend in density would not be expected if there were consistency in the behavioural controls over fish density in spawning areas. In contrast to the downward trend in fish density (Fig. 7), the cumulative spawning area shows varying trends but does not match that seen in Fig. 6. (Note: the cumulative spawn area is also shown in Appendix 2 Fig. 4, but is presented again here in a format similar to Fig. 6).

There are two main explanations for the apparent discrepancy between the two different trends shown in Figs. 6-7. One explanation is that the reductions in egg density are real and that herring spawning behaviour, or physiology (perhaps related to changes in size-at-age), or the regional environment, has changed over the last 20 years. The other is that the estimated spawning densities are incorrect, perhaps as a consequence of a systematic error in the herring spawn assessment methodology or and perhaps some undetected error in the database. It seems unlikely that herring spawning behaviour has changed in relation to the recent decline in SSB because the trend to diminishing layers has been gradual and continuous whereas SSB has fluctuated in most coastal regions of BC. Therefore it seems unlikely that the spawning density of herring would decline in accordance with a decline in SSB. This issue is examined in the following sections.

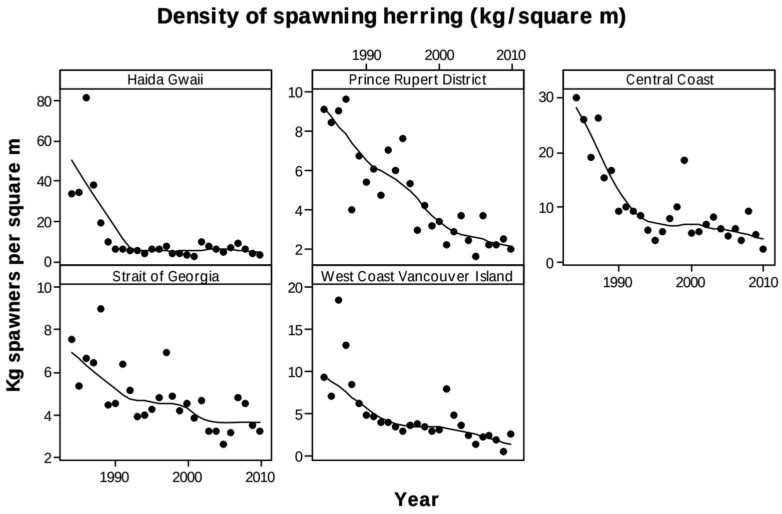

Figure 6. Changes in estimated density of spawning herring. The densities are estimated by dividing the total estimates SSB (in kg) assessment report (Cleary et al. 2010) for each region by the spawning area (in m2), estimated from the herring spawn database. The solid line is a Lowess smoother.

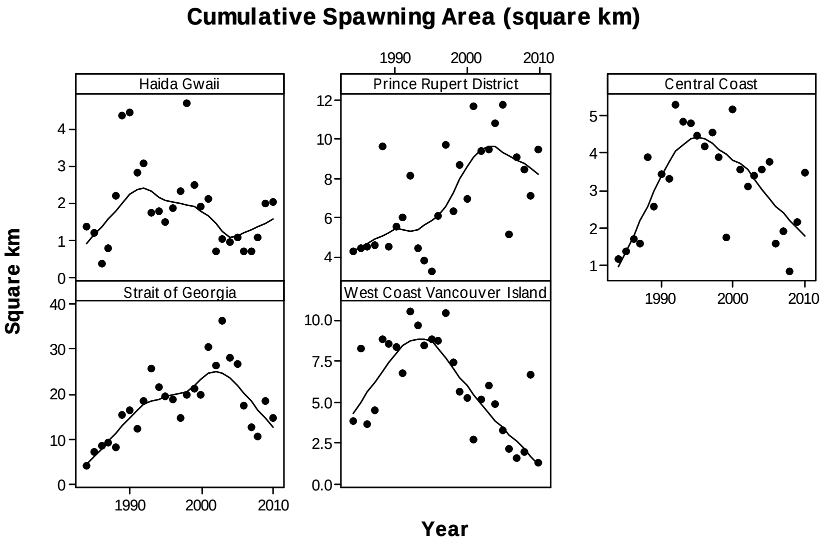

Figure 7. Changes in the total spawning area (km2). Cumulative spawning areas are estimated for each region from the herring spawn database. The solid line is a Lowess smoother.

3.6 SCHOOL STRUCTURE AND SIZE VERSUS SSB – IMPLICATIONS

Are there behavioural factors that reduce the density of spawning herring during periods of low abundance? There is developing evidence that the structure of schools and shoals is more complex than is generally recognized. In part, the uncertainty is related to inconsistent use of terminology, especially ‘shoal’ versus ‘school’. There is a developing consensus, however, that the term ‘shoal’ represents a loose aggregation that might consist of component schools. There is increasing recognition of a level of organization above the school where groups of schools associate and are known either as ‘clusters’ or ‘patches’ (Parrish 1999, Fréon et al. 2005). The concept of a school is that all members behave in a coordinated way, such as swimming direction, etc., so the term school is both a noun and a verb and has both structural and behavioural implications. Fish schools of single species are not necessarily homogeneous. It has long been recognized that fish schools vary by the size of members (fish of similar size school together, etc). There is increasing evidence that schools may consist of subunits of ‘neighbours’ (Parrish 1999) that Fréon et al. (2005) call a school ‘nucleus’ although there may be multiple nuclei within a school (Fig. 8).

There are two different kinds of evidence, based on tagging data and otolith microchemistry, that support the contention of structure below the level of the population in Pacific herring (Hay and McKinnel 2002, Sanborn 2003). If so, then the population and stock terminology used for management of Pacific herring may correspond to the proposed structure for pelagic fish (Fig. 8) as follows: Each of the five main stock groupings (Haida Gwaii, Prince Rupert District, etc). would compromise a population or stock. Within this there could be clusters of schools, and probably many more than those depicted in Fig. 8 that may segregate roughly into different geographic regions at spawning time. In this sense there may be a biological basis for the repetitive use of different spawning areas by a single biological population. Within the clusters, individual schools, and nuclei within schools, may achieve reproductive synchrony leading to the spawning ‘events’ referred to in this report. Probably most spawning events correspond to different schools, but some of the spawning events could involve the synchronous spawning of two or more schools in approximately the same area. An important implication of this conceptual model is that school structure is both dynamic, changing in spatial configuration and location but also relatively constant, in terms of fish packing density. This concept is explained clearly by Croft et al. (2003) and is reiterated below (in Italics)

“For shoals to encounter and interact, they need to be in close proximity. Encounters between shoals are required to allow the individual to make adjustments to the size of the shoal with which it associates, in response to environmental and behavioural changes. Intense fishing reduces population density, but mean shoal size may nevertheless be maintained (Ulltang 1980), reducing the rates of shoal encounters but increasing the catchability of fish to human fishers, ultimately leading to a stock collapse (Pitcher 1995). It is hypothesised that this will result in fish moving more rapidly in areas of low density until encountering other shoals, causing them to become concentrated in a local area (the size maintenance hypothesis of Pitcher 1997). The maintenance of a stable shoal size in association with a reduction in the range of movement of the fish means that a constant catch per unit effort can be maintained leading to an exacerbated stock collapse. The size maintenance hypothesis may provide a diagnostic tool for the identification of stock collapse, which would be achieved through the monitoring of the behavioural and spatial parameters of shoaling fish.”

Recent evidence from analysis of pre-spawning aggregations of herring on Georges Bank indicates that spawning shoals required a threshold density of about 0.2 fish/m^2 (Makris et al. 2009) before they would assemble and concentrate in potential spawning areas. Note that these densities are lower than those reported here from Pacific herring (e.g. Figure 6) but in this example the Georges Bank herring were examined well before spawning started. Based on analysis of herring egg densities (Hay 1985) it is probable that the spawning density of Atlantic herring is similar to that of Pacific herring. The work of Makris et al (2009) provides further evidence that the density of spawning herring does not become dilute as SSB decreases.

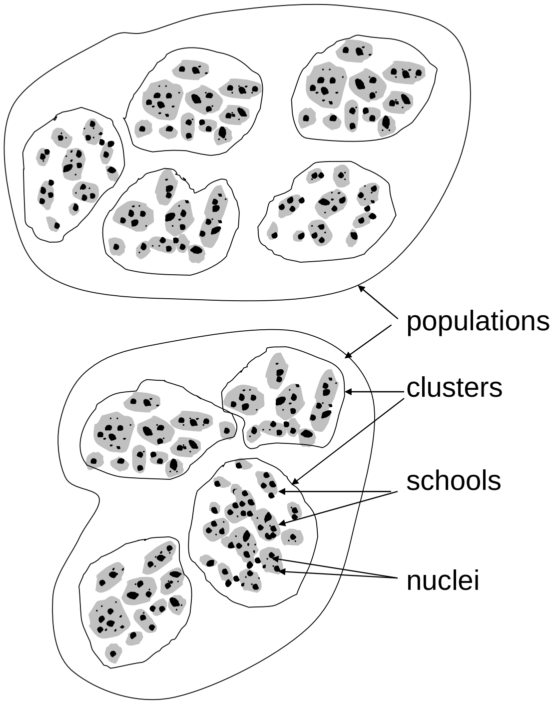

Figure 8. Conceptual model of herring population structure. The division into clusters, and schools is adapted from Fréon et al. 2005. Herring populations or stocks are organized into clusters or patches that consist of many schools or shoals. Within schools (shown as grey areas) there may be finer structure in the form of nuclei (dark areas), or a group of neighbouring fish that tend to maintain consistent associations. These relationships are not necessarily static in time, so as population density changes, nuclei within schools and schools within clusters may merge and maintain an approximately consistent packing density (see text for further explanation).

The fundamental premise of the conceptual model (Fig. 8 and related text) is that behavioural factors, not SSB, control the density of spawning herring in spawning areas and these behavioural factors are basically the same as those that operate to control school density at other times of year. It is becoming established in the literature that density *within* shoals of small pelagic fish is not a function of the SSB. Instead shoal density is the net balance between opposing forces of mutual attraction and repulsion that have evolved to maximize fitness by minimizing risk of predation. If the same forces operate during pre-spawning aggregation and spawning activity, then there would be no expectation that egg density, or spawn width would change as a function of SSB. Instead, it would mainly be a change in the number of spawn records (fewer during low SSB and vice versa).

3.7 THE POTENTIAL IMPACT OF PREDATION ON EGG LAYERS

A potential explanation for the temporal changes in egg layers is a change in predation rates. This might occur if the quantity of eggs removed by egg-eating predators increases in recent years. A review of the scientific literature (Table 7) provides no indication of whether predation rates could change but the review did establish that our knowledge and understanding of this subject is very limited. Fifty two of the papers are in primary, peer-reviewed journals, 14 were technical reports which may or may not be peer-reviewed. The remainder are a mixture of graduate theses, contract documents and some websites. A full list is shown in Appendix table 7a, which shows the category and origin of the literature followed by Appendix 7b which shows a brief summary of each report, as it pertains to egg loss.

Table 7. Review of scientific literature on egg loss in herring. This information is based on a more detailed review in Appendix 7. Probably the literature on Pacific herring (76 papers) is nearly complete but some literature on Atlantic and Baltic herring may be missing.

Egg loss cause	**Atlantic**	**Baltic**	**General**	**Pacific**	**All**
Bird predation	0	1	0	25	26
Fish predation	12	0	0	1	13
Whale predation	0	0	0	2	2
Invertebrate predation	0	0	0	0	1
Female condition	0	2	0	0	2
Environment	4	5	0	12	21
Overview	0	0	4	7	11
All	**16**	**8**	**4**	**48**	**76**

Most of the literature on predation of Pacific herring eggs is concerned with seabirds. Mainly the focus of the literature concerned with bird predation examines the dependence of seabird population on spawning herring as a source of food. There is only one published report (Haegele) and a thesis (Palsson) that describe invertebrate predation. There is only one paper that comments on fish predation in the Pacific but this topic dominates the literature on Atlantic herring. Two papers mention grey whales as egg predators but there are no quantitative estimates provided. There are several papers that comment on environmental factors that lead to egg mortality, and several that comment on egg quality, as a function of maternal condition, but none of these papers are comment directly on egg loss in a way that would affect estimates of spawn layers.

Tentative conclusions from this summary are that predation of herring eggs may have been overlooked as a factor affecting estimates of egg density. It not clear if there could be temporal changes in predation rates on eggs that would account for the observed changes in egg density, but the present scientific literature is insufficient to support any conclusions on this. One factor mentioned in several papers concerned with predation on Atlantic herring eggs is that benthic feeding fish predators may focus on locations where egg deposition is thickest – so several investigators have speculated independently that herring spawning behaviours may have evolved to avoid very thick egg depositions.

The most conspicuous weakness in the literature is the paucity of information on invertebrate predation and fish predation. It is plausible that predation on eggs by demersal fishes and invertebrates could be significant. Also such predation may be subject to naturally-caused temporal variation among years as the predator populations change in abundance and distribution. Clearly this subject needs more attention.

3.8 SYNOPSIS AND REVIEW

3.8.1 Decreases in spawn layers and density of spawning fish

The numbers of egg layers estimated by divers have declined annually for all regions of the BC coast (Fig. 5). Similarly, the density of spawning herring has also decreased (Fig. 6) and it seems that these two trends may have a common cause. The potential explanations for such a decline in egg layers fall into two categories:

(1) Biological or ecological change, including predation on eggs; density-dependent mortality; environmental factors; changes in size-at-age; limitations of spawning habitat; demographic effects.

(2) Methodology changes in spawn surveys: timing of spawn surveys.

With respect to explanation 1, does it follow that egg layers are lower at low levels of SSB? The difficulty of examining this is that SSB is derived from annual herring spawn assessment data, so SSB and spawn data are not independent. Since 1984 and the inception of SCUBA surveys, however, there is reason to believe that both spawn length and spawn widths that are *measured* during field surveys are valid. Therefore if we assume that two of the three key spawn parameters (length and width) are reasonably accurate and valid the only explanation for the discrepancy in the differences in trend between spawn area and herring spawning density (between Figs. 6 and 7) is a change in egg layers. Such a change might come from an unintentional change in the diver survey methodology or from a subtle biological change that somehow affects herring similarly in all areas of the BC coast. The following text considers potential explanations for changes in egg layers.

3.8.2 Predation and the interval between spawning time and survey time

Egg layer reduction could be associated with increased predation of incubating ages. Therefore changes in the duration of the interval between spawn deposition and the beginning of diver surveys could be important. It is established that egg mortality is substantial during the incubation period but estimates vary widely. Rooper et al. (1998, 1999) estimated daily loss rates of between 4.6 and 19.0 % per day depending on whether the eggs were exposed to air when their mortality was greatest. These estimates are generally higher than those reported for BC herring (Haegele and Schweigert 1991, Jones 1972). Egg mortality estimates vary according to location. There are instances of nearly complete egg mortality in BC (Purcell et al. 1990) but this may have been an exceptional instance attributable to a rare unusually warm, dry weather event during the incubation period. Among the highest reported mortality rates are those reported by Palsson (1974) for egg loss from Puget Sound herring. Egg deposition there is very light, perhaps reflecting the small sizes of herring that occur there. Palsson reported instances of daily egg loss exceeding 25%, but initial densities were low, mainly between a few thousand and 80,000 eggs/m^2.

Biologically, it is certain that egg density decreases rapidly during incubation as a consequence of predation. Consequently unless surveys were conducted immediately after spawning, all spawn surveys will underestimate total egg number. The potential scale of such possible under-estimates is uncertain, but even a relatively small daily loss (~2%) would result in a total loss of over 25% during a 14-day incubation period. A daily loss of 5% would result in total reduction of more than 50% during the same period. Perhaps the most important aspect about egg mortality, as a factor affecting estimates of egg layers, is that that the interval time, between the time of egg deposition and the time of the survey is important (Rooper et al. 1998). Therefore a particular concern is that as the financial and logistical support for spawn surveys has diminished in recent years, the timing of the surveys may be relatively later than during earlier surveys. Relatively later assessments of spawning by SCUBA surveys would be subject to longer periods of predation that could result in an under-estimate of spawn, hence an underestimate of the spawning biomass (see below). As shown in Table 5, however, there is no evidence for any systematic decrease in spawn survey effort that would account for the observed changes in spawn layers.

3.8.3 Density-dependent mortality – suffocation and predator swamping

The mortality of herring eggs may be affected by their density. Taylor (1971) and others have established that heavy egg deposition leads to increased mortality through *in situ* death caused by lack of oxygen.

On the other hand herring egg deposition is an example of 'predator swamping' (Ims 1990) where instances of relatively high egg depositions (say 10^6 eggs/m^2) minimize egg loss to predation. For example, with an initial density of 10^6 eggs/m^2 the loss of 50,000 eggs to predators would result in a lower mortality rate (5%) than those deposited at lower initial densities. In contrast the same egg loss by predation on an initial density of 10^5 eggs/m^2 would have a mortality rate (50%). Work by Haegele (1991) and others indicates than predation by small benthic organisms may be able to remove a relatively consistent amount each day.

This example illustrates two competing forces that operate on herring egg density. It is reasonable to assume that herring have evolved behaviour mechanisms that govern egg deposition to levels that maximize survival of eggs. If so, it follows that egg density during periods of low SSB would be relatively similar to those during periods of high SSB.

3.8.4 Environmental factors

Changes in the properties of seawater probably would not account for the systematic changes in egg layers. Although there are some unexpected changes in the temperature and salinity of spawning areas, the differences between Regions usually exceed those within. However, environmental change may be responsible for the change in size-at-age observed in all BC herring. The effect of climate may be indirect, but ultimately connected to a change in trophic conditions. *A priori* it may not seem reasonable to associate changes in size-at-age with decreases in egg layers but there is a possible relationship.

3.8.5 Effects of change in size-at-age and age composition on layers

Small fish produce smaller gonads so the gonosomatic index (gonad weight/whole body weight) is lower (Hay 1985). As a consequence, the same biomass of large herring would deposit a greater weight of eggs than smaller herring. The difference in egg production is substantial so it seems reasonable to ask whether the smaller size herring spawning in recent years could account for a reduction in the number of deposited eggs. Even if the density of spawning fish were the same (i.e., kg of spawners per unit volume of area), a uniform size aggregation of large fish with a GSI of about 30% would have about 1.5 times the weight of eggs as a uniformly size aggregation of small fish, with a mean GSI of 20%. On the other hand, larger herring have larger eggs (Hay 1985) and all sizes of herring tend to have a relative fecundity of about 200 eggs/gm of spawning female. So, even if there were a greater egg deposition from larger females, there might not necessarily be a greater deposition of egg number. The issue is complicated, however because the packing density of fish in schools varies as a function of size. Pitcher and Partridge (1979) estimate a size-dependent packing of herring to be approximately $N = 0.7L^3$ for Atlantic herring where N is the number of fish of length L (cm) that occupy a volume. As a consequence there are fewer large fish in a given volume than small ones. It seems probable that the diminishing size of herring has some impact on their egg density, but any effects cannot be determined from existing data. This would best be examined by field investigations that attempt to link the characteristics of spawning herring to egg deposition patterns.

It could be argued that egg layers vary with demographic change, with older or larger herring depositing eggs differently than smaller, younger herring. A brief review of the age data, however, can virtually rule out simple changes in age-structure as an explanation for the change in egg layers. In all years there is an assortment of age groups, mainly between ages 3-7, so demographic changes in the population are more likely. It is more difficult to exclude fish (female) size as a potential explanation. Herring size at age has been declining for several decades, but the change has been gradual, occurring over several decades whereas the decline in egg layers has been rapid.

3.8.6 Limitations of spawning habitat

A key point of this report is to ask how egg density (layers) or the density of herring on spawning areas responds to changes in herring spawning biomass, not the other way around. If the density of herring spawning (fish/m^2) changes as a function of overall spawning biomass the implication is that spawning habitat is limiting, so there may be periods when more fish are forced to spawn within the same limited area. There is evidence that this may occur in unique areas where spawning habitat is limited by ice (Tyurnin 1973) or by limited sheltered areas in California but there is no evidence that spawning areas are limited in BC (Hay and McCarter 1996), where herring have spawned on nearly 25 percent of the total BC coastline (Hay et al. 2009). The annual cumulative spawning maximal length may reach 500 km, whereas over 2500 km has been classified as spawning habitat, used at least once between 1937-2010 (Hay and McCarter 1996).

3.8.7 Changing survey methodology

A gradual change in the criteria divers use to classify egg layers, or associated variables such as percent vegetation cover, etc, might lead to systematic changes in the herring spawn index. This, in turn, could affect the estimates of SSB. The herring spawn index (HSI) is presented annually in appendix tables of the assessment report (see Appendix tables 2.1-2.5, pages 79-82 in the annual assessment report, Cleary et al. 2010). In recent years there tends to be clusters of negative residuals, indicating the HSI is disproportionately lower than the SSB. This is consistent with the downward trend in the HSI (see Appendix 2, Figure 2 of his report) and is also consistent with the downward trends in the estimates of mean layers (Appendix 2 Figure 6) and the increase in the frequency of the ‘trace’ category (Appendix 4, Figure 1).

Changes in criteria used to assess spawn density have occurred in the past (Hay and McCarter 2009) so it would not be surprising if there were a steady evolution of assessment criteria that can result in a ‘drift’ of egg density assessment criteria. There is no way, however to evaluate the possibility of this from a review of the existing herring spawn data but it is possible to conduct future tests to determine if new or recruit divers make the same types of observations as experienced divers. There are 164 divers listed in the herring spawn database and each year new divers participate for the first time, replacing others. Although there are impressive efforts made to ensure that divers adhere to a careful evaluation, there have not been direct tests to ensure that diver assessments are consistent, either among divers within years or between years. *Establishing this type of quality control review is a recommendation at the end of this report.*

The increased incidence of the ‘trace’ category will lead to a decrease in the estimate of mean layers used to summarize the egg density of each transect. It is clear, however, that ‘0.01’ layers is unrealistic and arbitrary and should not be used in the same way as other layer estimates that are intended to represent real values. *A recommendation of this report is to consider alternate, more realistic values for ‘trace’ layers and determine the potential effects on the computation of the HIS.*

3.8.8 A computational issue relative to ‘trace’ layers?

There is an additional possible issue with the increased assessment of ‘trace’ categories. If the designation of a ‘trace’ layer is a new development that represents a conscientious effort by divers to describe herring eggs in locations where they were once overlooked or ignored, because they were deemed to be inconsequential, then they might have the impact of increasing the estimated mean width of a transect. This would occur when the eggs are located on the deep edges of transects. The addition of a ‘trace’ category would have the impact of increasing the estimated transect width and this in turn would increase the estimate of total spawn width (see the underlined sentences in Appendix 1b) for an explanation of how this could happen). Such additional width, however, does not necessarily result in an increase in the herring spawn index. It would definitely increase the estimate of mean width for the spawn event, but it also would add additional area of very low egg density. Through simple, informal simulations we could construct scenarios where the addition of low density spawn at the margins of spawns could either inflate of deflate the SSB estimate compared to estimates made by ignoring such low-density, marginal spawns. Ironically, in some circumstances the consequence of such an addition could lower the arithmetic mean egg density to the extent that the total estimate of spawn is lower. In this circumstance, the decrease in the mean layer estimate has a greater, but negative, impact on the estimated egg number, than the positive effect of increasing the estimated spawning area. The severity of the impact of this issue on the estimate of the total spawn index is uncertain, and may be small. The potential for such an unexpected computational issue is uncertain but warrants further attention. Probably any error associated with the addition of additional, but low density spawning areas, would be mitigated if the density estimates were realistic. Therefore a revision of the ‘trace’ estimates of 0.01 layers to a less arbitrary number might be adequate as a solution to this concern. *In any event, a recommendation of this report is to review the computation used to estimate total egg number for spawns, with emphasis on the potential problems related to the treatment of the ‘trace’ category as a valid estimate of egg layers.*

SUMMARY AND RECOMMENDATIONS

The mean number of egg layers in herring spawn has decreased in all areas of the BC coast since the mid-1980’s, when coast-wide SCUBA diver surveys began (Fig. 5). In the last decade the category of ‘trace’ layers, which is recorded into the herring spawn database as 0.01 layers, has increased substantially, and contributes to the trend in the overall decrease in mean layers. The estimate of 0.01 layers is not a realistic number and should not be treated that way in the database. Concurrent with the decrease in mean layers, area-specific measurements of two other spawn metrics, mean length and width of individual spawn records (or spawn events), show no consistent or corresponding directional trends. If the mean size of individual spawn events expanded and contracted in accordance with changes in overall herring abundance (SSB), then all three spawn metrics (mean length, width and layers) would be expected to change in unison, but this has not occurred. It is only the estimate of mean layers that has decreased steadily with time.

At any location, the density of eggs must reflect, approximately, the density of herring that spawned there. Therefore the physiological and behavioural factors that control the density of spawning fish also affect the density of eggs. There is a voluminous scientific literature on the topic of schooling in pelagic fish. There appears to be general consensus that the species-specific packing density in fish schools is relatively constant, even at spawning times. Further, the consensus of the literature on the effect of fishing, or diminished abundance, is a reduction in the numbers of schools, and not a reduction of individual school size. The reason for this is that school size has important biological properties and small schools, perhaps the remnants after fishing, are unstable and will coalesce into larger groups of relatively consistent school size. This is consistent with the herring spawn database that shows that two dimensions of spawn (lengths and widths of spawn events) do not change with SSB. This raises the question of why mean egg layers change with SSB but not mean spawn lengths or widths.

Increased predation rates could reduce egg layers without a corresponding decrease in mean spawn length or widths. If increased predation on eggs were responsible for a decrease in mean egg layers, leading to an increase in the ‘trace’ category, it would have to reflect increased rates of predation, by increased numbers and kinds of predators, and not an increase in the duration of predation on incubating eggs. There is no evidence that widespread increases in predation have occurred – but on the other hand, this may reflect the relative paucity of literature on the subject. Although there is a lot of evidence for seabird predation on eggs, the understanding of possible invertebrate or fish predation on eggs is rudimentary.

A change in the interval between the time of spawning and the diver surveys could lead to an increase in the exposure time to predators. Therefore if the interval increased, there could be a decrease in mean layers without a corresponding decrease in spawn lengths or widths. However, when examined by several criteria, there is no evidence of any systematic decline in the total effort dedicated to spawn surveys.

It is likely that the change in mean of layers (Fig. 5) is a result of an unintentional and unnoticed change in diver surveys. Some change in survey methodology might be unavoidable because many different divers have participated in the surveys. The herring spawn database shows 164 different diver codes from 1984-2010 indicating that 164 different divers have been involved with the collection of data. Many would have had little prior experience in estimating egg layers. Part of the explanation for the discontinuity of the ‘layer’ evaluation may be related to the large number of different people associated with the dive surveys.

A consequence of the decrease in mean layers is a reduction in the annual herring spawn index, which in turn affects the estimated SSB in the annual assessments, although the extent of the effect is uncertain. It is possible that part of the explanation for the decline in mean egg layers reflects an unintentional change in the way that divers estimate spawn and perhaps, ironically, a response to well-intentioned enthusiasm to chronicle instances of egg deposition that might have been ignored as trivial in previous years.

Although it seems clear that the assessments of layers have changed, it also is clear that the effect of such a change – even if it is a methodological error – may have led to moderately overly-conservative assessments. Even so, there are other criteria that make it clear that BC herring stocks have declined significantly in the last 5 years. This can be ascertained in this report simply by noting the reduction in the number of spawn events. Therefore, while it is important to examine the issue of past inconsistencies in diver methodology, it is important to avoid rushing to judgment about the impact of such a change on SSB estimates. <u>To provide further insight into this question a recommendation is to conduct a series of quality control tests on herring spawning grounds. These tests should examine diver variability in the assessment of egg layers and determine if experienced DFO divers use the same evaluation criteria as non-DFO contract divers.</u>

The sharp increase in the frequency of the 'trace' (0.01) category of egg layers is not caused by a key-punching error, which is a possibility mentioned in the herring spawn assessment manual (Fort et al. 2009). Therefore such an increase must reflect a change in herring biology or an unintentional change in survey protocols. Regardless, the estimate of 0.01 layers is not realistic. <u>A recommendation is to examine ways to establish more realistic estimates of a 'trace' observation, because the present use of the 0.01 layers may be contributing to error in the herring spawn index, possibly leading to unwarranted conservatism in the annual assessment of herring.</u> Several options should be examined to determine the effect on the estimates of the HSI (herring spawn index) used in the assessments. One option could be to re-classify all 'trace' observations to zero, but this would impact the estimates of spawn width. Another would be to take field measurements, or egg counts, to determine realistic estimates of egg density. There may be other options, but ignoring the issue would be the worst.

There may be a computational problem with the present calculation of the herring spawn index used for assessment, although the severity of the problem is uncertain. The problem arises indirectly because of the increased frequency of the 'trace' category at the ends of transects. In some instances the addition of a "0.01" trace estimate at the end-points of transects will have the dual effect of (1) lowering the mean egg density both for the transect and the entire spawning bed and (2) increasing the estimated area of the spawning bed. Intuitively it would seem that adding more spawning area, even with very low egg densities (0.01 layers) would increase the estimate of spawning biomass, but not always. The egg density (eggs/m^2) for a spawning bed is estimated as the 'mean of all transect means' where the transect mean is the mean egg number for each station on the transect, weighted by the transect length. In some instances the additional area may not be sufficient to compensate for the effect of reduction in mean layers so the overall estimate of egg number for the entire spawning bed is reduced. The frequency and severity of this circumstance on the estimate of the total spawn index is uncertain, and may be small. <u>Regardless, a recommendation is that the computational procedures for estimating eggs (within the assessment methodology that pertains to the estimation of the herring spawn index) should be re-examined to determine if there is a better way to add peripheral, low-density spawning data without negatively impacting the estimation of the most abundant sections of transects.</u> The inclusion of 'trace' layers as representing real density estimates is a problem that should be addressed (see the preceding recommendations).

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APPENDIX 1A. THE HERRING SPAWN DATABASE

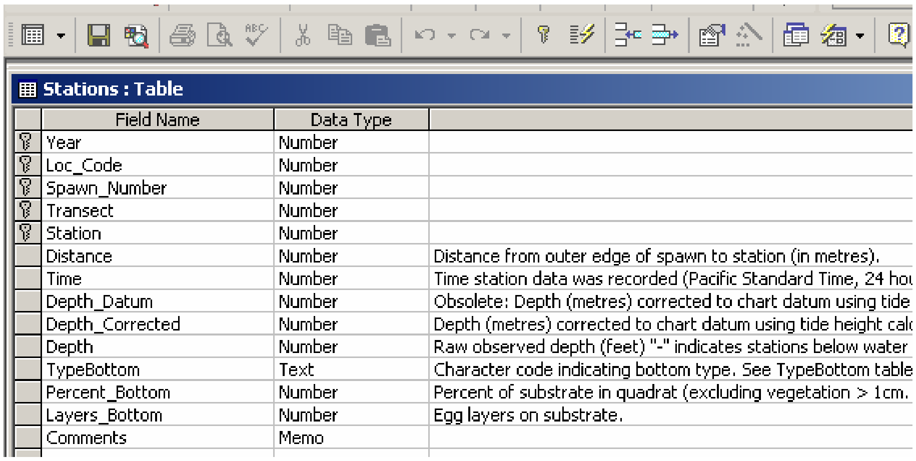
The herring spawn database maintained in Access© at the Pacific Biological Station in Nanaimo consists of a number of key tables. Four main tables described briefly here are: (1) the STATION Table; (2) the VEGETATION Table; (3) the VEGTRANS Table; (4) the ALLSPAWN table.

STATION Table

This table has data on each sample station examined with quadrat along the spawn survey transects. Data include:

- station number (position along transect);
- time (of day);
- depth (at time of sample but later corrected, for tidal variation);
- type of bottom - range of several bottom types, such as sand, rocks etc.;
- percent bottom – percent of bottom quadrat covered with eggs;
- bottom egg layers - number of egg layers on substrate;
- vegetation cover and the number of egg layers on bottom substrates.

This table consists of 121,537 rows of data collected since 1984.



	Field Name	Data Type	
🔑	Year	Number	
🔑	Loc_Code	Number	
🔑	Spawn_Number	Number	
🔑	Transect	Number	
🔑	Station	Number	
	Distance	Number	Distance from outer edge of spawn to station (in metres).
	Time	Number	Time station data was recorded (Pacific Standard Time, 24 hou
	Depth_Datum	Number	Obsolete: Depth (metres) corrected to chart datum using tide
	Depth_Corrected	Number	Depth (metres) corrected to chart datum using tide height cal
	Depth	Number	Raw observed depth (feet) "-" indicates stations below water
	TypeBottom	Text	Character code indicating bottom type. See TypeBottom table
	Percent_Bottom	Number	Percent of substrate in quadrat (excluding vegetation > 1cm.
	Layers_Bottom	Number	Egg layers on substrate.
	Comments	Memo	

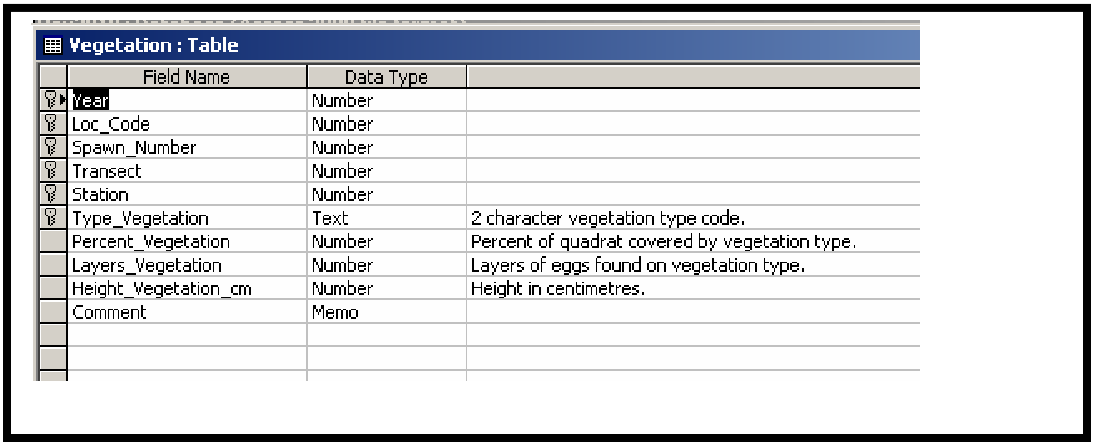
VEGETATION Table

The VEGETATION table consists of nine columns including:

- location number that corresponds to each of >2000 coastal locations;
- transect and station number;
- type vegetation - a two character code for six vegetation categories;
- percent vegetation - % of the quadrat that is covered by the vegetation type;

- layers of vegetation - estimated for each vegetation types; (may be several entries for single stations;
- height of vegetation (in cm).

The VEGETATION table has 129,200 entries of which 1,731 have estimates that exceed 100 percent vegetation. The rational for this is that estimates exceeding 100 percent are warranted to adjust to tall vegetation (see diver manual). *It may be a concern about whether the incidence or frequency of the high (>100%) estimates is consistent over time.*

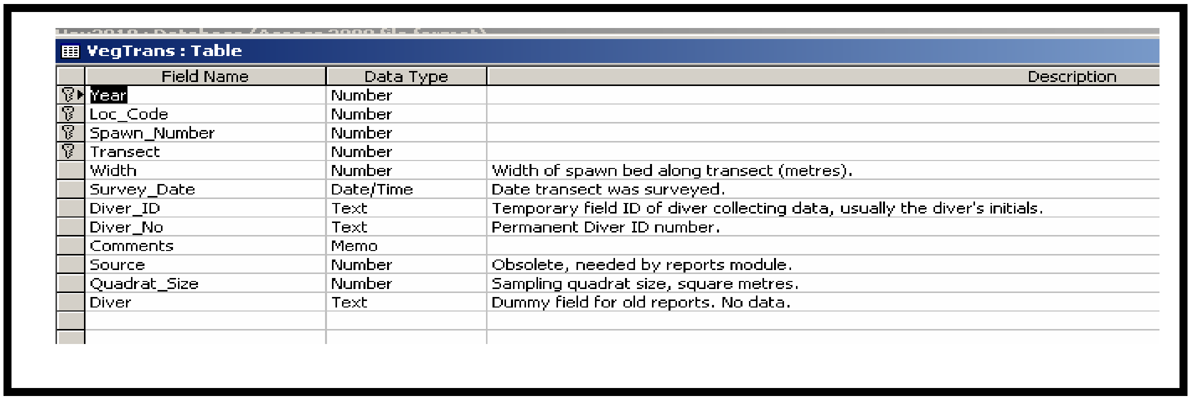

Vegetation : Table

Field Name	Data Type	
Year	Number	
Loc_Code	Number	
Spawn_Number	Number	
Transect	Number	
Station	Number	
Type_Vegetation	Text	2 character vegetation type code.
Percent_Vegetation	Number	Percent of quadrat covered by vegetation type.
Layers_Vegetation	Number	Layers of eggs found on vegetation type.
Height_Vegetation_cm	Number	Height in centimetres.
Comment	Memo	

The VEGTRANS Table represents each transect. Data include:

- codes to link to other tables;
- transect code (identical to entries in other tables);
- width (or a derivative) of the estimate of maximal distance along transects where spawn was found;
- diver identification number.

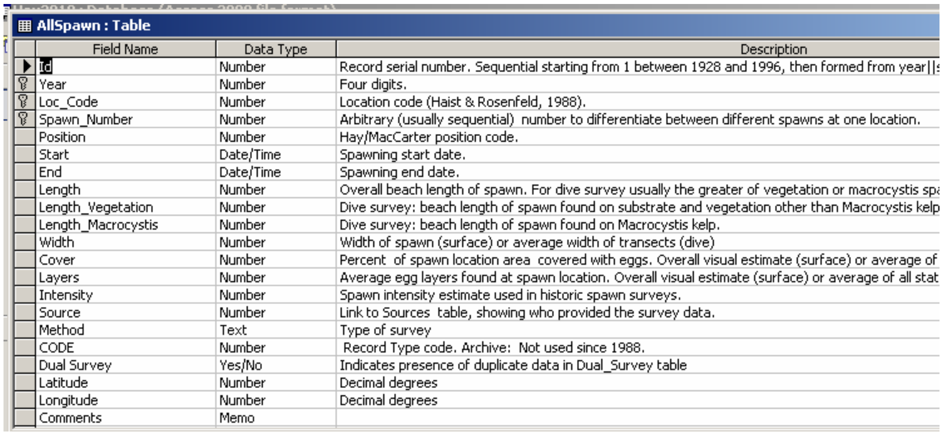
The VEGTRANS table consists of 21,777 records of transect data from 1984-2010. For each spawn event examined by divers, there were one or more transects that are differentiated in the table as the spawn number for each date. This table records key information about spawn widths.


VegTrans : Table

Field Name	Data Type	Description
Year	Number	
Loc_Code	Number	
Spawn_Number	Number	
Transect	Number	
Width	Number	Width of spawn bed along transect (metres).
Survey_Date	Date/Time	Date transect was surveyed.
Diver_ID	Text	Temporary field ID of diver collecting data, usually the diver's initials.
Diver_No	Text	Permanent Diver ID number.
Comments	Memo	
Source	Number	Obsolete, needed by reports module.
Quadrat_Size	Number	Sampling quadrat size, square metres.
Diver	Text	Dummy field for old reports. No data.

ALLSPAWN Table

The ALLSPAWN table consists of 29,866 spawn records from 1928 to 2010.
The ALLSPAWN table represents a merger of all spawn data collected by both surface and divers surveys and includes 11,807 records collected since 1984. **<u>These records represent spawn events.</u>** Each record will have a unique date, estimated spawn length, width, estimated layers (a composite of all estimates from each calculation using input from the preceding tables).



Field Name	Data Type	Description
Id	Number	Record serial number. Sequential starting from 1 between 1928 and 1996, then formed from year||
Year	Number	Four digits.
Loc_Code	Number	Location code (Haist & Rosenfeld, 1988).
Spawn_Number	Number	Arbitrary (usually sequential) number to differentiate between different spawns at one location.
Position	Number	Hay/MacCarter position code.
Start	Date/Time	Spawning start date.
End	Date/Time	Spawning end date.
Length	Number	Overall beach length of spawn. For dive survey usually the greater of vegetation or macrocystis sp
Length_Vegetation	Number	Dive survey: beach length of spawn found on substrate and vegetation other than Macrocystis kelp
Length_Macrocystis	Number	Dive survey: beach length of spawn found on Macrocystis kelp.
Width	Number	Width of spawn (surface) or average width of transects (dive)
Cover	Number	Percent of spawn location area covered with eggs. Overall visual estimate (surface) or average of
Layers	Number	Average egg layers found at spawn location. Overall visual estimate (surface) or average of all stat
Intensity	Number	Spawn intensity estimate used in historic spawn surveys.
Source	Number	Link to Sources table, showing who provided the survey data.
Method	Text	Type of survey
CODE	Number	Record Type code. Archive: Not used since 1988.
Dual Survey	Yes/No	Indicates presence of duplicate data in Dual_Survey table
Latitude	Number	Decimal degrees
Longitude	Number	Decimal degrees
Comments	Memo	

APPENDIX 1B. EGG ESTIMATION METHODS

The text in the box is a summary of the egg estimation method presented in Cleary et al. 2010. The text shown here is unaltered except for one sentence that is underlined. See the text for the explanation.

Scuba Surveys

For scuba surveys, spawning bed lengths are determined by exploratory grabs with a spawn drag, rake or snorkelling to define the limits of the areas of egg deposition. A systematic sampling regime is employed whereby transects are set across the egg bed perpendicular to shore at 350 m intervals. Corresponding spawning bed widths are estimated as the mean of all transect lengths within the spawning bed. Estimates of mean egg density are based on a two-stage sampling design (Schweigert et al. 1985, 1990). Average egg density for each spawning bed is estimated, as the weighted mean of the means of a series of quadrats located along each transect, where the weighting is based on the length of each transect. For each quadrat, observations are made on several variables: type of algal substrate; proportion of the quadrat covered by each algal type; number of layers of eggs on each algal type; proportion of the bottom substrate covered by eggs; and an estimate of the number of egg layers on the bottom substrate. In some areas, assessments are also made of the egg deposition on the giant kelp as described in a following section.

Egg deposition for each sampling quadrat is estimated from the predictive equation described in the 1989 assessment (Haist and Schweigert 1990, Schweigert 1993). Egg density for each vegetation subfraction is estimated as follows using non-linear regression (P<0.0001):

$$Eggs_{ij} = 1033.6694\, L_{ij}^{0.7137}\, P_{ij}^{1.5076}\, V_{ij}\, Q_j.$$

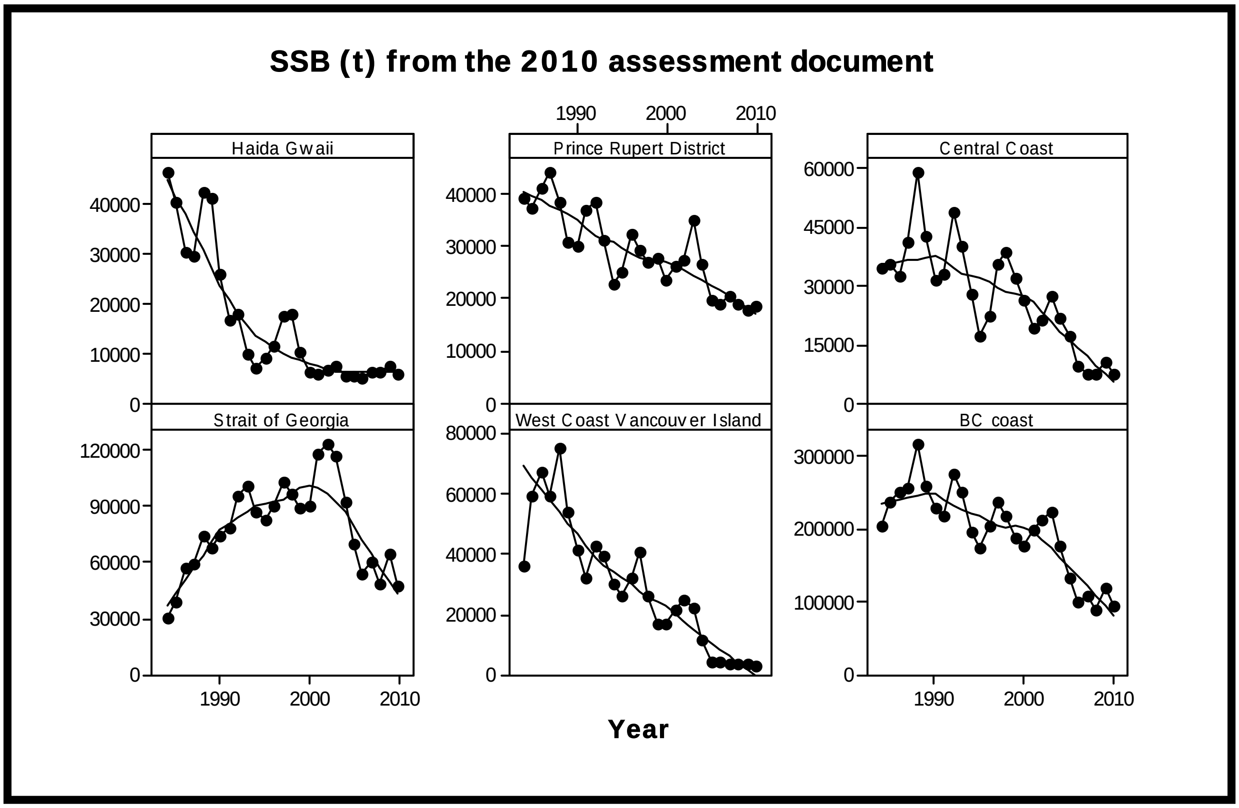
where

$Eggs_{ij}$ = estimated number of eggs in thousands per m^2 on vegetation type i in quadrat j

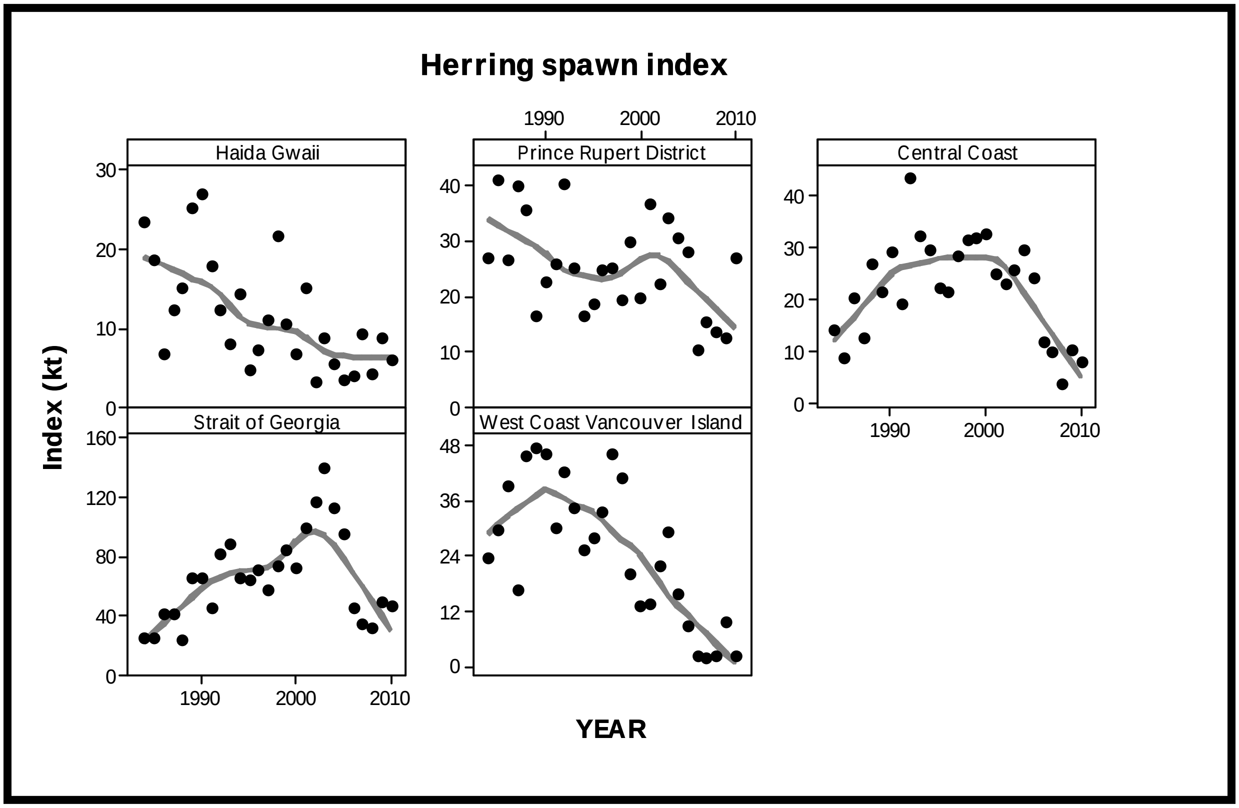
L_{ij} = number of layers of eggs on algal substrate i in quadrat j,
P_{ij} = proportion of quadrat covered by algal substrate i in quadrat j,
V_{1j} = 0.9948 parameter for sea grasses in quadrat j,
V_{2j} = 1.2305 parameter for rockweed in quadrat j,
V_{3j} = 0.8378 parameter for flat kelp in quadrat j,
V_{4j} = 1.1583 parameter for other brown algae in quadrat j,
V_{5j} = 0.9824 parameter for leafy red and green algae in quadrat j,
V_{6j} = 1.0000 parameter for stringy red algae in quadrat j,
Q_1 = 0.5668 parameter for 1.00 m^2 quadrats,
Q_2 = 0.5020 parameter for 0.50 m^2 quadrats,
Q_3 = 1.0000 parameter for 0.25 m^2 quadrats.

APPENDIX 2. SPAWN METRICS COMPARED BY REGION AND EVENT

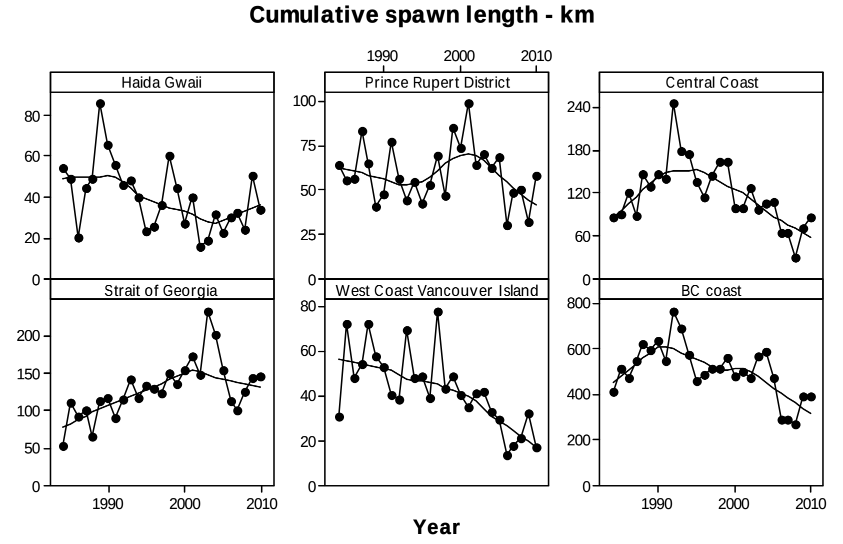
Appendix 2. Figure 1. Spawning stock biomass estimates from the annual assessment report (Cleary et al. 2010). The line between the points is a Lowess smoother.



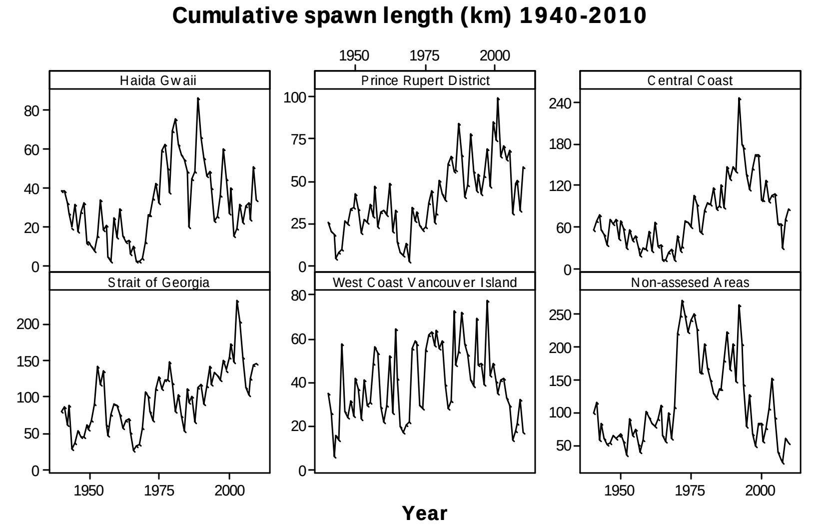
Appendix 2. Figure 2. Herring spawn index from the 2010 assessment report (Cleary et al. 2010) shown by region and year. The grey line between the points is a Lowess smoother.



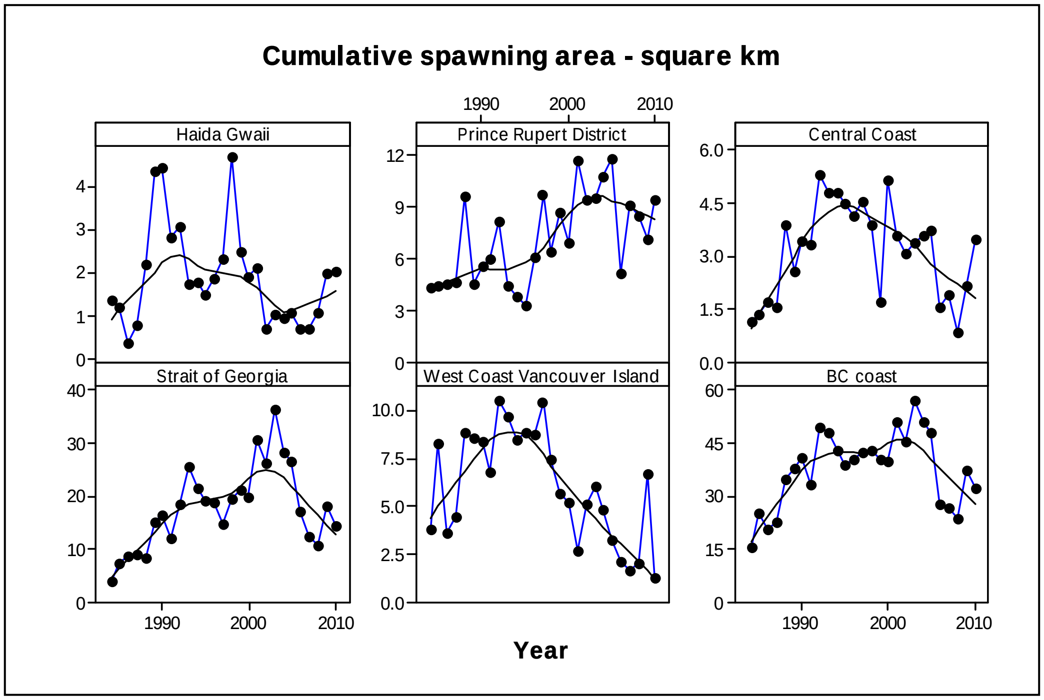
Appendix 2. Figure 3a. The cumulative spawn length (km) for each region and year from the dive survey period of 1984-2010. The line between the points is a Lowess smoother.



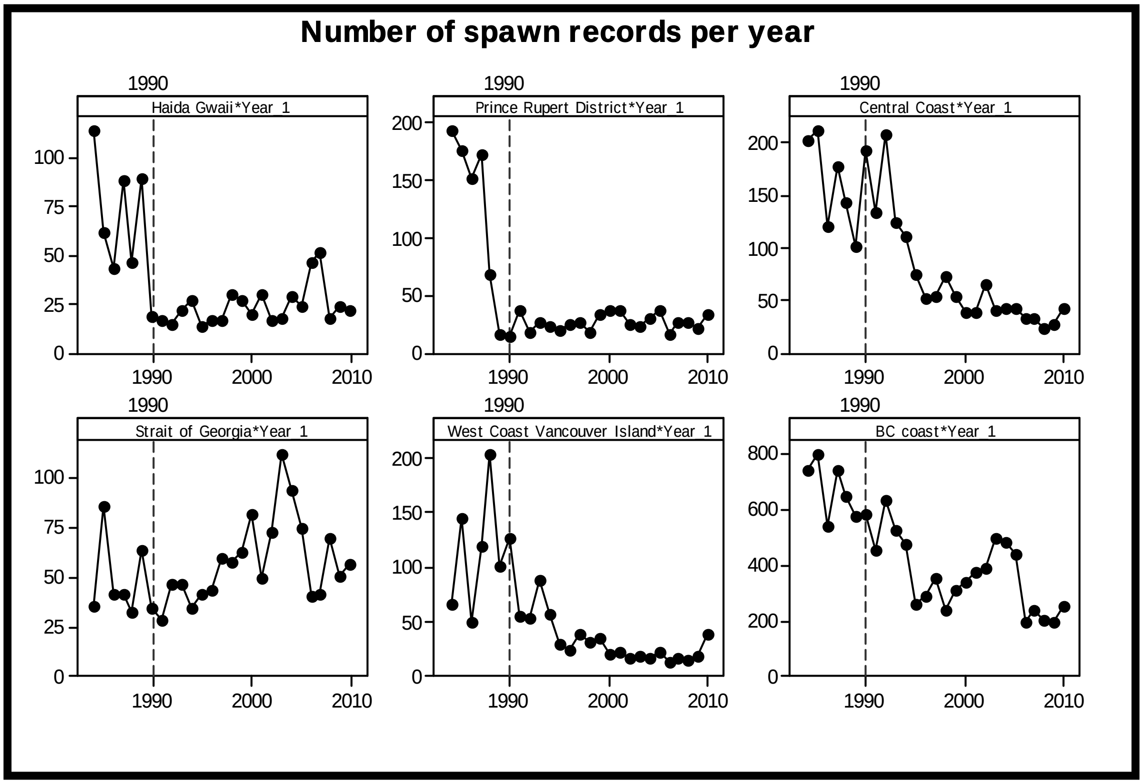
Appendix 2. Figure 3b. The cumulative spawn length (km) shown for each region and year since 1940.



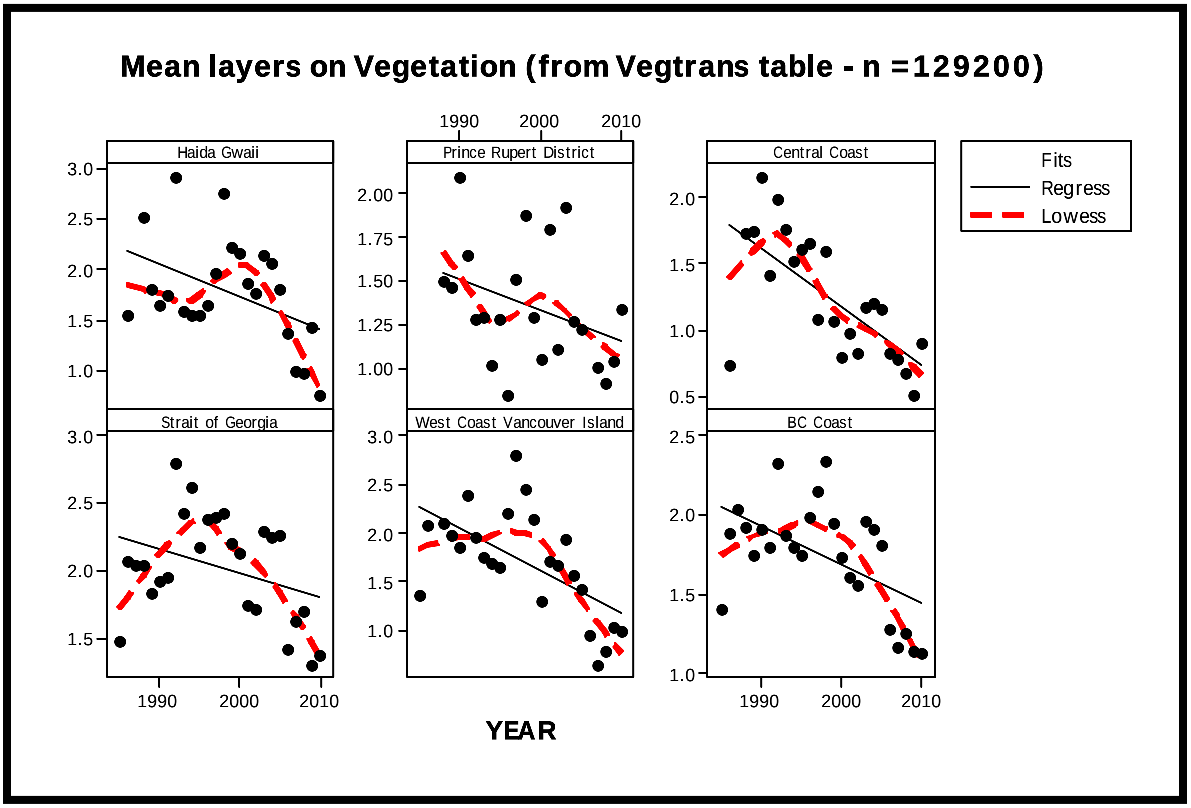
Appendix 2. Figure 4. The cumulative spawn area (square km) per year for each region. The line is a Lowess smoother.



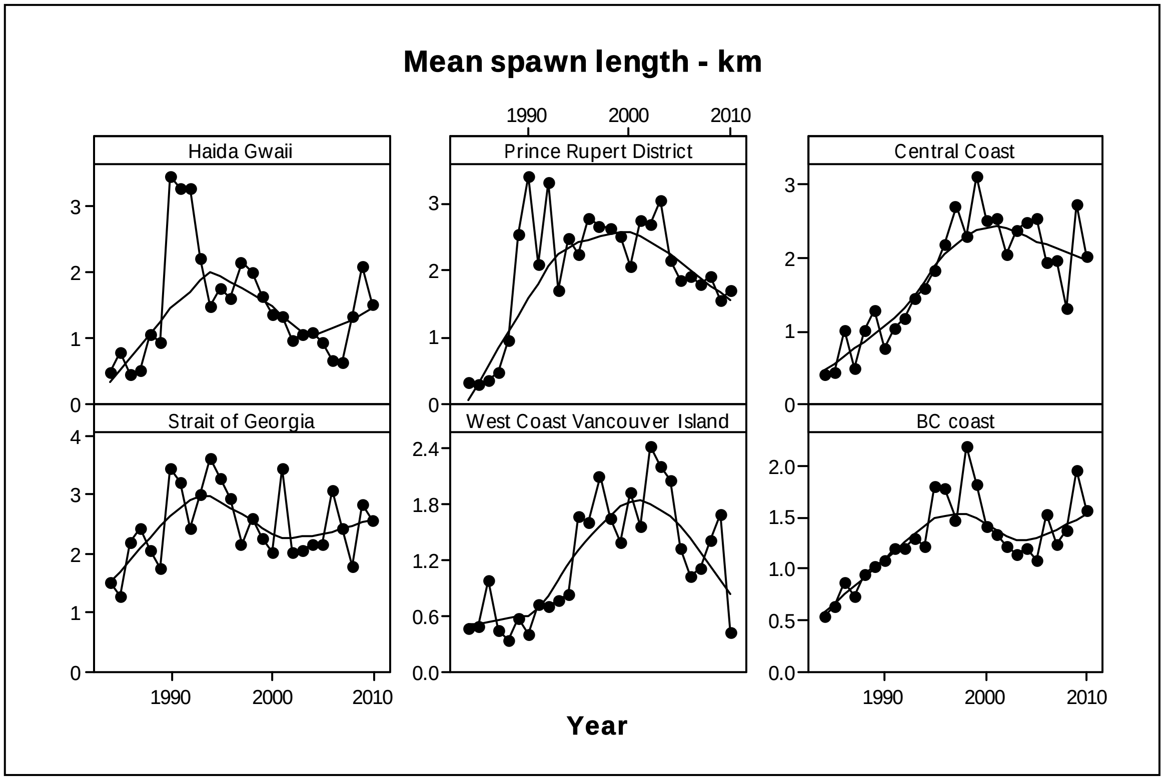
Appendix 2. Figure 5. The number of spawn records per year for each region. The data prior to 1990 (dashed line) were not collected consistently relative to the determination of spawn records or event. In those earlier years there was a tendency to record a larger number of smaller spawn units that might not have been distinct spawns.



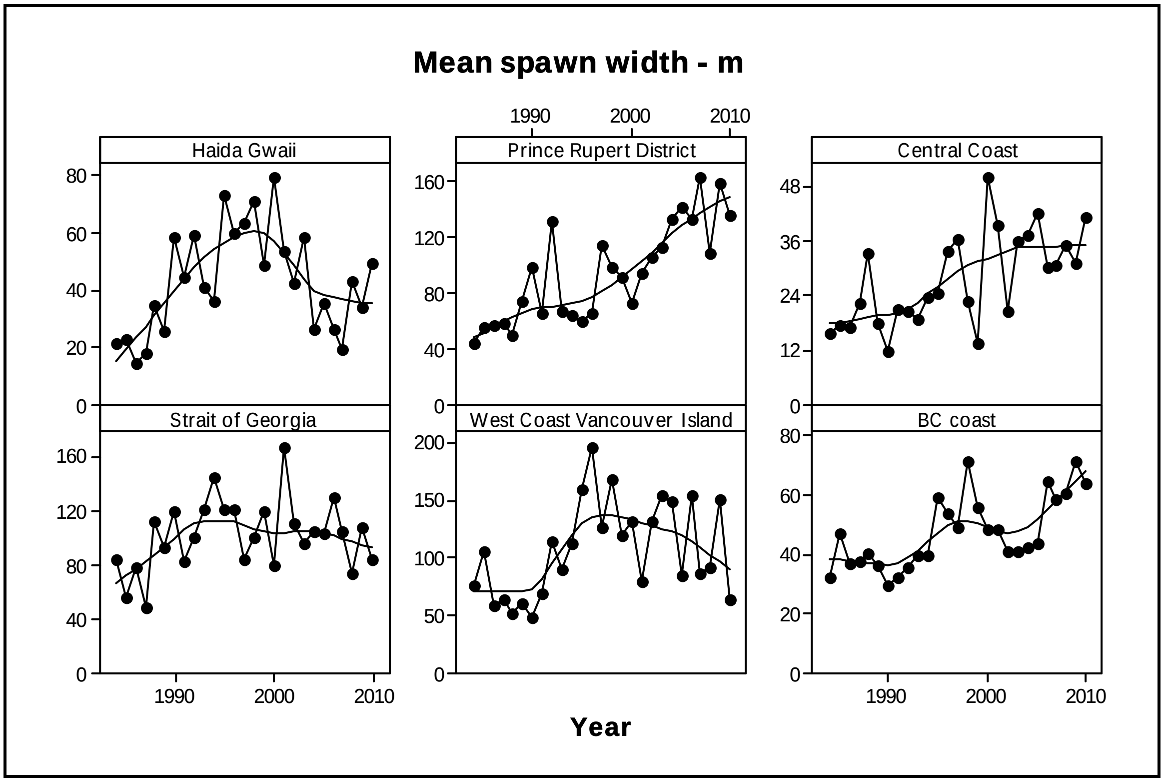
Appendix 2. Figure 6. Mean layers on vegetation, by year and Region. These estimates are derived from 129,200 records in the VEGTRANS table. The solid line shows a linear regression that is significant for are Regions. The dashed line is a Lowess smoother.



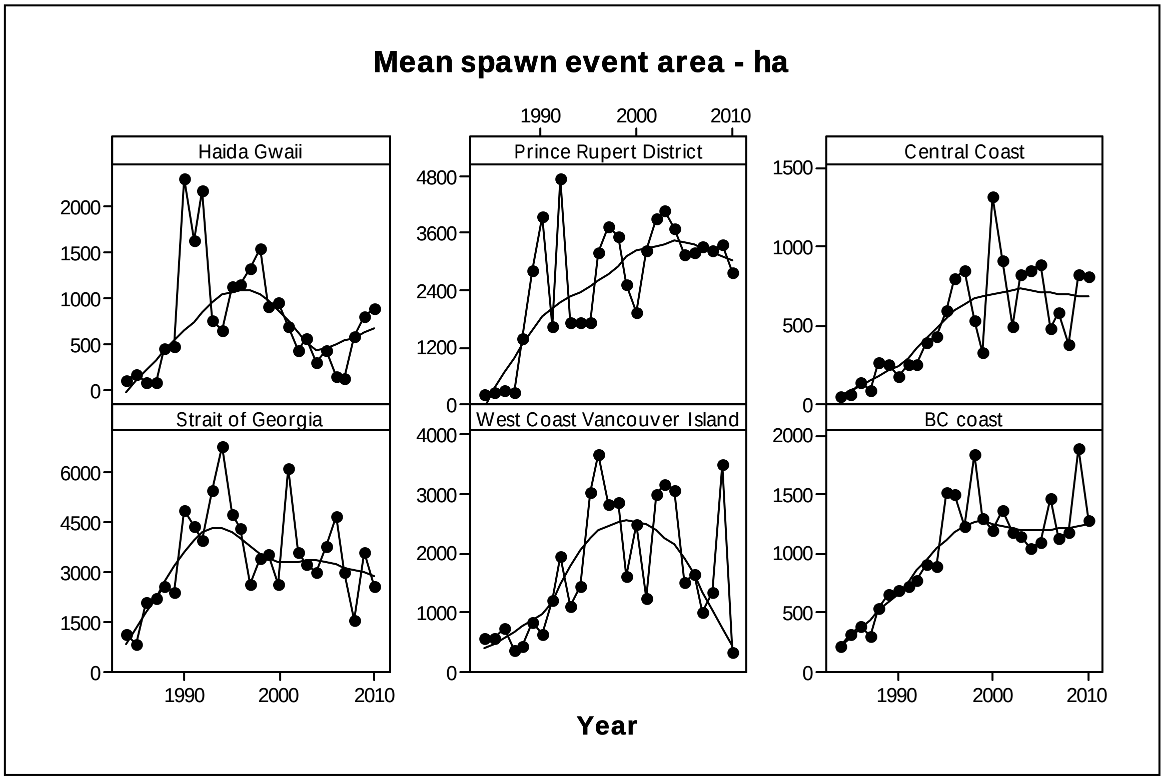
Appendix 2. Figure 7. Mean spawn length (km) of spawn events (from the ALLSPAWN table). The line is a Lowess smoother.



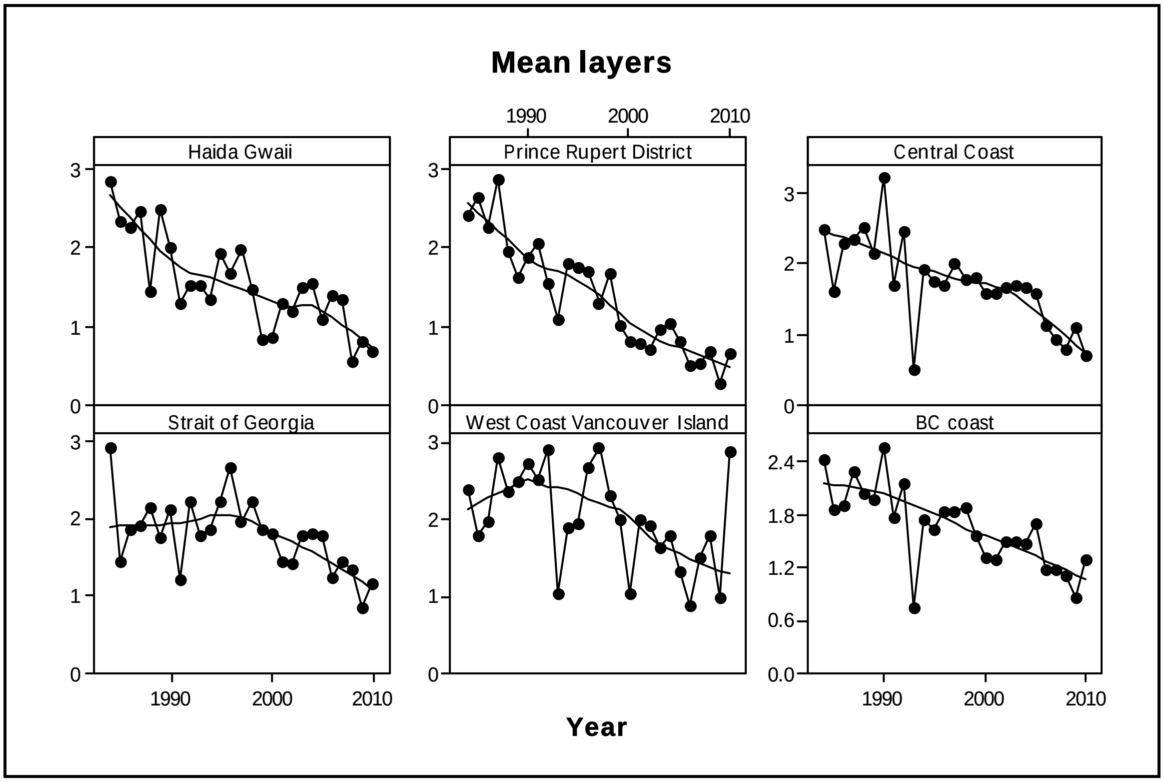
Appendix 2. Figure 8. Mean spawn width (m) of spawn events (from the ALLSPAWN table). The line is a Lowess smoother.



Appendix 2. Figure 9. Mean spawn area (ha) of spawn events (from the ALLSPAWN table). The line is a Lowess smoother.



Appendix 2. Figure 10. Mean spawn layers (m) of spawn events (from the ALLSPAWN table). The decrease in mean layers was examined by linear regression and was significant (p<0.01) in all regions. The solid line is a Lowess smoother.



APPENDIX 3. CORRELATION MATRIX OF SPAWN METRICS

Correlation matrices between different spawn metrics for five different stock assessment regions. In each box the top number is the correlation coefficient and the bottom number is the probability of significance. Nearly all spawn metrics examined at the level of the region co-vary significantly. Many of the metrics from spawn events are either not significant or have negative correlation coefficients. The shaded boxes (top three rows) on the top left represent metrics of the entire region.   The lower boxes represent metrics from spawn events. The bottom line compares the frequency of low egg numbers (0+ represents all egg layers between 0.01 and 0.49) with the SSB (all are significant) and two main spawn event metrics (mean length and mean width) and most comparisons are not significant.

Appendix 3. Table 1. Haida Gwaii

	SSB	Spawn index	Sum length	Number records	Mean length	Mean width	Mean layers
Spawn index	0.700						
p	*0.00*						
Sum length	0.591	0.872					
p	*0.001*	*0.000*					
Number records	0.727	0.478	0.450				
p	*0.00*	*0.01*	*0.02*				
Mean length	-0.164	0.273	0.344	-0.580			
p	*0.414*	*0.168*	*0.079*	*0.002*			
Mean width	-0.382	-0.047	-0.118	-0.663	0.581		
p	*0.05*	*0.82*	*0.56*	*0.00*	*0.00*		
Mean layers	0.769	0.542	0.380	0.688	-0.220	-0.348	
p	*0.000*	*0.004*	*0.051*	*0.000*	*0.271*	*0.075*	
0+ layers	**-0.588**	-0.455	-0.340	-0.191	**-0.150**	**-0.161**	-0.386
p	***0.00***	*0.03*	*0.11*	*0.38*	***0.50***	***0.46***	*0.07*
	SSB	**Spawn index**	**Sum length**	**Number records**	**Mean length**	**Mean width**	**Mean layers**

Appendix 3. Table 2. Prince Rupert District

	SSB	Spawn index	Sum length	Number records	Mean length	Mean width	Mean layers
Spawn index	0.685						
p	*0.00*						
Sum length	0.331	0.644					
p	*0.09*	*0.00*					
Number records	0.640	0.476	0.252				
p	*0.00*	*0.01*	*0.20*				
Mean length	-0.321	-0.179	-0.003	-0.840			
p	*0.10*	*0.37*	*0.99*	*0.00*			
Mean width	-0.647	-0.267	-0.220	-0.530	0.365		
p	*0.00*	*0.18*	*0.27*	*0.00*	*0.06*		
Mean layers	0.822	0.466	0.149	0.698	-0.423	-0.775	
p	*0.00*	*0.01*	*0.46*	*0.00*	*0.03*	*0.00*	
0+ layers	**-0.613**	-0.197	0.021	-0.039	**-0.135**	**0.606**	-0.633
p	***0.00***	*0.35*	*0.92*	*0.85*	***0.52***	***0.00***	*0.00*
	SSB	**Spawn index**	**Sum length**	**Number records**	**Mean length**	**Mean width**	**Mean layers**

Appendix 3. Table 3. Central Coast

	SSB	Spawn index	Sum length	Number records	Mean length	Mean width	Mean layers
Spawn index	0.550						
p	*0.00*						
Sum length	0.664	0.844					
p	*0.000*	*0.000*					
Number records	0.700	0.148	0.428				
p	*0.00*	*0.46*	*0.03*				
Mean length	-0.448	0.254	-0.044	-0.849			
p	*0.019*	*0.201*	*0.826*	*0.000*			
Mean width	*-0.440*	*-0.080*	*-0.420*	*-0.673*	*0.561*		
p	*0.02*	*0.69*	*0.03*	*0.00*	*0.00*		
Mean layers	*0.641*	*0.407*	*0.424*	*0.637*	*-0.415*	-0.433	
p	*0.000*	*0.035*	*0.027*	*0.000*	*0.032*	*0.024*	
0+ layers	**-0.496**	-0.374	-0.325	-0.204	**0.082**	**0.138**	-0.361
p	***0.01***	*0.07*	*0.11*	*0.33*	***0.70***	***0.51***	*0.08*
	SSB	**Spawn index**	**Sum length**	**Number records**	**Mean length**	**Mean width**	**Mean layers**

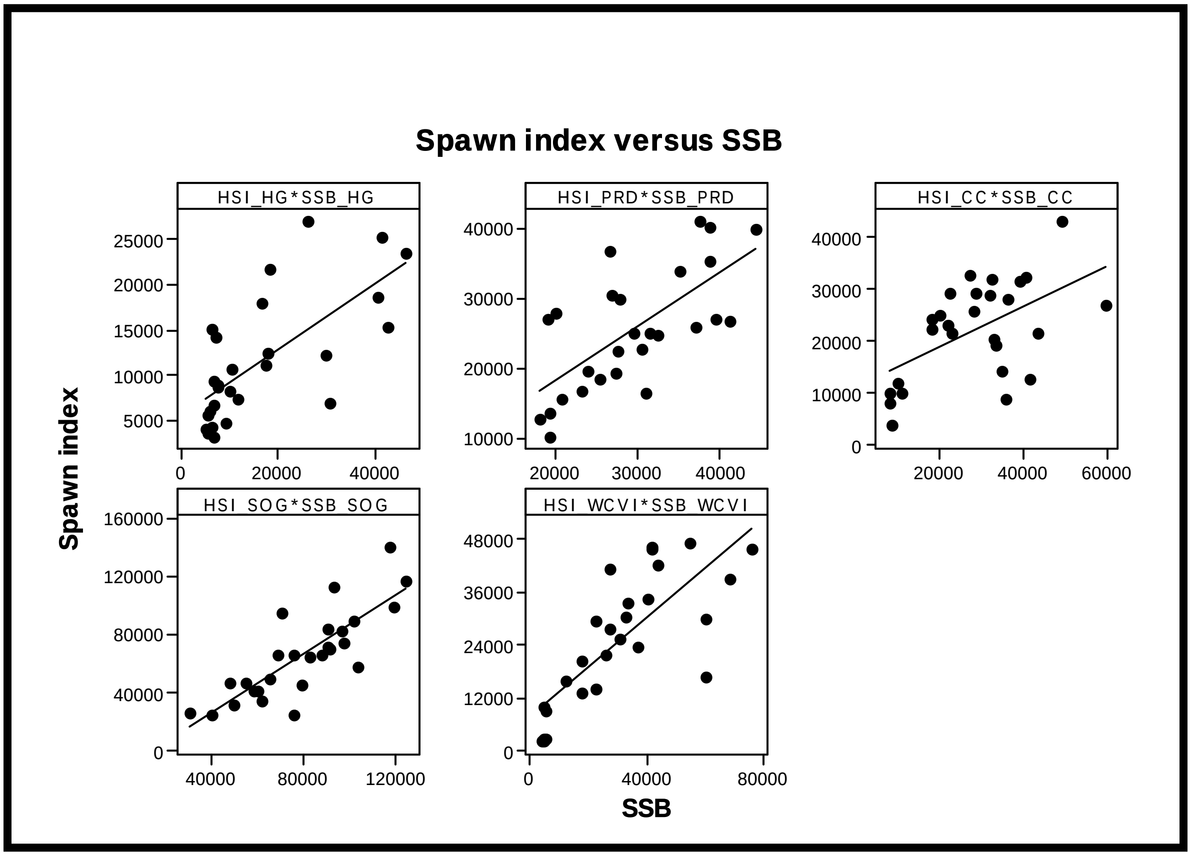
Appendix 3. Table 4. Strait of Georgia

	SSB	Spawn index	Sum length	Number records	Mean length	Mean width	Mean layers
Spawn index	0.818						
p	*0.00*						
Sum length	0.604	0.835					
p	*0.00*	*0.00*					
Number records	0.271	0.567	0.755				
p	*0.17*	*0.00*	*0.00*				
Mean length	0.312	0.145	0.086	-0.551			
p	*0.11*	*0.47*	*0.67*	*0.00*			
Mean width	0.505	0.416	0.246	-0.253	0.678		
p	*0.01*	*0.03*	*0.22*	*0.20*	*0.00*		
Mean layers	0.073	0.026	-0.249	-0.197	-0.090	0.023	
p	*0.72*	*0.90*	*0.21*	*0.33*	*0.66*	*0.91*	
0+ layers	**-0.735**	-0.610	-0.409	-0.225	**-0.226**	**-0.257**	-0.204
p	***0.00***	*0.00*	*0.03*	*0.26*	***0.26***	***0.20***	*0.31*
	SSB	**Spawn index**	**Sum length**	**Number records**	**Mean length**	**Mean width**	**Mean layers**

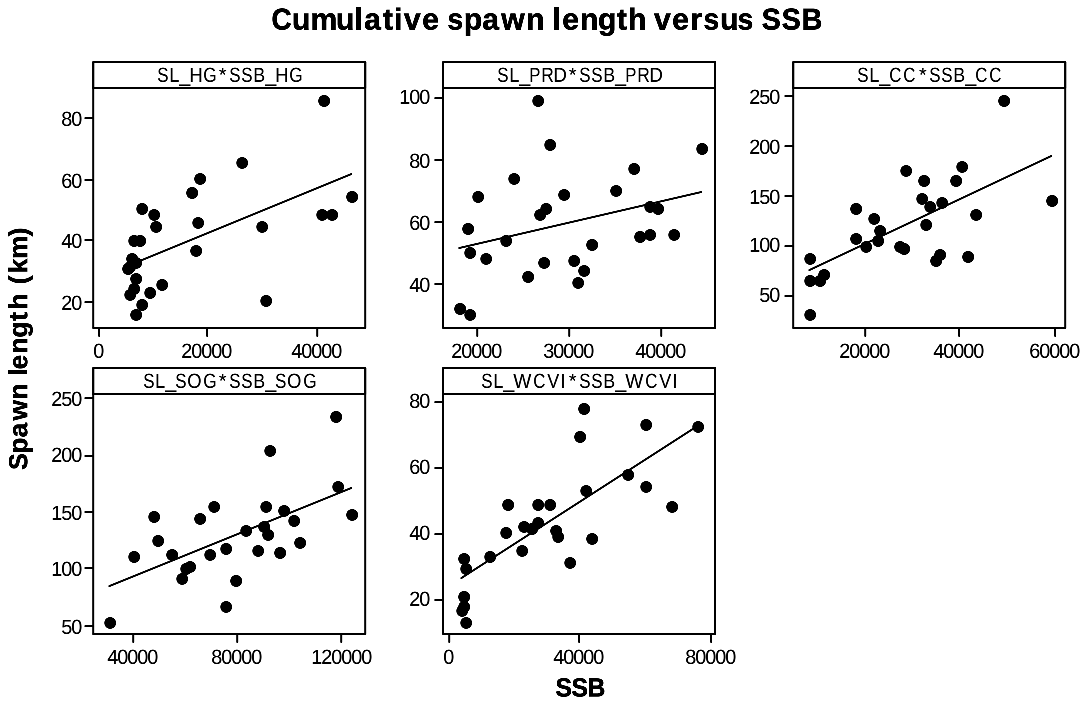
Appendix 3. Table 5. West Coast of Vancouver Island

	SSB	Spawn index	Sum length	Number records	Mean length	Mean width	Mean layers
Spawn index	0.777						
p	*0.00*						
Sum length	0.781	0.765					
p	*0.000*	*0.000*					
Number records	0.801	0.538	0.674				
p	*0.00*	*0.00*	*0.00*				
Mean length	-0.471	-0.176	-0.144	-0.710			
p	*0.013*	*0.380*	*0.473*	*0.000*			
Mean width	-0.406	-0.096	-0.163	-0.575	0.712		
p	*0.04*	*0.63*	*0.42*	*0.00*	*0.00*		
Mean layers	0.467	0.514	0.270	0.347	-0.325	-0.284	
p	*0.014*	*0.006*	*0.173*	*0.076*	*0.098*	*0.152*	
0+ layers	**-0.784**	-0.732	-0.709	-0.600	**0.200**	**0.242**	-0.494
p	***0.00***	*0.00*	*0.00*	*0.00*	***0.33***	***0.23***	*0.01*
	SSB	**Spawn index**	**Sum length**	**Number records**	**Mean length**	**Mean width**	**Mean layers**

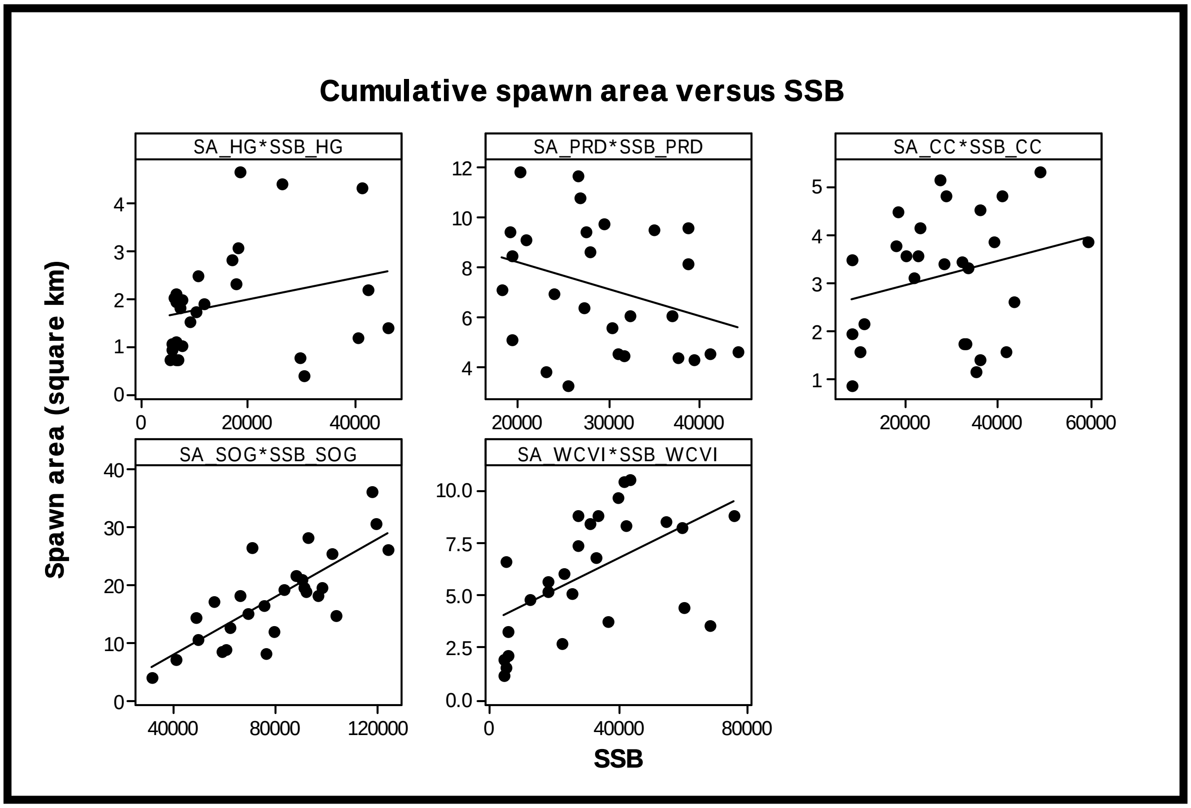
Appendix 3. Figure 1. Herring spawn index versus spawning stock biomass (SSB). The line shows a linear regression fit. These figures correspond to the summary in Table 2, row 1.



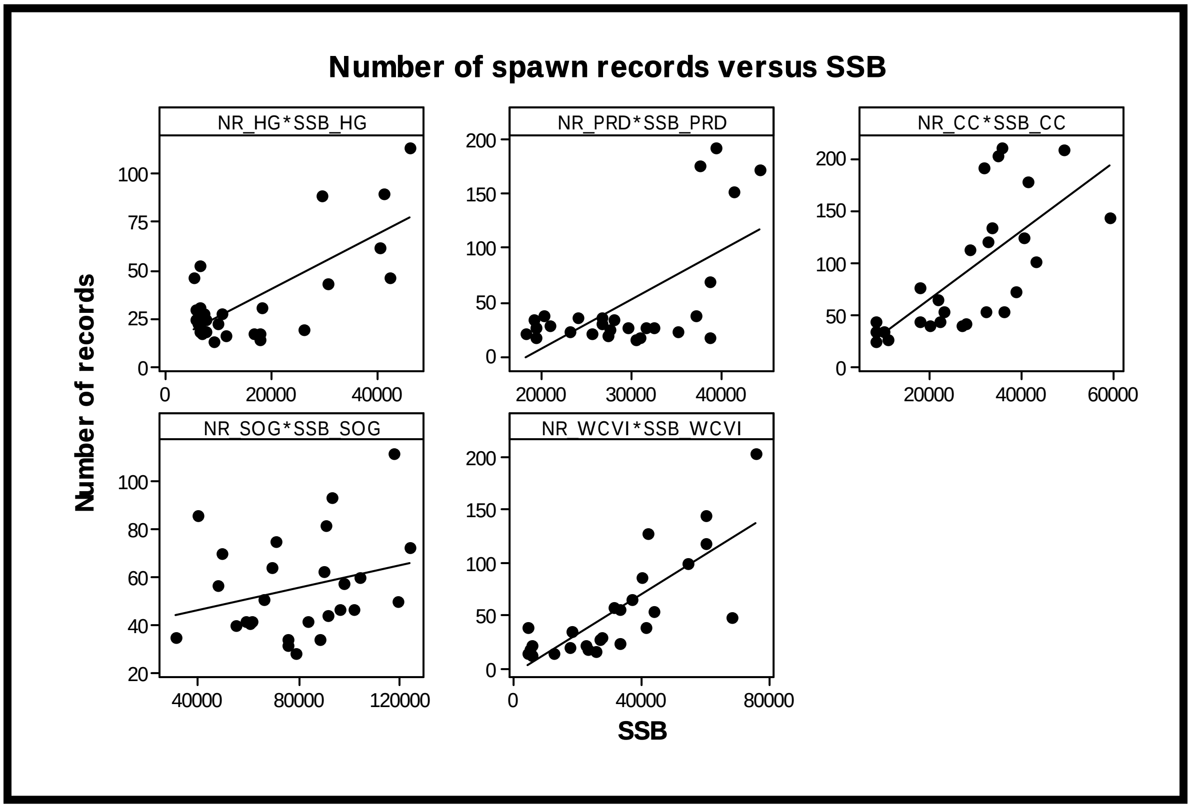
Appendix 3. Figure 2. Cumulative spawn length (km) versus the spawning stock biomass (SSB). The line shows a linear regression fit. These figures correspond to the summary in Table 2, row 2.



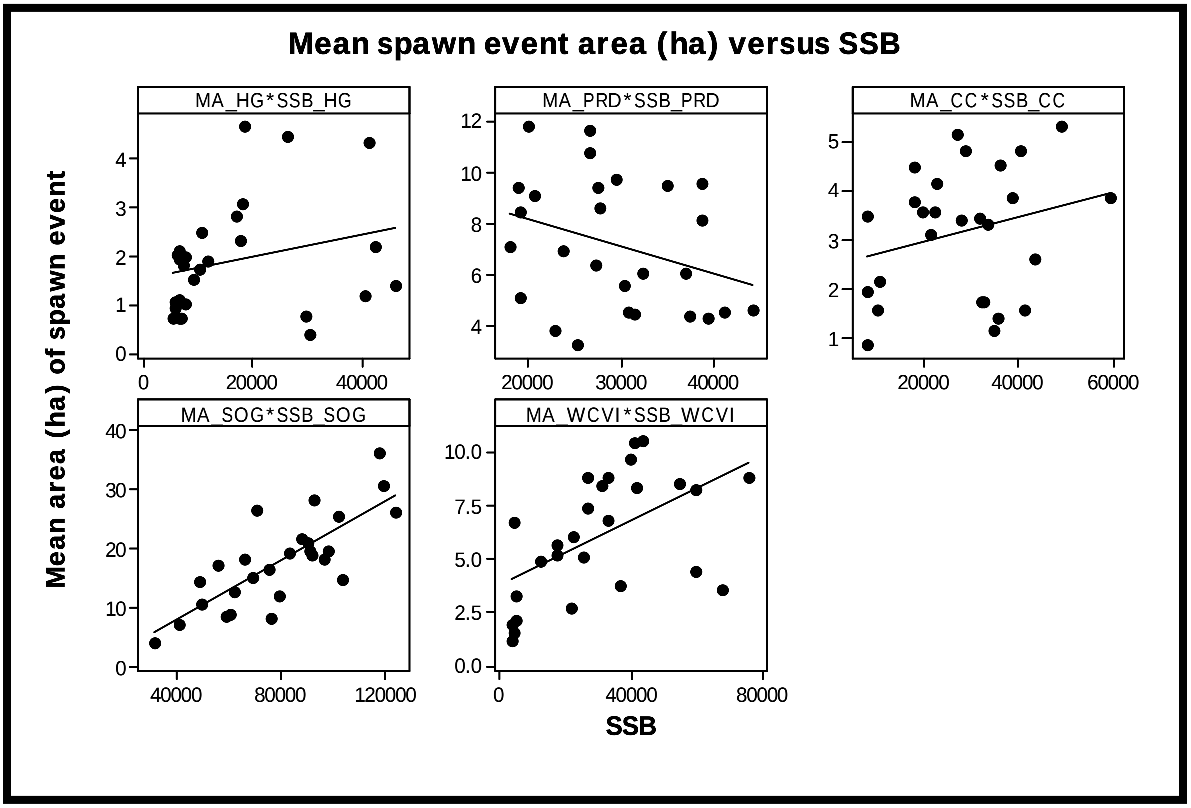
Appendix 3. Figure 3. Cumulative spawn area (km^2) index versus spawning stock biomass (SSB). These figures correspond to the summary in Table 2, row 3.



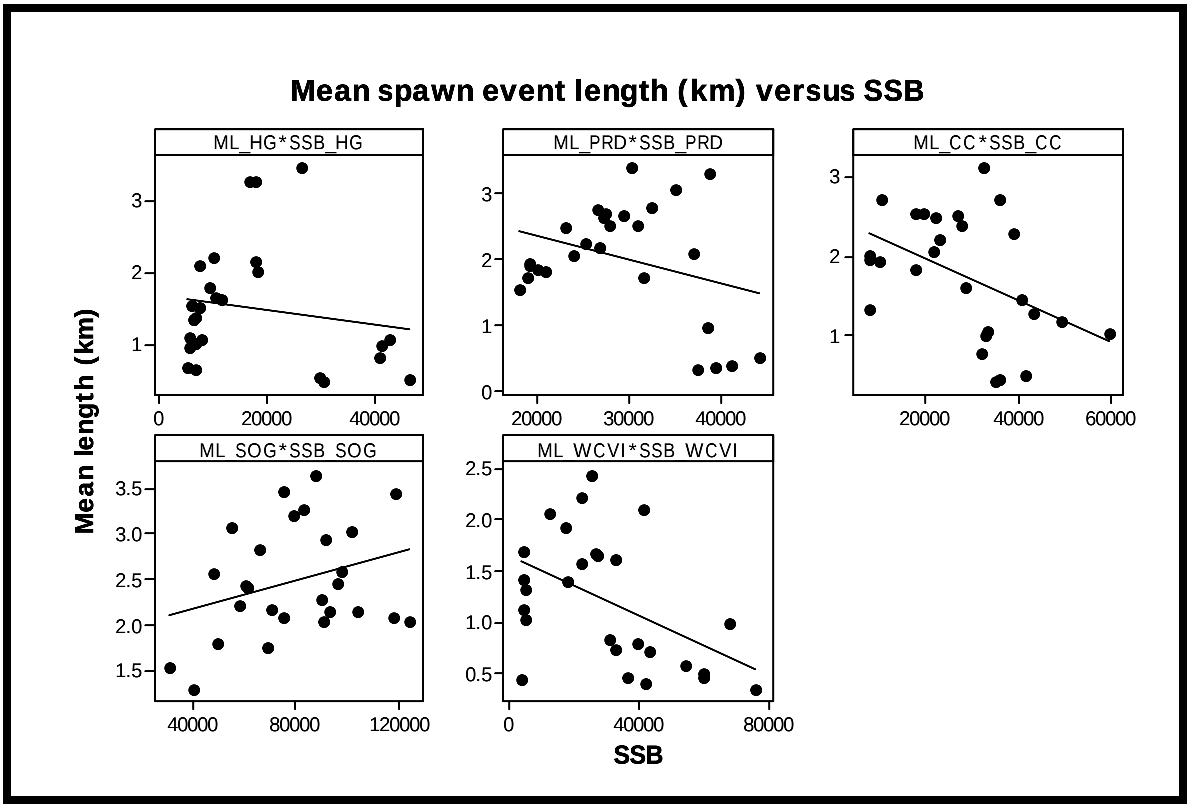
Appendix 3. Figure 4. Number of herring spawn records versus spawning stock biomass (SSB). The line shows a linear regression fit. These figures correspond to the summary in Table 2, row 4.



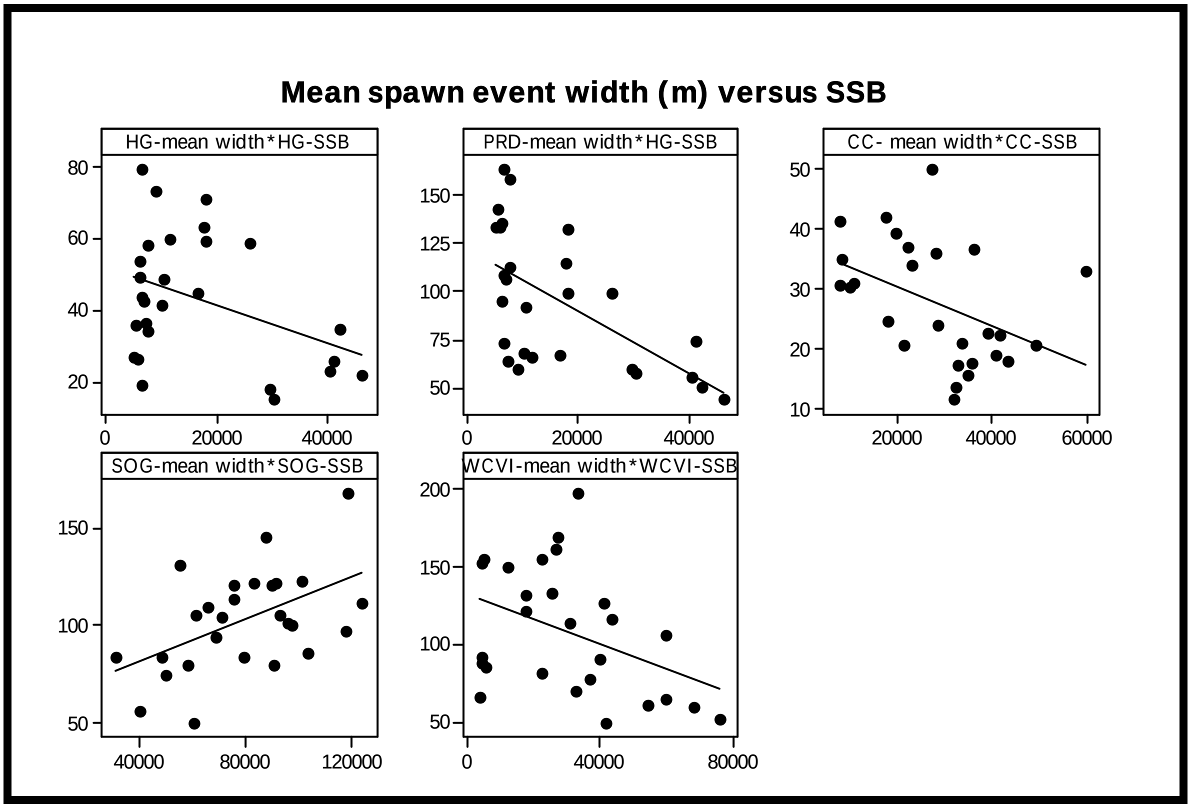
Appendix 3. Figure 5. Mean spawn event area (ha^2) versus spawning stock biomass (SSB). The line shows a linear regression fit. These figures correspond to the summary in Table 3, row 1.



Appendix 3. Figure 6. Mean spawn event length (km) versus spawning stock biomass (SSB). The line shows a linear regression fit. These figures correspond to the summary in Table 3, row 2.

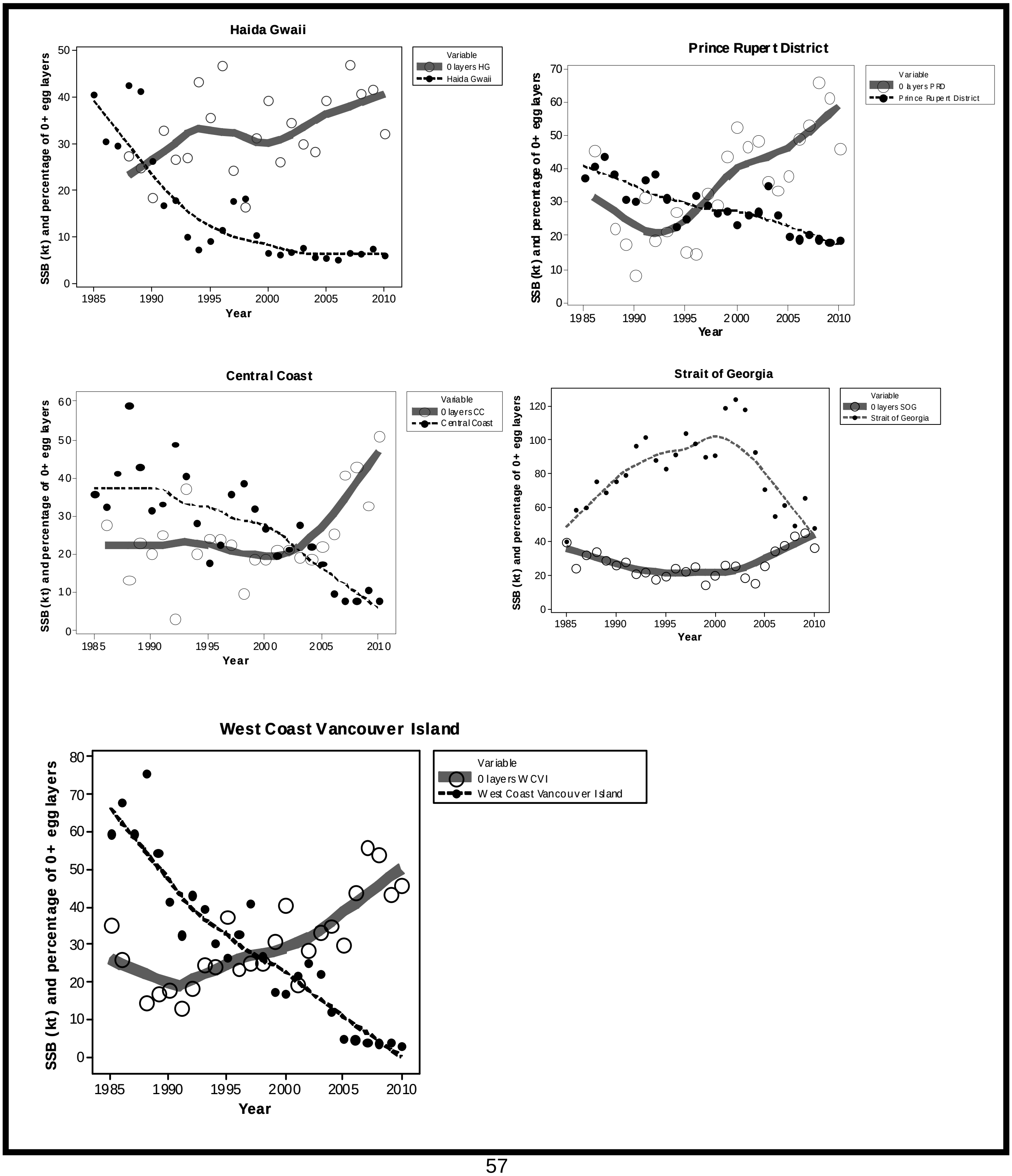


Appendix 3. Figure 7. Mean spawn event width (m) versus spawning stock biomass (SSB). The line shows a linear regression fit. The data points corresponding to the last 5 years are shown by year. These figures correspond to the summary in Table 3, row 3.

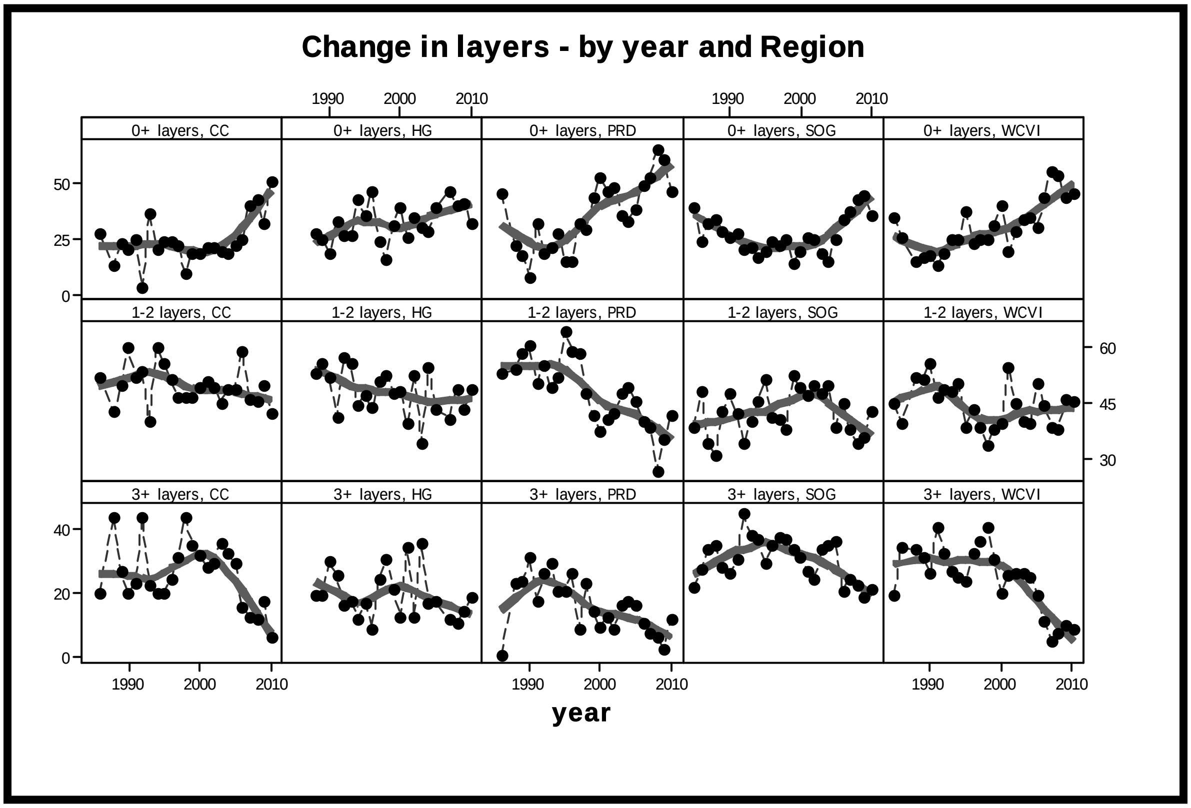


APPENDIX 4. EGG LAYER ANALYSIS

Appendix 4. Figure 1. Changes in egg layers and concurrent changes in SSB. The frequency of the ‘trace’ category of egg layers has increased in time. The open circles indicate the percentage of such observations made for each year. The SSB (in kt or kilotonnes) is shown on the same axis. The grey line is a Lowess smoother. Note that the scale of the y-axis varies among the 5 panels.

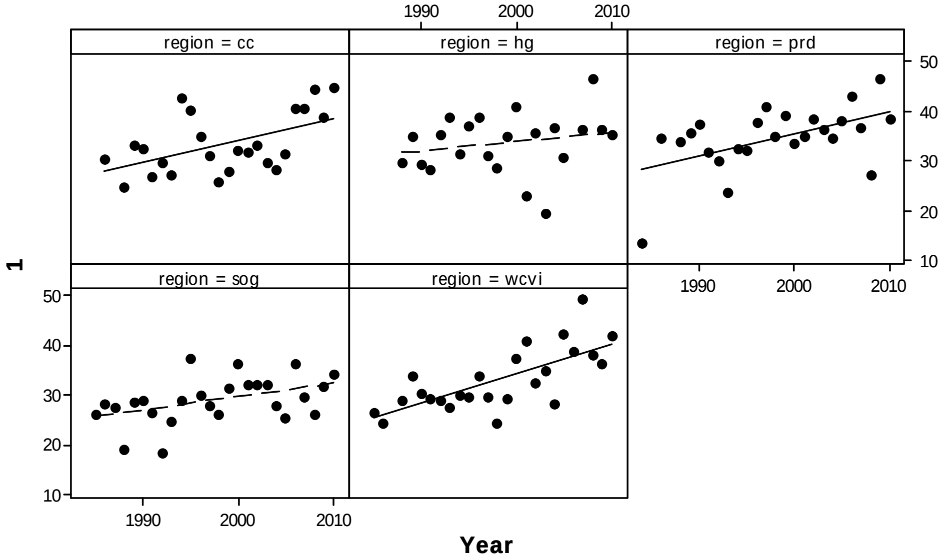


Appendix 4. Figure 2. (a) Changes in frequency of egg layers by category. The grey line is a Lowess smoother. The top panels show frequency changes for the 0+ layer (or the percentage of all observations between 0.01 and 0.49 layers, rounded to 0 (zero). The middle row ("1-2 layers") shows egg layers between 1.5 and 2.49 layers. The bottom row shows the cumulative percentage of all egg layer observations of 2.5 or greater. The grey line is a Lowess smoother.

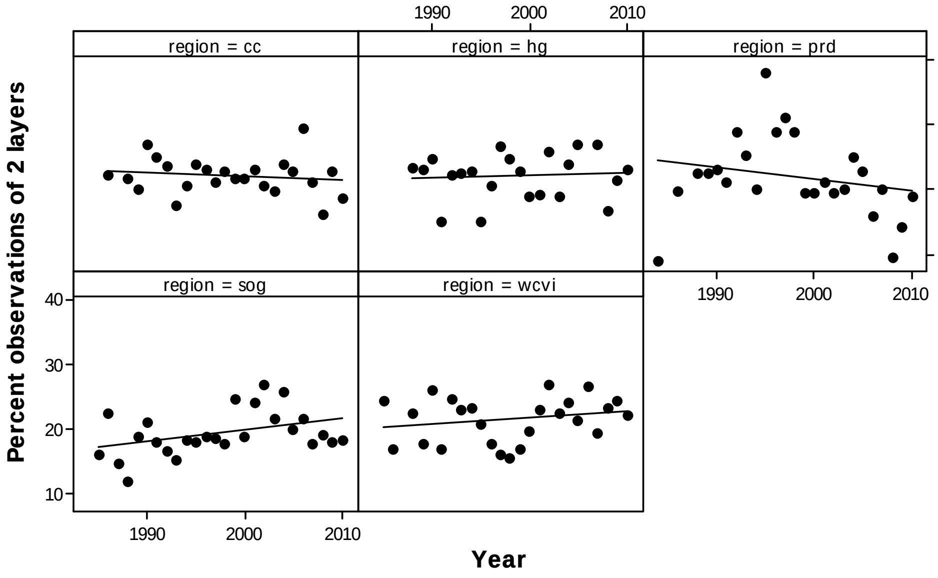


Appendix 4. Figure 2 b-g. Changes in frequency of egg layers by category when trace layers are excluded from the analysis, shown by region for 1 layer (Fig. 2b) 2 layers (Fig. 2c), 3 layers (Fig. 2d), 4 layers (Fig. 2e) 5 layers (Fig. 2f) and 6 layers (Fig. 3g). In each graph the solid line shows a linear regression fit for all years.

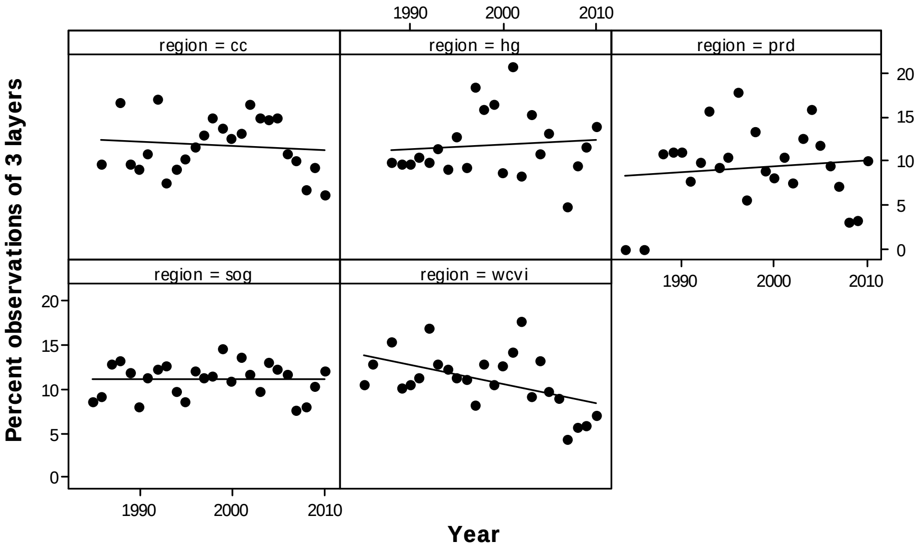
(b) Percentage of 1 layer observations (no trace layers)



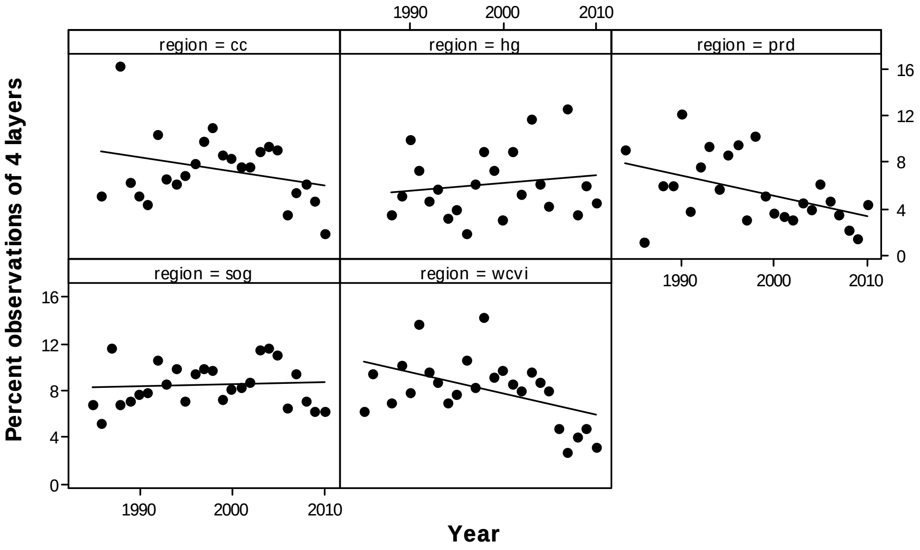
(c) Percentage of 2 layer observations (no trace layers)



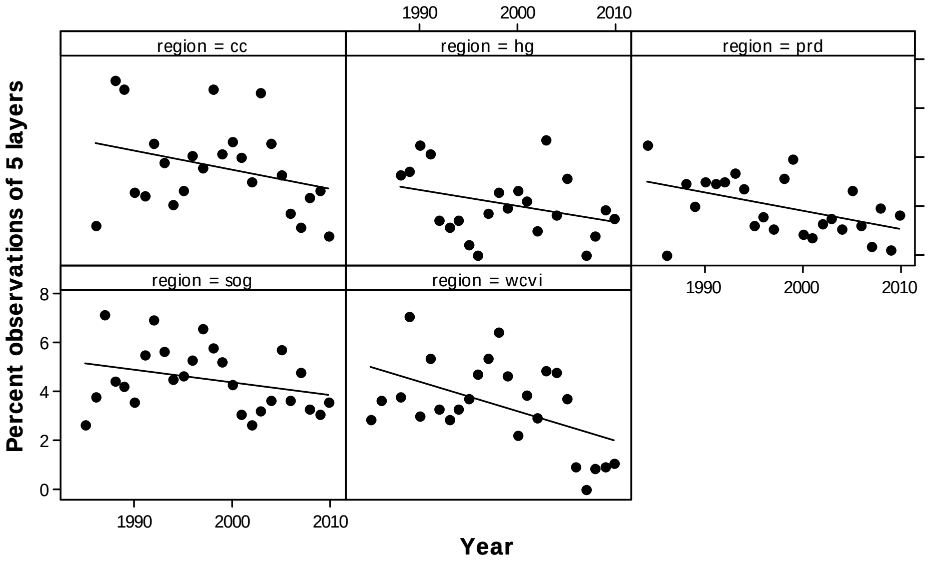
(d) Percentage of 3 layer observations (no trace layers)



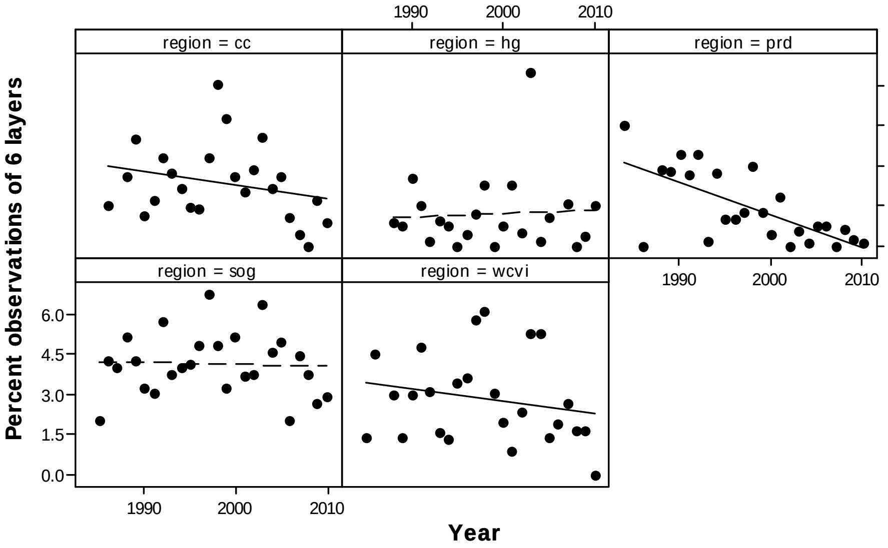
(e) Percentage of 4 layer observations (no trace layers)



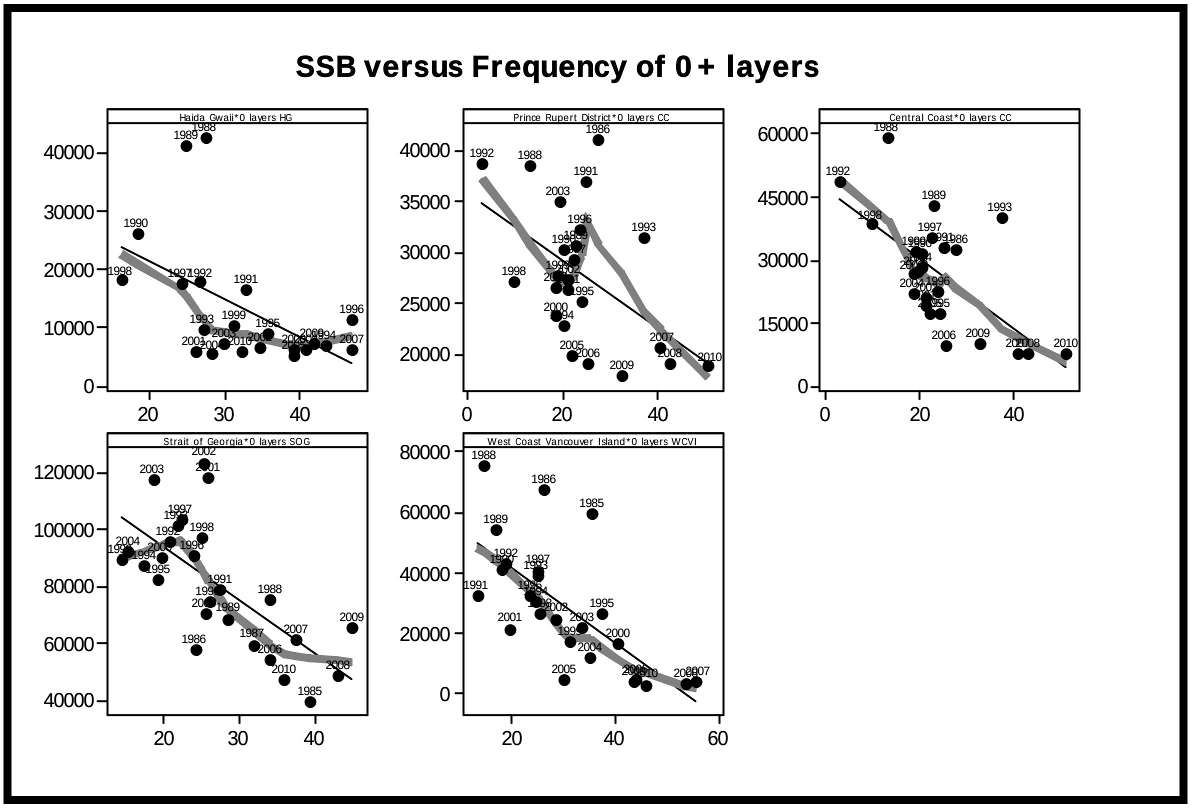
(f) Percent of 5 layer observations (no trace layers)



(g) Percent of 6 layer observations (no trace layers)

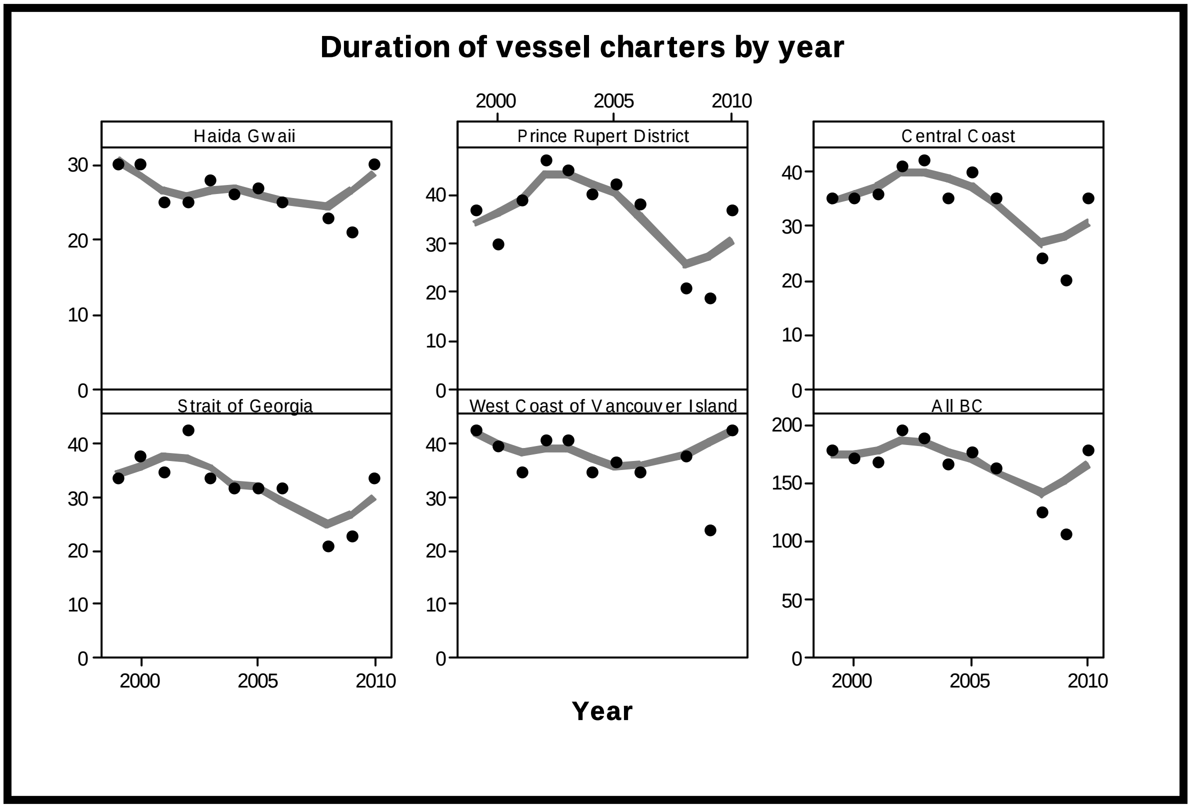


Appendix 4. Figure 3. Plots of SSB (metric tonnes) on the y-axis by the frequency of 0+ egg layers (x-axis). The solid line is a liner regression. The grey line is a Lowess smoother.

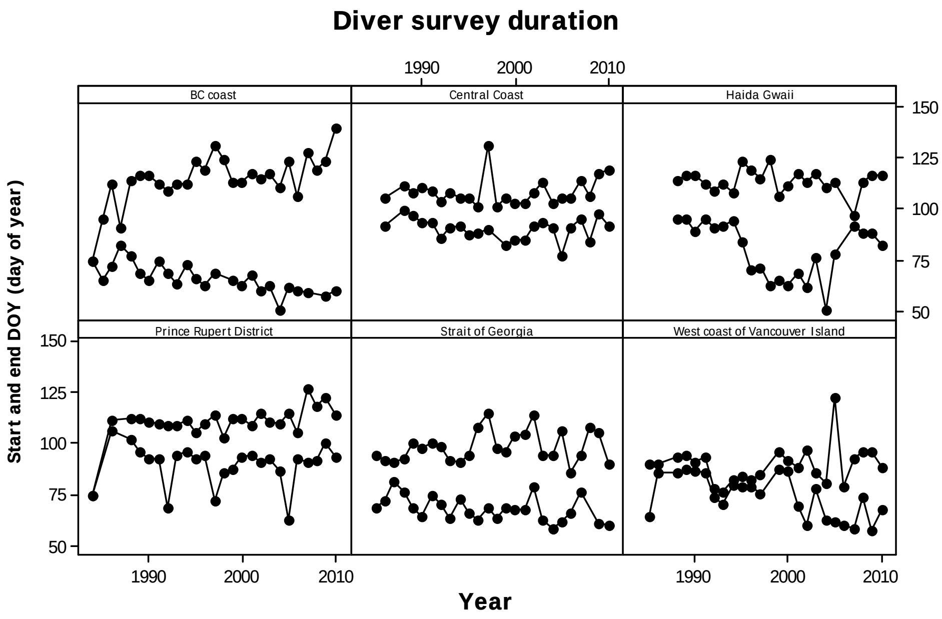


APPENDIX 5. SPAWN SURVEY METRICS

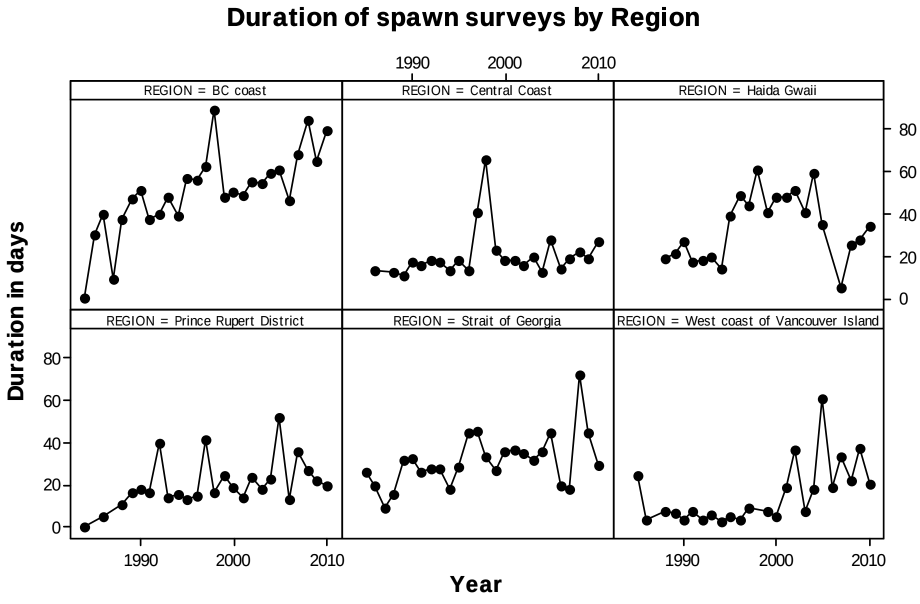
Appendix 5. Figure 1. Duration of vessel surveys by region and year. The grey line is a Lowess smoother. These data (provided by L. Hamer) show the duration of vessel charters use to support contract divers. The duration of the survey, by year, may not be complete in all years. The data indicate a slight decreasing trend in recent years in some areas.



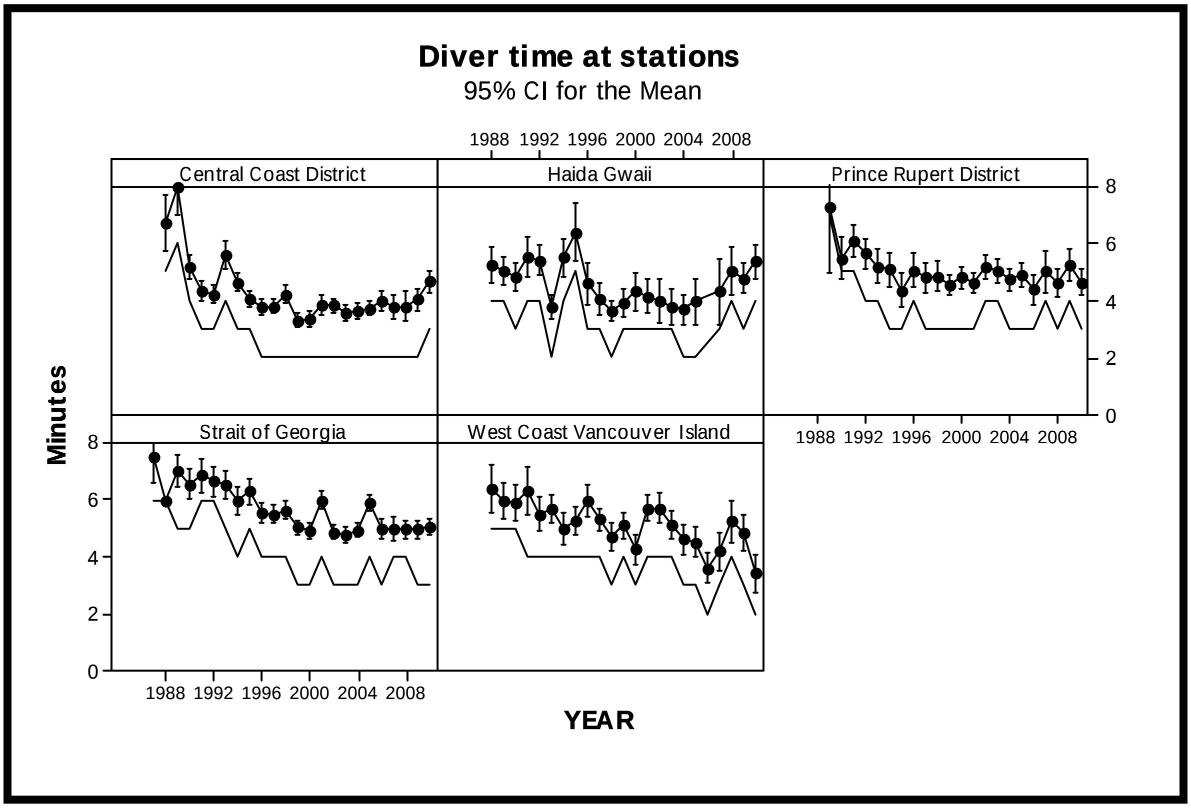
Appendix 5. Figure 2(a). Beginning and end of diver surveys, extracted mainly from the VEGTRANS tables. The day of the year (January 1 = day 1) was determined for the earliest and latest spawn survey. The difference, called the duration, is shown below by year and region in Figure 2(b). Some of the surveys were done by DFO staff on dates that were earlier or later than the those surveyed by contract divers. Data in some years may have been incomplete, so probably these estimates may be conservative.



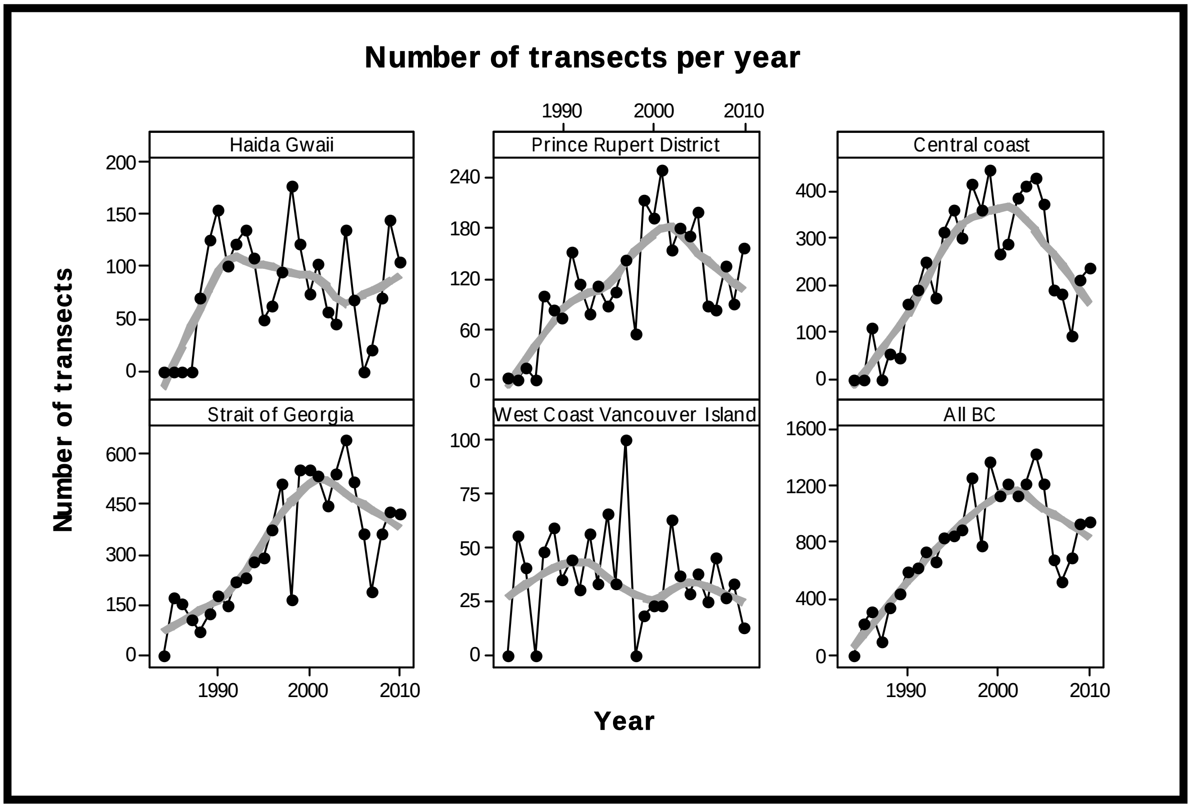
Appendix 5. Figure 2(b) Duration of diver surveys,



Appendix 5. Figure 3. Estimated time (minutes) spent by divers at each quadrat, by year and area**.** The minutes per quadrat were estimated by comparing the differences in the time-of-day (to the nearest minute) between adjacent stations on each transect. Outliers in the data were eliminated by assuming that the maximal time could not exceed 20 minutes. The solid top line shows the mean time (with 95% confidence limits). The bottom line indicates the median times spent at each station. There is a decrease over the entire period, in most regions, but little change in most regions since the mid-1990's. The data from the west coast of Vancouver Island may be misleading because surveys have been limited there in recent years.

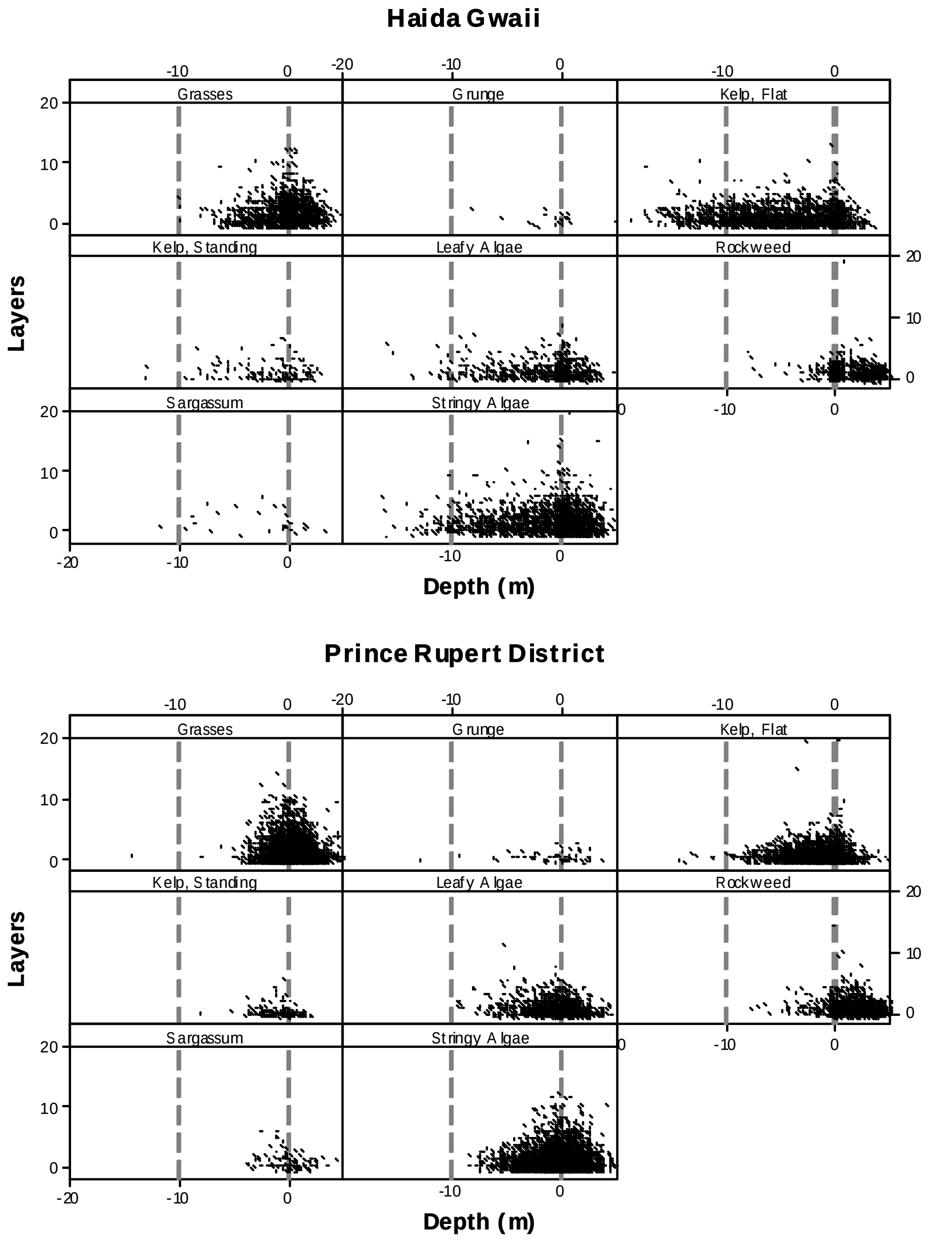


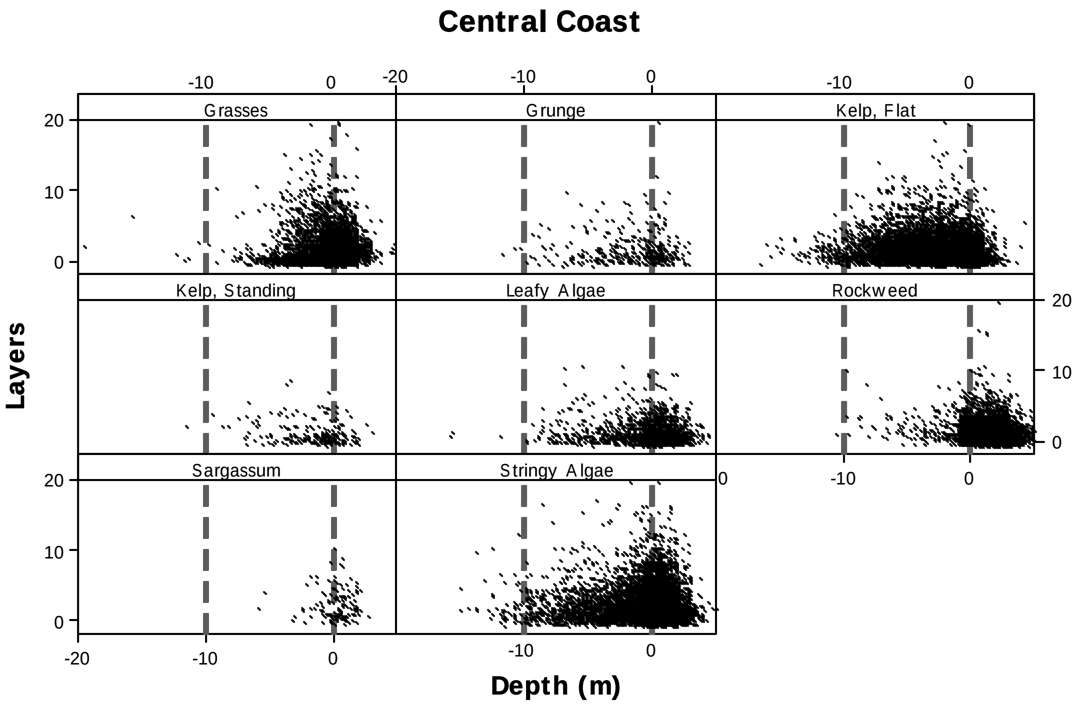
Appendix 5. Figure 4. The total number of transects made each year, by region. The grey line is a Lowess smoother. There is a tendency for a slight decrease in recent years. This trend may be difficult to interpret because, in part, the number of transects will depend on the amount of spawning activity. The number increased in all areas in the last 2-4 years.

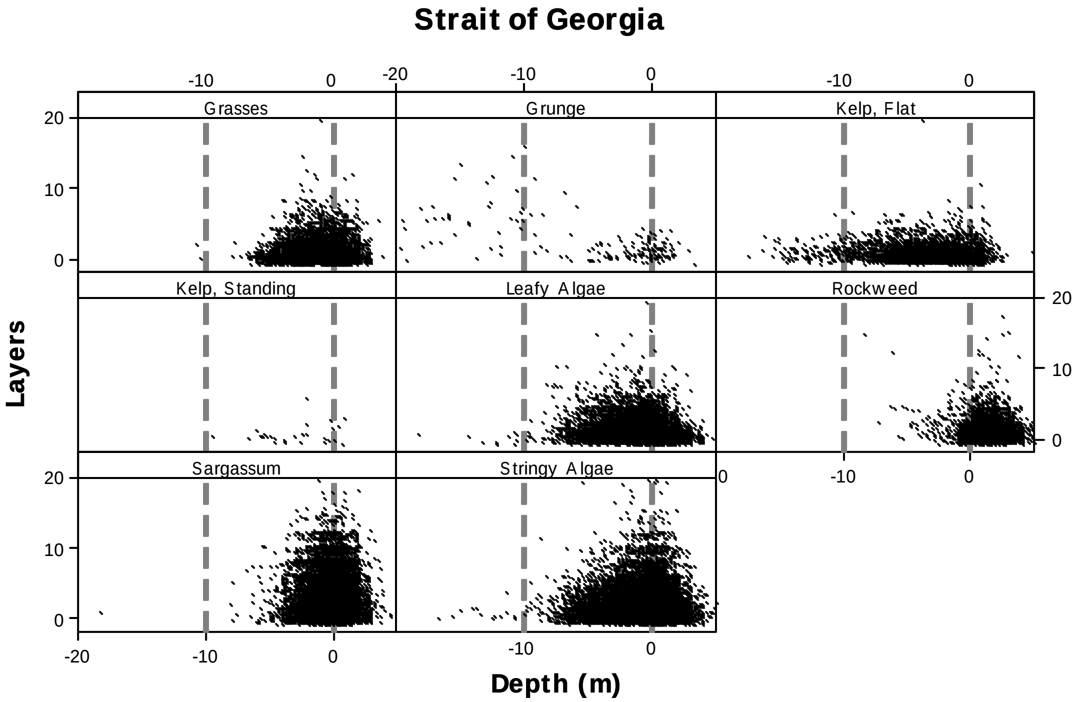


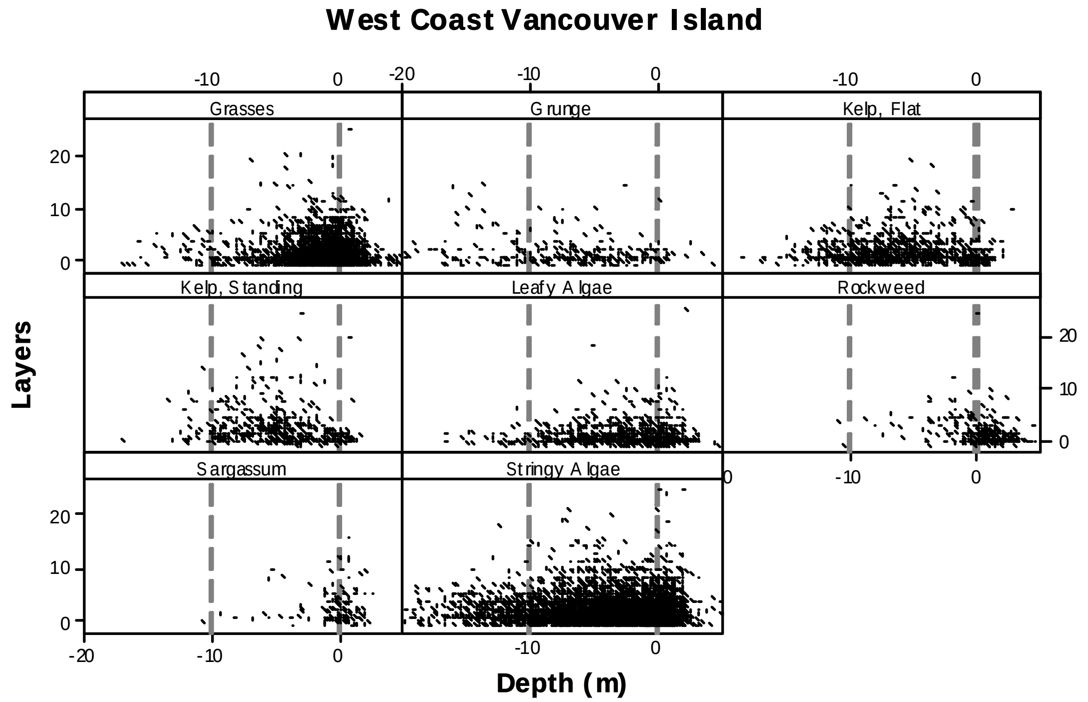
APPENDIX 6. THE SPAWNING ENVIRONMENT

Appendix 6. Figure 1. Scatterplot of all egg layers by depth (corrected for tidal variation), showing layers and depth for each vegetation type in each region. The vertical lines show the low water mark (0 m) and -10 m depth. The plots show clearly that most egg layers are concentrated near the intertidal zones in all regions.

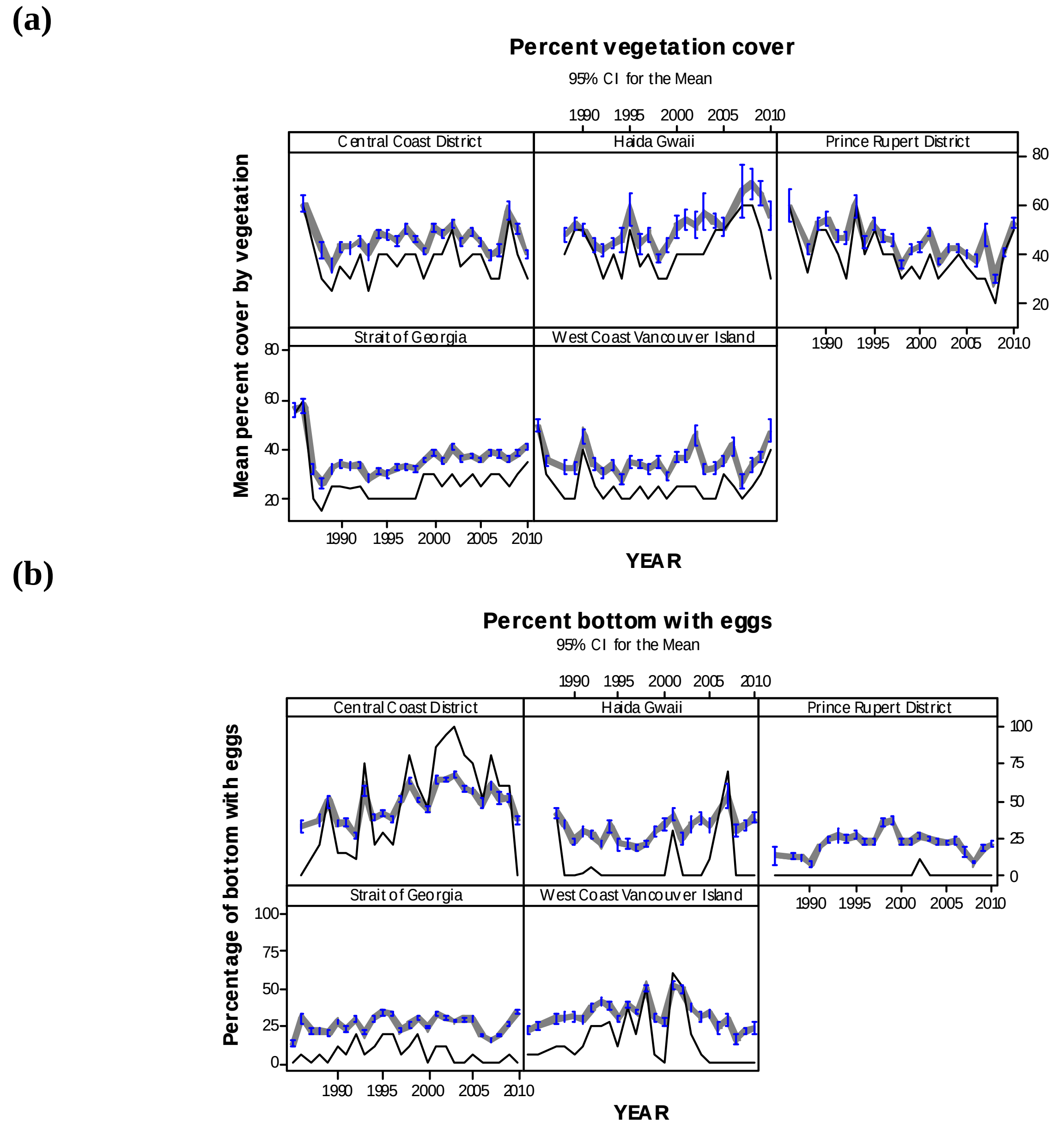



Central Coast
Grasses
Grunge
Kelp, Flat
Kelp, Standing
Leafy Algae
Rockweed
Sargassum
Stringy Algae
Layers
Depth (m)
-20
-10
0
10
20


Strait of Georgia
Grasses
Grunge
Kelp, Flat
Kelp, Standing
Leafy Algae
Rockweed
Sargassum
Stringy Algae
Layers
Depth (m)
-20
-10
0
10
20


West Coast Vancouver Island
Grasses
Grunge
Kelp, Flat
Kelp, Standing
Leafy Algae
Rockweed
Sargassum
Stringy Algae
Layers
Depth (m)
-20
-10
0
10
20

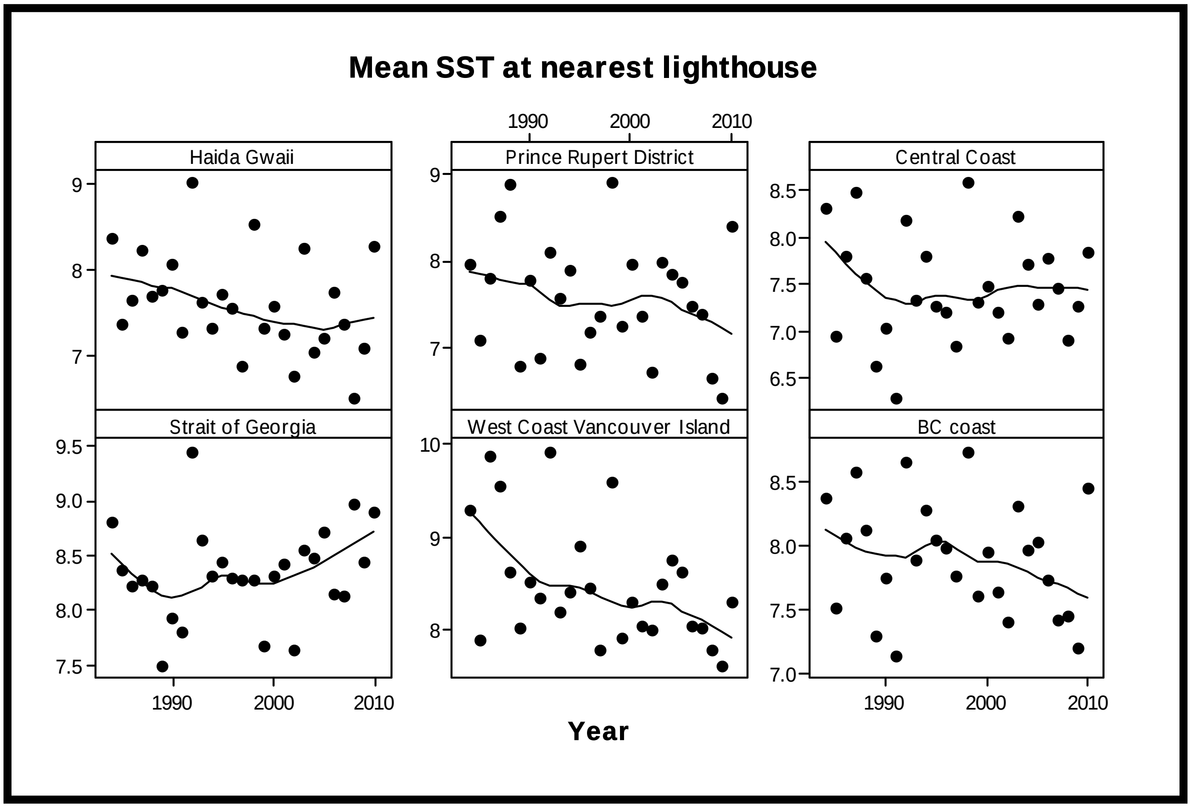
Appendix 6. Figure 2. (a) Mean percent vegetation cover by year and region. The dark vertical lines indicate the 99% confidence limits. Estimates vary, especially in recent years. This may be related to an apparent increase in the estimates of percent cover exceeding 100%, that is used to describe certain types of vegetation. The impact of this is uncertain and warrants further analysis. (b) Percent of the bottom covered with eggs. The dark vertical lines indicate the 99% confidence limits. There is a trend for a decrease in recent years. In both panels the thick grey line represents the mean and 95% confidence limits. The thin line represents the median.



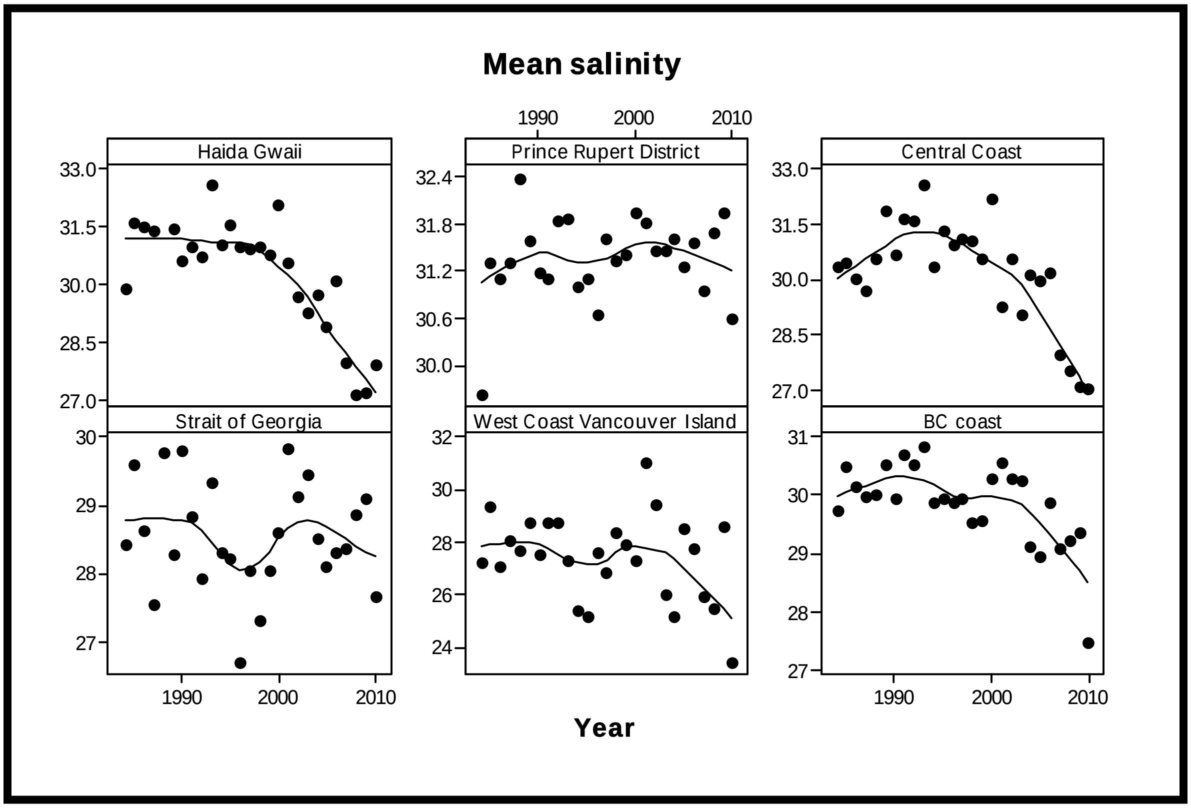
The is the percent of the bottom of the quadrat (excluding vegetation < 1 cm) covered with eggs.

Appendix 6. Figure 3a. Sea surface temperatures determined from DFO lighthouse data (**http://www.pac.dfo-mpo.gc.ca/science/oceans/data-donnees/lighthouses-phares/index-eng.htm**) closest to spawning areas in each region at spawning times. The specific lighthouse and number of times it was used (in parentheses) is as follows: Active Pass (79); Amphitrite (112); Bonilla Is. (1487); Cape St. James (459); Cape Mudge (28); Chrome Is. (1487); Egg Is (525); Entrance Is. (463); Kains Is. (293); Langara Is. (437); McInnes Is. (3208); Nootka Pt. (341); Pine Is. (1862); Race Rocks (26). Mean sea-surface temperature (C) and salinity were weighted by the Spawn Habitat Index (see **http://www.pac.dfo-mpo.gc.ca/science/species-especes/pelagic-pelagique/herring-hareng/herspawn/pages/default5-eng.htm**).

There is a decreasing trend for salinity and temperature in recent years in all areas except the Strait of Georgia. The implications of these changes on herring spawning are not clear. In each panel the line is a Lowess smoother.



Appendix 6. Figure 3b. Surface salinity.



APPENDIX 7A. ANNOTATED SUMMARY OF LITERATURE ON PREDATION OF HERRING EGGS

Appendix 7. (a) Summary of literature on predation of herring eggs. Each row shows the authors, year of publication, study area (when applicable), the approximate type of publication ('primary' refers to a peer-reviewed journal paper), the title and reference source. **(b).** Annotated summary of each reference as it applies to the issue of egg loss or predation on herring eggs.

	Author	Year	Area	Causes	Type	Title	Journal/Source
1	Anderson, E. M., J. R. Lovvorn, D. Esler, W. S. Boyd, and K. C. Stick	2009	Pacific	Bird predation	Primary	Using predator distributions, condition, and diet to evaluate seasonal foraging sites: sea ducks and herring spawn.	Marine Ecology Progress Series 386:287–302.
2	Aneer, G.	1987	Baltic	Environment	Primary	High natural mortality of Baltic herring (*Clupea harengus*) eggs caused by algal exudates?	Mar. Biol. 94, 163–169.
3	Aneer, G.	1989	Baltic	Environment	Primary	Herring (*Clupea harengus L.*) spawning and spawning ground characteristics in the Baltic Sea.	Fisheries Research 8: 169-195.
4	Bailey, K. M. and E. D. Houde.	1989	Pacific	Overview	Primary	Predation on eggs and larvae of marine fishes and the recruitment problem.	Adv. Mar. Biol. 25, 82 p.
5	Bayer, R.D	1980	Pacific	Bird predation	Primary	Birds feeding on herring eggs at the Yaquina estuary, Oregon.	Condor 82: 193-198.
6	Bishop, M.A. and S.P. Green	2001	Pacific	Bird predation	Primary	Predation on Pacific herring (*Clupea pallasi*) spawn by birds in Prince William Sound, Alaska.	Fish. Oceanogr. 10:149–158.
7	Blaxter, J.H.S. and F.G.T. Holliday.	1963	General	Overview	Primary	The behaviour and physiology of herring and other clupeids.	Advances in Marine Biology 1:261-393.
8	Bond J.C. and D. Esler	2006	Pacific	Bird predation	Primary	Nutrient acquisition by female Harlequin Ducks prior to spring migration and reproduction: evidence for body mass optimization.	Can. J. Zool. 84: 1223–1229.
9	Bunn, N., C.J. Fox, and T. Webb.	2000	General	Overview	Technical	A literature review of studies on fish egg mortality: implications for the estimation of spawning stock biomass by the annual egg production method.	Science Series Technical Report 111, CEFAS. Lowestoft. 37 pp.
10	Calambokidis, J., J.D. Darling, V. Deeke, P.Gerrin, M. Gosho, W. Megill, C.M. Tombach, D. Goley, C. Toropova, and B. Gisborne.	2002	Pacific	Whale predation	Primary	Abundance, range and movements of a feeding aggregation of gray whales (*Eschrichtius robustus*) from California to southeastern Alaska in 1998.	J. Cetacean Res. Manage. 4:267–276.
11	Cleaver, F. C. and D. M. Franett.	1946	Pacific	Bird predation	Technical	The predation by sea birds upon the eggs of the Pacific herring *(Clupea pallasi)* at Holmes Harbor during 1945.	Washington State Dept. Fish. Biol. Rep. 46B, 18 p.

12	Cooper, J.R., J.R. Uzmann, R.A. Clifford and K.J. Pecci.	1975	Atlantic	Fish predation	Technical	Direct observations of herring (*Clupea harengus harengus*) egg beds on Jeffreys Ledge, Gulf of Maine in 1974.	Int. Comm. Northwest Atl. Fish. (ICNAF) Res. Doc. 75/93. 6 p.
13	Dahlberg, M.D.	1979	General	Overview	Primary	A review of survival rates of fish eggs and larvae in relation to impact assessments.	Marine Fisheries Review 41: 1–12.
14	Darling, J.D, K. E. Keogh and T.M. Steeves.	1998	Pacific	Whale predation	Primary	Gray whale (*Eschrichtius robustus*) habitat utilization and prey species off Vancouver Island, B. C.	Marine Mammal Science: 14:692–720.
15	De La Cruz, S.E.W., J.Y. Takekawa, M.T. Wilson, D.R. Nysewander, J.R. Evenson, D. Esler and D.H. Boyd.	2009	Pacific	Bird predation	Primary	Spring migration routes and chronology of surf scoters (*Melanitta perspicillata*): a synthesis of Pacific coast studies.	Can. Journal Zoology 87: 1069-1086.
16	Esler, D., R. Ydenberg, J. Bond and S. LeBourdais.	2007	Pacific	Bird predation	Contract	Variation in harlequin duck distribution and productivity: the roles of habitat, competition, and nutrient acquisition.	Contract report for BC Hydro http://www.bchydro.com/bcrp/projects/docs/bridge_river/05.W.BR.03.pdf
17	Grass. A.	1973	Pacific	Bird predation	Primary	Mew gulls and black turnstones feeding on herring eggs.	Murrelet 54:38–39'
18	Griffin F.J., E.H. Smith, C.A. Vines and G.N. Cherr.	2009	Pacific	Environment	Primary	Impacts of suspended sediments on fertilization, embryonic development, and early larval life stages of the Pacific herring, *Clupea pallasi*.	Biol. Bull. 216: 175–187.
19	Grosse, D. and T. Sibley.	1984	Pacific	Environment	Contract	Projected effects of co -induced climate change on the Pacific herring (*Clupea harengus pallasi*) fishery in the northeast Pacific ocean.	Contract Report 4524910 to the Lawrence Berkeley Laboratory, Fisheries Research Institute, School of Fisheries WH-1O, University of Washington, Seattle, Washington.
20	Haegele, C.W.	1991	Pacific	Overview	Technical	Spawn estimates and associated predator data for herring egg loss in Lambert Channel, Georgia Strait - 1989 and 1990.	Can. Data Rep. Fish. Aquat. Sci. 821: 103 p.
21	Haegele, C.W.	1993	Pacific	Invertebrate predation	Primary	Epibenthic invertebrate predation of Pacific herring, *Clupea pallasi*, spawn in British Columbia.	Canadian field-naturalist 107: 83-91.
22	Haegele, C.W.	1993	Pacific	Bird predation	Primary	Seabird predation of Pacific Herring, *Clupea pallasi*, spawn in British Columbia.	Canadian Field-Naturalist 107: 73–82.
23	Haegele, C. W. and J. F. Schweigert	1989	Pacific	Overview	Technical	Egg loss from Pacific herring spawns in Barkley Sound in 1988.	Can. Manag. Rep. Fish. Aquat. Sci. 2037. 40p.
24	Haegele, C. W. and J. F. Schweigert	1991	Pacific	Overview	Primary	Egg loss in herring spawns in Georgia Strait, British Columbia.	Proceedings of the International Herring Symposium, Anchorage, Alaska, October 23–25, 1990, p. 309–322. Univ. Alaska, Fairbanks, AK
25	Hardwick, J. E.	1973	Pacific	Bird predation	Primary	Biomass estimates of spawning herring, *Clupea harengus pallasi*, herring eggs, and associated vegetation in Tomales Bay.	Calif. Fish Game 59:36-61.

26	Hay, D.E. and M.J. Marliave.	1988	Pacific	Overview	Primary	Transplanting Pacific herring spawn: a stocking experiment. Publication of Amer. Fish. Soc. Symposium 5:49-59.	Amer. Fish. Soc. Symposium 5:49-59.
27	Hay, D.E. and Miller, D.C.	1982	Pacific	Environment	Technical	A quantitative estimate of herring spawn lost by storm action in French Creek. Can. MS. Rep. Fish. Aquat. Sci. 1636: 9p.	Can. MS. Rep. Fish. Aquat. Sci. 1636: 9p
28	Hempel, I., and G. Hempel.	1971	Atlantic	Fish predation	Primary	An estimate of mortality in eggs of North Sea herring (*Clupea harengus L*.).	Rapp. P.-V. Reun. Cons. Int. Explor.Mer 160:24–26.
29	Hoines, A., O.A. Bergstad and O.T. Albert	1992	Atlantic	Fish predation	Technical	Hoines, A., O.A. Seasonal variation of the diet of cod (*Gadus morhua* L.) and haddock (*Melanogrammus aeglefinus* L.) at a herring spawning ground.	ICES C.M. 1992/G:9. 23p.
30	Hoeines, A.S. and O.A. Bergstad.	1992	Atlantic	Fish predation	Primary	Food partitioning by flatfishes on a herring spawning ground.	Sarsia 87: (1) 19–34.
31	Høines, Å.S., O.A. Bergstad and O.T. Albert.	1995	Atlantic	Fish predation	Conference	The food web of a coastal spawning ground of the herring (*Clupea harengus*).	Proceedings of the Mare Nor Symposium on the Ecology of Fjords and Coastal Waters. In: Skjoldal, H.R., C. Hopkins, K.E. Erikstad, and H.P. Leinaas, (Eds.). Ecology of Fjords and Coastal Waters. Elsevier Science., Amsterdam. pp. 17–22.
32	Hoeines, A.S. and O.A. Bergstad.	1999	Atlantic	Fish predation	Primary	Resource sharing among cod, haddock, saithe and pollock on a herring spawning ground.	Journal of Fish Biology 55: 1233–1257.
33	Hourston, A. S., H. Rosenthal and H Westerhagen.	1981	Pacific	Environment	Technical	Data summaries for viable hatch from Pacific herring eggs deposited at different intensities on a variety of substrates.	Can. Data Rep. Fish. Aquat. Sci. 267: 56 p.
34	Hourston, A. S., H. Rosenthal and H Westerhagen.	1984	Pacific	Environment	Technical	Viable hatch from eggs of Pacific herring (*Clupea harengus pallasi*) deposited at different intensities on a variety of substrates.	Can. Tech. Rep. Fish. Aquat. Sci. 1274: 19 p.
35	Johannessen, A.	1986	Atlantic	Fish predation	Thesis	Recruitment studies of herring in Lindaaspollene, western Norway. Chapter 1.	Fiskeridir. Skr. Ser. Havunders. 18:139-240.
36	Jones, B.C.	1971	Pacific	Environment	Thesis	The effect of intertidal exposure on survival and embryonic development of Pacific herring spawn.	MSc thesis. Dept. Zoology. University of BC. 56 p.
37	Jones, B.C.	1972	Pacific	Environment	Primary	Effect of intertidal exposure on survival and embryonic development of Pacific herring spawn.	Can. J. Fish. Aquat. Sci. **29**: 1119–1124.
38	Kelly, J.P. and S.L. Tappen	2003	Pacific	Bird predation	Primary	Distribution, abundance, and implications for conservation of winter waterbirds on Tomales Bay, California.	Western Birds 29: 103-120. On web at http://elibrary.unm.edu/sora/wb/v29n02/p0103-p0120.pdf

39	LaCroix, D. L, . S. Boyd, D. Esler, M. Kirk, T. Lewis and S. Lipovsky.	2005	Pacific	Bird predation	Primary	Surf scoters *Melanitta perspicillata* aggregate in association with ephemerally abundant polychaetes.	Marine Ornithology 33: 61–63.
40	Laine, P. and M. Rajasilta.	1998	Baltic	Female condition	Primary	Changes in the reproductive properties of Baltic herring females during the spawning season.	Fisheries Research 36: 67-73.
41	Laine, P. and M. Rajasilta.	1999	Baltic	Female condition	Primary	The hatching success of Baltic herring eggs and its relation to female condition.	J. Exp. Mar. Biol. Ecol. 237, 61–73.
42	Lewis T. L., D. Esler and W.S. Boyd	2007	Pacific	Bird predation	Primary	Foraging behaviors of surf scoters and white-winged scoters during spawning of Pacific herring.	The Condor 109:216–222
43	Lok, E. K.	2008	Pacific	Bird predation	Thesis	Site use and migration of scoters (*Melanitta spp.*) in relation to the spawning of Pacific herring (*Clupea pallasi*).	Thesis, Simon Fraser University, Burnaby, Canada.
44	Lok, E. K., M. Kirk, D. Esler and W. S. Boyd. 2008	2011	Pacific	Bird predation	Primary	Movements of pre-migratory surf and white-winged scoters in response to herring spawn in the Strait of Georgia, British Columbia.	Waterbirds 31:385–393.
45	McGurk, M.D.	1986	General	Overview	Primary	Natural mortality of marine pelagic fish eggs and larvae: role of spatial patchiness.	Marine Ecology Progress Series, 34: 227–242.
46	Messieh, S. H. and H. Rosenthal.	1989	Atlantic	Environment	Primary	Mass mortality of herring eggs on spawning beds on and near Fisherman's Bank, Gulf of St. Lawrence, Canada.	Aquat. Living Resourc. 2:1-8.
47	Morrison, J.A., J. C. Gamble and I. R. Napier	1991	Atlantic	Environment	Primary	Mass mortality of herring eggs associated with a sedimenting diatom bloom.	ICES J. Mar. Sci. (1991) 48 (2): 237-245.
48	Munro, J.A. and W.A. Clemens.	1931	Pacific	Bird predation	Primary	Waterfowl in relation to the spawning of herring in British Columbia.	Bulletin of the Biological Board of Canada 1 17: 1 1–46.
49	Outram, D. M.	1958	Pacific	Bird predation	Technical	The magnitude of herring spawn losses due to bird predation on the west coast of Vancouver Island.	Fish. Res. Board Can. Pac. Biol. Stat. Prog. Rep. 111:9–13.
50	Palsson, W. A.	1984	Pacific	Bird predation	Thesis	Egg mortality upon natural and artificial substrata within Washington state spawning grounds of Pacific herring (*Clupea harengus pallasi*).	M.S. thesis, Univ. Washington, Seattle, WA, 191 p.
51	Purcell, J.E., D. Grosse and J.J. Grover.	1990	Pacific	Environment	Primary	Mass abundance of abnormal Pacific herring larvae at a spawning ground in British Columbia.	Transactions of the American Fisheries Society 119:463- 469.
52	Rajasilta, M., J. Eklund, J. Hanninen, M. Kurkilahti, M.J. Kaaria, P. Rannikko, and M. Soikkeli.	1993	Baltic	Environment	Primary	Spawning of herring (*Clupea harengus membras L.*) in the Archipelago Sea.	ICES J. Mar. Sci. 50:223–246.
53	Rajasilta, P. Laine and J. Eklund	2006	Baltic	Environment	Primary	Mortality of herring eggs on different algal substrates (*Furcellaria* spp. and *Cladophora* spp.) in the Baltic Sea – an experimental study.	Hydrobiologia 554: 127-130.
54	Richardson, D.	2010	Atlantic	Fish predation	Web	The role of haddock egg predation in the decline of an Atlantic herring population.	Web Abstract. http://sh.nefsc.noaa.gov/seminar_abstracts.htm

55	Richardson, D.E. and J.A. Hare. 2009.	2009	Atlantic	Fish predation	Conference	Does haddock egg predation decouple the abundance of Atlantic herring larvae from spawning stock biomass on Georges Bank?	Larval Fish Conference 2008. Portland, Oregon.
56	Richman, S. E. and J. R. Lovvorn.	2009	Pacific	Bird predation	Primary	Predator size, prey size, and threshold food densities of diving ducks: does a common prey base support fewer larger animals?	Journal of Animal Ecology 78:1033-1042.
57	Rodway, M.S., H.M. Regehr, J. Ashley, P.V. Clarkson, R.I. Goudie, D.E. Hay, C.M. Smith and K.G. Wright.	2003	Pacific	Bird predation	Primary	Aggregative response of Harlequin Ducks to herring spawning in the Strait of Georgia, British Columbia.	Canadian Journal of Zoology 81: 504–514.
58	Rodway, M.S. and F. Cooke	2002	Pacific	Bird predation	Primary	Use of fecal analysis to determine seasonal changes in the diet of wintering Harlequin Ducks at a herring spawning site.	J. Field Ornithol. 73:363-371
59	Rooper, C.N. and L.J. Haldorson.	2000	Pacific	Fish predation	Primary	Consumption of Pacific herring (*Clupea pallasi*) eggs by greenling (Hexagrammidae) in Prince William Sound, Alaska.	Fishery Bulletin 98: 655-659.
60	Rooper, C.N., L.J. Haldorson and T.J. Quinn II.	1999	Pacific	Environment	Primary	Habitat factors controlling Pacific herring (*Clupea pallasi*) egg loss in Prince William Sound, Alaska.	Canadian Journal of Fisheries and Aquatic Sciences 56: 1113-
61	Rooper, C.N. L. J. Haldorson, and T.J. Quinn	1998	Pacific	Overview	Primary	An egg-loss correction for estimating spawning biomass of Pacific herring in Prince William Sound, Alaska.	Alaska Fishery Research Bulletin 5: 137-142.
62	Rounsefell, G.A.	1930	Pacific	Bird predation	Primary	Contribution to the biology of the Pacific herring, *Clupea pallasii*, and the condition of the fishery in Alaska.	Bulletin of the U.S. Bureau of Commercial Fisheries 45:227-320
63	Runnstrom, S.	1941	Atlantic	Environment	Primary	Quantitative investigations on herring spawning and its yearly fluctuations at the west coast of Norway.	Fiskeridir. Skr. Ser. Havunders. 6(8):5-71
64	Skaret, G., B. E. Axelsen, L. Nøttestad, A. Fernö and A. Johannessen.	2005	Atlantic	Fish predation	Primary	Herring as cannibals.	Journal of Fish Biology 61:1050–1052
65	Skaret, G., A. Fernö, L. Nøttestad, L.A. Johannessen and B.E. Axelsen	2001	Atlantic	Fish predation	Technical	*Impact of herring spawning behaviour on acoustic abundance estimates.*	ICES C.M. Q22.
66	Stratoudakis, Y., Gallego, A., Morrison, J.A.	1998	Atlantic	Environment	Primary	Spatial distribution of developmental egg ages *within a herring* Clupea harengus spawning ground.	Marine Ecology Progress Series, 174: 27-32.

67	Sullivan, T.M., Butler, R.W., and Boyd, W.S.	2002	Pacific	Bird predation	Primary	Seasonal distribution of waterbirds in relation to spawning Pacific herring, *Clupea pallasi*, in the Strait of Georgia, British Columbia.	Can. Field-Nat. 116: 366–370.
68	Taylor, FCH.	1971	Pacific	Environment	Primary	Variation in hatching success in Pacific herring (*Clupea pallasi*) eggs with water depth, temperature, salinity, and egg mass thickness.	Rapp.P.-v. Reun. Cons. Int. Explor. Mer. 160, 34-41.
69	Toom, M. M	1958	Baltic	Environment	Primary	Experiments in the incubation of Baltic herring eggs.	Trudy VNIRO, 34: 19-29. (In Russian, translation by Office of Technical Services. U.S. Dept. of Commerce, Washington 25, D.C.).
70	Toreson, R.	1991	Atlantic	Fish predation	Primary	Predation on the eggs of Norwegian spring-spawning herring (Clupea harengus L.) on a spawning ground on the west coast of Norway.	ICES J. Mar. Sci. 48:15–21.
71	Wahl, T.R., S.M. Speich, D.A. Manuwal, K.V. Hirsch, and C. Miller.	1981	Pacific	Bird predation	Technical	Marine bird populations of the Strait of Juan de Fuca, Strait of Georgia and adjacent waters in 1978 and 1979.	U.S. Environmental Protection Agency, DOC/EPA Interagency Energy/Environment R&D Progr. Rep. EPA/600/f-81/156.
72	Weathers, W.W. and J.P. Kelly	2007	Pacific	Bird predation	Primary	Energy Footprints on Tomales Bay.	The Ardeid. 2007. p7-9.
73	Wilcock, J.A., E.D. Brown, and E. Debevec	1995	Pacific	Environment	Technical	Herring spawn deposition and reproductive impairment.	EVOSTC Restoration Project Annual Report (Project 94 166- l), Alaska Dept. Fish and Game,Cordova, Alaska.
74	Willson, M.F., and Womble, J.N.	2006	Pacific	Overview	Primary	Vertebrate exploitation of pulsed marine prey: a review and the example of spawning herring.	Rev. Fish Biol. Fish. **16**(2): 183–200
75	Willette, T.M., G.S. Carpenter, and K. Hyer.	1997	Pacific			Herring spawn deposition and reproductive impairment.	EVOSTC Restoration Project Annual Report (Project 96166), Alaska Dept. Fish and Game, Cordova, Alaska
76	Zydelis, R. and D. Esler. 2005	2005	Pacific	Bird predation	Primary	Response of wintering Steller's Eiders to herring spawn.	Waterbirds 28: 344-350.

APPENDIX 7B. ANNOTATED SUMMARY OF EACH REFERENCE AS IT APPLIES TO THE ISSUE OF EGG LOSS OR PREDATION ON HERRING EGGS

1. Anderson, E. M., J. R. Lovvorn, D. Esler, W. S. Boyd, and K. C. Stick. 2009. Using predator distributions, condition, and diet to evaluate seasonal foraging sites: sea ducks and herring spawn Marine Ecology Progress Series 386:287–302. This paper is among the most recent and detailed of any paper examining the interaction of seabirds and herring. It makes a case that sea ducks and other seabird species may be dependent on herring spawn as a vital component of their diet. The paper concludes with some comments about protection of herring spawning habitat and other issues, some of which were not necessarily examined in the paper.

2. Aneer, G. 1987. High natural mortality of Baltic herring (*Clupea harengus*) eggs caused by algal exudates? Mar. Biol. 94, 163–169. This report examined the relationship between egg survival of Baltic herring eggs and oxygen concentration that is implicated with egg survival. No relationship was detected but the paper implicates naturally occurring toxic exudates associated with brown, filamentous algae.

3. Aneer, G. 1989. Herring (*Clupea harengus L.*) spawning and spawning ground characteristics in the Baltic Sea. Fisheries Research 8: 169-195. This report has a short section reviewing egg mortality of Baltic herring eggs. In general predation is discounted as a significant source of mortality. Instead the main sources of mortality for the Baltic herring examined in this paper were related to unfavourable temperatures and excessive amounts of filamentous algae.

4. Bailey, K. M. and E. D. Houde. 1989. Predation on eggs and larvae of marine fishes and the recruitment problem Adv. Mar. Biol. 25, 82 p. The focus of this lengthy review is mainly on larvae and pelagic eggs. There is some speculative discussion about the role of patches of eggs or larvae relative to predation, but there are few direct implications for Pacific herring. There is nothing in the paper that refers to predation as a factor that would limit or reduce egg layers.

5. Bayer, R.D. 1980. Birds feeding on herring eggs at the Yaquina estuary, Oregon. Condor 82: 193-198. This short paper documents 17 species of birds feeding on herring eggs and comments on the feeding habits of some of the most abundant species (brant, wigeon, coots diving ducks gulls, buffleheads and scaups). The paper has no relevance to factors affecting the numbers of egg layers.

6. Bishop, M.A. and S.P. Green. 1991. Predation on Pacific herring (Clupea pallasi) spawn by birds in Prince William Sound, Alaska. Fisheries Oceanography 10, Supplement 1:149–158. The authors modeled egg consumption by five seabirds including two gull species (glaucous-winged gull (*Larus glaucescens*) and mew gull (*Larus canus*), surf scoters (*Melanitta perspicillata*), surfbirds (*Aphriza virgata*) and black turnstone (*Arenaria melanocephala*). The authors estimate that these five species consumed 31% of the total spawn deposition in Prince William Sound Alaska, in 1994. This work provides evidence that bird predation can have important implications for total egg removal, but the impact on the numbers of egg layers in not clear.

7. Blaxter, J.H.S. and F.G.T. Holliday. 1963. The behaviour and physiology of herring and other clupeids. Advances in Marine Biology 1:261-393. There is only a single page (page 273) of this 132-page review devoted to the subject of herring egg mortality. Three mortality sources are listed: (1) egg density; (2) fungal and bacterial attack; (3) predation. The review suggests there is an optimal egg density, above and below which the proportion of eggs surviving to hatching decreases. Presumably the increased mortality at high density is related to oxygen limitation, but no explanation is provided for lower hatching at low egg density. Only one study is cited (Toom 1958) that comments on fungus – apecifically that fungal infections are more common in the laboratory than in nature. The review noted that predation of eggs occurs from fish in the North Sea by coalfish (*Pollachius virens)* and ophiuroids (echinoderms). Two references are cited (Rounsfell 1930 and Cleaver and Franett 1946) that comment on predation by seabirds in the Pacific.

8. Bond, J. C., and D. Esler. 2006. Nutrient acquisition by female harlequin ducks prior to spring migration and reproduction: evidence for body mass optimization. Canadian Journal of Zoology

84:1223–1229. Body weight gain of adult female Harlequin Ducks was greater among ducks feeding on herring roe compared to those consuming marine invertebrates (crabs, limpets and snails). The report confirms that harlequin ducks may consume herring roe but other than that there are no specific implications for changes in egg layers.

9. Bunn, N., C.J. Fox, and T. Webb. 2000. A literature review of studies on fish egg mortality: implications for the estimation of spawning stock biomass by the annual egg production method. Science Series Technical Report 111, CEFAS. Lowestoft. 37 pp. This is a very useful literature review of all aspects of egg and larval fish mortality from all fish species. It does not capture some of the technical and non-peer-reviewed reports on egg predation of Pacific herring.

10. Calambokidis, J., J.D. Darling, V. Deeke, P. Gerrin, M. Gosho, W. Megill, C.M. Tombach, D. Goley, C. Toropova and B. Gisborne. 2002. Abundance, range and movements of a feeding aggregation of gray whales (*Eschritius robustus*) from California to southeast Alaska in 1998. Journal of Cetacean Research and Management 4(3): 267-271. This paper (like the Darling paper below) was added to this list because it was one of the few sources of definitive evidence that gray whales consume herring eggs. It is probable that the removal of eggs would be so complete so such predation would not necessarily reduce the number of egg layers but rather result on complete removal of entire patches. A potential implication for egg layers is that intelligent whale predators may target the thickest egg patches, perhaps resulting in a decrease in the overall number of egg layers.

11. Cleaver, F.C., and D.M. Franett. 1946. The predation by seabirds upon the eggs of the Pacific herring (*Clupea pallasi*) at Holmes Harbor during 1945. Washington State Department Fisheries Biology Report 46B. This paper investigated the role of seabird predation on herring in Puget Sound, as a possible explanation for the reduction of herring there. The authors examined stomach contents of scaups, surf scoters and white-winged scoters and provide quantitative estimates of the numbers of eggs found. They conclude that in previous times (prior to 1946), when herring abundance was higher, the removal of eggs might not have been a concern, but in the period when herring stocks (and egg production) is lower, the relative proportion of eggs removed is lower. The authors do not recommend the widespread killing of seabirds as a solution to the perceived problem, but instead recommend high speed vessels that can scare birds away from spawning areas.

12. Cooper, J.R., J.R. Uzmann, R.A. Clifford, and K.J. Pecci. 1975. Direct observations of herring (*Clupea harengus harengus*) egg beds on Jeffreys Ledge, Gulf of Maine in 1974. Int. Comm. Northwest Atl. Fish. (ICNAF) Res. Doc. 75/93. 6 p. This brief report documents fish predation on Atlantic herring spawn in the Gulf of Maine. The main predators were the cunnner (*Tautogolabrus adspersus*), Atlantic cod (*Gadus morhua)*, bluefish (*Pomatomus saltarrix*) and pollock (*Pollachias virens*). An interesting comment is that predation by fish tends to occur at night.

13. Dahlberg, M.D. 1979. A review of survival rates of fish eggs and larvae in relation to impact assessments. Marine Fisheries Review 41: 1–12. This is a dated but useful review of the literature on egg and larval survival of all fish species including herring.

14. Darling, J.D., K. E. Keogh and T.M. Steeves. 1998. Gray whale (*Eschrichtius robustus*) habitat utilization and prey species off Vancouver Island, B.C. Marine Mammal Science, 14(4):692-720. Also see annotated comments about Calambokidis et al. 2002 (above). This paper describes how northward migrating gray whales interrupt their journey to feed on herring eggs in the vicinity of Hesquiat Harbour in Clayoquot Sound. The specific site of whale feeding activity varied each year. This egg-eating activity usually lasted several weeks starting as early as mid-February and sometimes lasting until early April. Numbers of whales can vary from “dozens to hundreds”. This type of feeding would probably have considerable impacts on the numbers of egg layers but it appears that no one has documented the effects on the impacted spawning areas or estimated the quantity of eggs consumed.

15. De La Cruz, S.E.W, J. Y.Takekawa, M. T. Wilson, D. R Nysewander J. Evenson, D. Esler, W. S. Boyd and D. H. Ward. 2009. Spring migration routes and chronology of surf scoters (*Melanitta perspicillata*): a synthesis of Pacific coast studies. Canadian Journal of Zoology, 87: 1069-1086.

This paper covers many topics but part of the review is concerned with the significance of 'once predictable' herring spawning in Puget Sound and the Strait of Georgia as a factor affecting the migration route of surf scoters –specially whether they choose a coastal versus an inland route. Although this is an information-rich review, there in little in the paper that has direct relevance to the issue of the effect of seabird predation on egg layers, except one might anticipate that surf scoter predation would be less during periods of low (herring) abundance.

16. Esler, D., R. Ydenberg, J. Bond and S. LeBourdais. 2007. Variation in harlequin duck distribution and productivity: the roles of habitat, competition, and nutrient acquisition. Contract report for BC Hydro: http://www.bchydro.com/bcrp/projects/docs/bridge_river/05.W.BR.03.pdf This lengthy contract report contains two reports. While it is clear that harlequin ducks consume herring eggs, both reports tend to discount the importance of herring spawn as a factor affecting the migration or reproduction of the ducks because other food sources are used.

17. Grass. A. 1973. Mew gulls and black turnstones feeding on herring eggs. Murrelet 54:38–39. This older paper was not examined.

18. Griffin F.J., E.H. Smith, C.A. Vines and G.N. Cherr. 2009. Impacts of suspended sediments on fertilization, embryonic development, and early larval life stages of the Pacific herring, *Clupea pallasi*. Biol. Bull. 216: 175–187. This paper provides definitive evidence of the detrimental effect of sediments on egg mortality. The authors suggest a number of factors that may link sedimentation to egg layers. One is that the presence of sediments may compromise egg adhesion, thereby making it more probable that some eggs may break off of egg masses. Another is that the presence of sediments in the water may discourage spawning at affected sites, so there is reason to suspect that egg deposition may be less in areas where sediments occur. These suggestions are, however, speculative.

19. Grosse, D. and T. Sibley. 1984. Projected effects of CO_2-induced climate change on the Pacific herring (*Clupea harengus pallasi*) fishery in the northeast Pacific ocean. Contract Report 4524910 to the Lawrence Berkeley Laboratory, Fisheries Research Institute, School of Fisheries WH-1O, University of Washington, Seattle, Washington. There are several pages in this review that present a list of literature and overview of herring egg mortality. There is no reference made to the effect of predation on estimates of egg layers.

20. Haegele, C. W. and J. F. Schweigert. 1989. Egg loss from Pacific herring spawns in Barkley Sound in 1988. Can. Manag. Rep. Fish. Aquat. Sci. 40p.
See text under '24'.

21. Haegele, C.W. 1993. Seabird predation of Pacific herring, *Clupea pallasi*, spawn in British Columbia Canadian Field-Naturalist 107: 73–82.
See text under '24'.

22. Haegele, C.W. 1993. Epibenthic invertebrate predation of Pacific herring, *Clupea pallasi*, spawn in British Columbia Canadian field-naturalist 107: 83-91.
See text under '24'.

23. Haegele, C. W. and J. F. Schweigert. Egg loss from Pacific herring spawns in Barkley Sound in 1988. Can. Manag. Rep. Fish. Aquat. Sci. 2037. 40p.
See text under '24'.

24. Haegele, C. W., and J. F. Schweigert. 1991. Egg loss in herring spawns in Georgia Strait, British Columbia. In Proceedings of the International Herring Symposium, Anchorage, Alaska, October 23–25, 1990, p. 309–322. Univ. Alaska, Fairbanks, AK. The five references above all describe similar work: field and laboratory studies of seabird and invertebrate predation. These represent the most detailed study of this topic from the perspective of egg loss. Egg loss was described for the Lambert Channel area of the Strait of Georgia in 1989 and in Barkley Sound in 1988. Egg loss was estimated by two methods: (1) examination of egg layers at 5-6 different times (usually 2-day intervals) during a 14-day incubation period and (2) counts of birds and invertebrates and estimated consumption by individuals. There was no clear temporal trend in the estimation of egg layers, perhaps because the data were so variable. Total egg loss from bird and invertebrate predation was estimated at about 7%, of which about 3% was from birds and the remainder was from invertebrates. Degrees of bird predation was not spatially uniform so in specific locations the predation rate was higher. Further gull species tended to concentrate in intertidal areas whereas scoters and diving ducks too inter-tidal spawn. Of invertebrates most predation was from kelp crabs followed by snails and starfish. The 1991 paper points out that 'physical translocation' of spawn through storms may lead to greater egg loss (26-40%) but concludes that (i) unless herring stock biomass is very low, egg loss from predation is low, and mainly undetectable from surveys of spawn; (ii) predation rates are so variable in time and space, that a general model of predation is not possible.

25. Hardwick, J. E. 1973. Biomass estimates of spawning herring, *Clupea harengus pallasi*, herring eggs, and associated vegetation in Tomales Bay. Calif. Fish Game 59:36-61. This paper reports on personal observations of the author about extensive bird predation in Tomales Bay. It also recounts observations of local fishers who indicate that predators on herring eggs also include sturgeon, silversides (Atherinids), surf perches (Embiotocidae) and crabs.

26. Hay D.E. and DC. Miller. 1982. A quantitative assessment of herring spawn lost by storm action in French Creek, 1980. Canadian Manuscript Report Fisheries Aquatic Sciences 1636. 9 p. A storm event in 1980 dislodged massive amounts of vegetation and herring spawn, equivalent to about 25 percent of the entire spawning deposition in the area. Probably this estimate is high relative to the amount of egg loss in most years. This report also includes an estimate of the weight of an incubating egg that, curiously, is not described elsewhere in the literature.

27. Hay, D.E. and M.J. Marliave. 1988. Transplanting Pacific herring spawn: a stocking experiment. Publication of Amer. Fish. Soc. Symposium 5:49-59. This paper shows that eggs that are detached from vegetation are not necessarily dead or destined to die. Many survive to hatch and grow into viable larvae.

28. Hempel, I., and G. Hempel. 1971 An estimate of mortality in eggs of North Sea herring (*Clupea harengus L*. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 160:24–26. This short report examined herring eggs captured from the stomachs of hake in the North Sea – and then using microscopic analysis of the eggs attempted to estimate the proportion of eggs that were alive prior to being consumed by the hake. The average proportion of eggs that were apparently alive and normal prior to being eaten was 95.8 percent. This was the first estimate of egg survival (excluding predation) for North sea herring. This paper has few implications for egg loss of Pacific herring except to point out that fish predation (haddock) is common elsewhere.

29. Hoines, A., O.A. Bergstad and O.T. Albert. 1992. Seasonal variation of the diet of cod (*Gadus morhua* L.) and haddock (*Melanogrammus aeglefinus* L.) at a herring spawning ground. ICES C.M. 1992/G:9. 23p Cod and haddock have different diets but at times when herring spawn is available both piscivores switch and include herring spawn.

30. Hoeines, A.S. and O.A. Bergstad. 1992. Food partitioning by flatfishes on a herring spawning ground. Sarsia 87: 19–34. This short paper shows that pleuronectids consume herring spawn.

31. Høines, Å.S., O.A. Bergstad and O.T.Albert. 1995. The food web of a coastal spawning ground of the herring (*Clupea harengus*). Proceedings of the Mare Nor Symposium on the Ecology of Fjords and CoastalWaters. In: Skjoldal, H.R., C. Hopkins, K.E. Erikstad, and H.P. Leinaas, (Eds.). Ecology of Fjords and Coastal Waters. Elsevier Science., Amsterdam. Pp. 17–22. This paper focuses on the potential significance of increasing herring spawning in Norwegian waters for the production of coastal fish population. The structural and nutritional significance of predator-prey interactions between coastal populations and the herring was assessed. Food webs were constructed based on fish diet studies and literature data. For most central fish species, annual consumption of different prey, including herring and herring eggs, was estimated using simple stomach evacuation models. In the absence of herring, the most important pathway from phytoplankton to piscivorous fish went via copepods and a single planktivorous fish, the sandeel, *Ammodytes marinus*. This and several other pathways were broken in the presence of herring or herring eggs during the 6-8-week spawning season in March to April. In that period, several piscivores and benthivores showed pronounced diet shifts, abandoning their normal prey in favour of herring eggs and herring, i.e., food sources not produced locally. Herring eggs contributed significantly to the annual prey consumption of several coastal species of fish, but only very low proportions of the herring and herring eggs available at the spawning ground were lost due to predation by fish.

32. Hoeines, A.S. and O.A. Bergstad. 1999. Resource sharing among cod, haddock, saithe and pollack on a herring spawning ground. Journal of Fish Biology 55: 1233–1257. This 1999 paper describes work conducted in 1991-1993 that was reported in a preliminary version in the 1991 ICES report (above by same authors). More detail is added but the main conclusions are the same: fish predators with different diets will switch to herring spawn when it is available.

33. Hourston, A. S., H. Rosenthal and H. Westerhagen. 1981. Data summaries for viable hatch from Pacific herring eggs deposited at different intensities on a variety of substrates.Can. Data Rep. Fish. Aquat. Sci. 267: 56 p. This report briefly describes 53 laboratory experiments where the measurements were taken on the larvae incubated under different conditions. The remainder of the report consists of data.

34. Hourston, A. S., H. Rosenthal and H. Westerhagen. 1984. Viable hatch from eggs of Pacific herring (*Clupea harengus pallasi*) deposited at different intensities on a variety of substrates. Can. Tech. Rep. Fish. Aquat. Sci. 1274: 19 p. The essence of this paper is that larval viability and survival is compromised from eggs deposited at high density. The major weakness of the paper, according to the authors, is that the estimates of density were made on a subjective scale, and not estimated according to the numbers of egg layers.

35. Johannessen, A. 1986. Recruitment studies of herring in Lindaaspollene, western Norway. Chapter 1. Fiskeridir. Skr. Ser. Havunders. 18:139-240. This paper is one of a three-part report (or published thesis) on a herring population in the Lindaaspollene fjord in Norway. The paper also indicates that maximal egg densities appear to be limited so that the spatial extent of spawning increases as the size of the herring spawning population increases. The paper comments that diving ducks can consume about 1/3 and haddock (fish predator) about 2/3 of herring spawns in locations when egg density is low. In years when spawn was more dense, however, the impact of such predation, in terms of the amount removed, would be insignificant.

36. Jones, B.C, 1971. The effect of intertidal exposure on survival and embryonic development of pacific herring spawn. MSc thesis. Dept. Zoology. University of BC. 56 p.
See next reference.

37. Jones, B.C. 1972. Effect of intertidal exposure on survival and embryonic development of pacific herring spawn. Can. J. Fish. Aquat. Sci. 29: 1119–1124.
This report is based on an MSc thesis (Jones 1971) that examined the development of herring eggs according to the amount of intertidal exposure egg received. Egg survival rates varied from 13-31 percent. These are not necessarily natural survival rates because the work was conducted in a laboratory and therefore subject to other factors (such as disease) that were not documented.

38. Kelly J.P and S.L. Tappen. 2003. Distribution, abundance, and implications for conservation of winter waterbirds on Tomales Bay, California. Western Birds 29: 103-120. On web at http://elibrary.unm.edu/sora/wb/v29n02/p0103-p0120.pdf
This report points out the spatial connection between over-wintering seabirds and herring spawning in Tomales Bay between 1990 and 1996. There are no estimates of consumption of spawn by birds.

39. LaCroix, D. L, . S. Boyd, D. Esler, M. Kirk, T. Lewis and S. Lipovsky. 2005. Surf scoters *Melanitta perspicillata* aggregate in association with ephemerally abundant polychaetes. Marine Ornithology 33: 61–63. This brief report is more about scoter behaviour than the relationship between scoters and herring spawn. The report describes how scoters congregated at a specific site to forage intensely on polychaetes that was not in the immediate vicinity of herring spawning in the Strait of

Georgia. The report has no implication for egg layers except to point out that there are alternate prey that are attractive to seabirds.

40. Laine, P. & Rajasilta, M. 1998. Changes in the reproductive properties of Baltic herring females during the spawning season. Fisheries Research 36: 67-73.
See next reference.

41. Laine, P. and M. Rajasilta. 1999. The hatching success of Baltic herring eggs and its relation to female condition. J. Exp. Mar. Biol. Ecol. 237, 61–73. These papers make a case that female condition affects egg quality and hence egg survival. It is uncertain whether the physical properties of a female could affect the egg survival of Pacific herring, although related work shows that larger females have larger eggs. Therefore if egg size has a bearing on egg survival, then female size might also have some impact on egg survival.

42. Lewis, T. L., D. Esler, and W. S. Boyd. 2007. Foraging behaviors of surf scoters and white-winged scoters at spawning sites of Pacific herring. Condor 109:216-222.
During winter surf and white-winged scoters (*Melanitta perspicillata and M. fusca*) are feed mainly on clams but shift to herring eggs after spawning. Although clams could provide the nutritional and energetic requirements of scoters, they were required to spend about half of their time foraging. Foraging time was much less when herring eggs were available, so one advantage of feeding on herring eggs is a reduction in the cost of energy for feeding. Hay note: It is not clear, however, if such a reduction would occur when herring eggs were lightly deposited (i.e. few layers).

43. Lok, E. K. 2008. Site use and migration of scoters (*Melanitta spp.*) in relation to the spawning of Pacific herring (*Clupea pallasi*). Thesis, Simon Fraser University, Burnaby, Canada.
See next reference

44. Lok, E. K., M. Kirk, D. Esler, and W. S. Boyd. 2008. Movements of pre-migratory surf and white-winged scoters in response to herring spawn in the Strait of Georgia, British Columbia. Waterbirds 31:385–393. This paper (and thesis) is mainly about the importance of the Berner's Bay herring in Southeast Alaska for scoters. There are interesting implications that scoters are dependent on certain herring spawning areas for their migratory behaviour but there is no information on the extent of herring consumption by scoters.

45. McGurk, M.D. 1986. Natural mortality of marine pelagic fish eggs and larvae: role of spatial patchiness. Marine Ecology Progress Series, 34: 227–242. This is mainly a theoretical paper that included Pacific herring as part of an explanation that egg size (or dry weight) is a useful predictor of natural mortality rate. The paper makes a compelling case for this when examined over a range of egg weights and a variety of species. However, in spite of the title, there are no direct implications for explaining factors affecting egg loss in herring.

46. Messieh, S. H., and H. Rosenthal. 1989. Mass mortality of herring eggs on spawning beds on and near Fisherman's Bank, Gulf of St. Lawrence, Canada. Aquat. Living Resourc. 2:1-8. This paper documents two unique but related events: excessive spawn density of 20-30 layers followed by mass mortality of eggs. Such intense egg deposition is rare and the authors speculate that it was associated with rapid temperature change. There are no specific implications for egg loss of BC herring except that this example provides a rationale for why herring have evolved to avoid (usually) intense egg density.

47. Morrison J.A., I.R. Napier and J.C. Gamble. 1991. Mass mortality of herring eggs associated with a sedimenting diatom bloom. ICES Journal of Marine Science 48(2):237-245. This paper reports on a unique incident in which a heavy diatom bloom covered a large (163,000 m^2) herring spawning site in Scotland. Eggs were deposited in densities between 2 and 12 layers. Egg development began normally but gradually succumbed to the effects of sedimentation and diminished oxygen concentration. This paper is not directly relevant to the topic of factors affecting egg density or egg survival of BC herring.

48. Munro, J.A. and W.A. Clemens. 1931. Water fowl in relation to the spawning of herring in British Columbia. Bulletin 17. Biological Board of Canada. 46 pp. This 46-page report is one of the first that was dedicated to examining seabird predation on herring. The study was confined to the east coast of Vancouver Island, in the vicinity of Departure Bay (Nanaimo). Although the paper rambles it is rich with data on stomach contents of seabirds and natural observations. In part the paper takes issues with earlier reports that indicate that sea ducks may be causing serious harm to herring spawning. Instead these authors point out that some of the prior accounts of sea duck consumption of herring eggs were grossly over-estimated and that the predatory ducks have intrinsic worth (which was not necessarily a perspective held by many in 1931). The paper also advises that although gulls (Glaucous-winged herring and short-billed) consume substantial quantities of herring eggs, they are mainly from sources that have been dislodged from submerged vegetation and blown onto beaches.

49. Outram, D. M. 1958. The magnitude of herring spawn losses due to bird predation on the west coast of Vancouver Island. Fish. Res. Board Can. Prog. Rep. 111:9-13. In controlled predator-exclusion tests on the west coast of Vancouver Island, seabird predation accounted for most egg loss, with declines ranging between 66-85% in four separate plots. In contrast, predator-excluded plots lost between 7-50%. Glaucous-winged gulls and herring gulls accounted for most of the predation. Egg predation was confirmed by examination of bird stomachs. The report advises that the amount of egg loss from seabirds may vary among years.

50. Palsson, W. A. 1984. Egg mortality upon natural and artificial substrata within Washington state spawning grounds of Pacific herring (*Clupea harengus pallasi*). M.S. thesis. University of Washington, Seattle, Washington. 191 p. This 207-page thesis provides especially valuable information about factors affecting egg survival of herring in Puget Sound. It describes innovative field experiments using ‘predator exclusion devices’ and provides rigorous quantitative estimates of egg loss. The main limitation of the work, relative to most BC herring populations, is that the initial egg densities were extremely low. It is not clear whether the very low egg densities described in this paper represented typical spawning areas in Puget Sound or whether the experimental sites were exceptionally low relative to other areas in Puget Sound. It is regrettable that the work was not formally published but regardless this report is one of the most definitive studies on approaches to studying herring egg loss.

51. Purcell, J.E., D. Grosse, J.J. Grover. 1990. Mass abundance of abnormal Pacific herring larvae at a spawning ground in British Columbia. Transactions of the American Fisheries Society 119:463-469. A high proportion of abnormal herring larvae were noted in a spawning site that had unusually high temperatures and dry weather. The egg deposition producing the larvae was only 1-2 layers thick, so heavy egg deposition, resulting in low oxygen of high CO_2 would not explain the observations.

52. Rajasilta, M.J., J. Eklund, J. Kaaria, and K. Ranta-aho. 1989. The deposition and mortality of eggs of the Baltic herring, *Clupea harengus membras* L., on different substrates in the south-west archipelago of Finland. J. Fish. Biol. 34: 417-427. Eggs density varied between 6000 and 2,300,000 eggs/m^2 in the study in the western Baltic. Tidal range is limited in the Baltic Sea so egg the depth range was only from 0-4 m. Although overall egg mortality was low, it was higher at deeper and warmer sites. It also varied greatly with substrate.

53. Rajasilta,M., Laine, P. & Eklund, J. 2006. Mortality of herring eggs on different algal substrates (*Furcellaria* spp. and *Cladophora* spp.) - an experimental study. Hydrobiologia 554: 127-130. The ultimate cause of egg mortality was shown to be closely related to temperature and substrate (vegetation type). Total egg mortality was relatively low (~15%) but the actual cause of mortality was not mentioned.

54. Richardson, D.E. and J.A. Hare. July 2009. Does haddock egg predation decouple the abundance of Atlantic herring larvae from spawning stock biomass on Georges Bank? *Larval Fish Conference* 2008-Portland Oregon. There is no publication with this citation but there is a brief abstract at: **http://sh.nefsc.noaa.gov/seminar_abstracts.htm**. An interesting aspect is authors contention that predation at the egg stage may be sufficient to compromise estimates of spawning stock biomass made from surveys at the early larval stage.

55. Richardson D. 2010. The role of haddock egg predation in the decline of an Atlantic herring population. Web Abstract. http://sh.nefsc.noaa.gov/seminar_abstracts.htm*.* This reference was included as an example of recent work on fish predation on Atlantic herring eggs. The potential significance is that fish predation on Pacific herring eggs does not appear to have been examined carefully or quantified.

56. Richman, S. E. and J. R. Lovvorn. 2009. Predator size, prey size, and threshold food densities of diving ducks: does a common prey base support fewer larger animals? Journal of Animal Ecology 78:1033-1042. This subject of this paper is not specifically on seabird predation of herring or herring eggs, but rather uses seabird predation to examine fundamental issues about efficiency of foraging relative to predator and prey size. Although it is not mentioned in the paper this approach may be useful to consider relative to seabird consumption of herring eggs: specifically what are the minimal densities (layers) of herring eggs required for seabird foraging?

57. Rodway, M.S., H.M. Regehr, J. Ashley, P.V. Clarkson, R.I. Goudie, D.E. Hay, C.M. Smith and K.G. Wright. 2003. Aggregative response of Harlequin Ducks to herring spawning in the Strait of Georgia, British Columbia. Can. J. Zool. 81: 504-514. Contrary to the conclusions of some previous work, this paper shows that most Harlequin Ducks (55-87%) in the northern Strait of Georgia consume herring eggs. However during the study period of 1999-2000 the total consumption of eggs was estimated to be from 11.3-17.8 tonnes, which represents a relatively small amount of the total amount of spawn deposited in that area.

58. Rodway, M.S. and F. Cooke. 2002. Use of fecal analysis to determine seasonal changes in the diet of wintering Harlequin Ducks at a herring spawning site. J. Field Ornithol. 73:363–371. This paper examines season changes in the diets of Harlequin Ducks and shows that herring eggs probably are the main prey during the first week of spawning. The paper advises that at this time the digestion of eggs is nearly complete so egg remains are not noticed in the feces but later, after about a week, some herring egg remains can be seen in duck feces indicating incomplete digestion. The authors speculate that such egg remains may be indicative of consumption of dead, desiccated eggs, perhaps taken from the intertidal areas.

59. Rooper, C.N., L.J. Haldorson and T.J. Quinn II. 1998. An egg-loss correction for estimating spawning biomass of Pacific herring in Prince William Sound, Alaska. Alaska Fishery Research Bulletin 5: 137-142. This short but useful paper describes egg loss as a function of depth and air exposure, based on studies in Prince William Sound, Alaska, that is subject to large tidal fluctuation. Estimates of egg loss are higher than estimates made for most other areas in the eastern Pacific, reaching nearly 30% for the full incubation period but among specific sample sites the range was from a low of 18.9% to a high of 89.6%. The important implication of this work is that spawn surveys will be under-estimated unless the estimates account for egg mortality.

60. Rooper, C.N., L.J. Haldorson and T.J. Quinn II. 1999. Habitat factors controlling Pacific herring (*Clupea pallasi*) egg loss in Prince William Sound, Alaska. Canadian Journal of Fisheries and Aquatic Sciences 56: 1113-1142. Model studies based on field studies between 1990-1995 in Prince William Sound, Alaska, indicate that mortality rates of incubating eggs are very high with egg loss rates approaching 100% among intertidal eggs experiencing more than 200 hours of air exposure. It is interesting that the maximal egg densities (120,000 egg/m^2) found in this study are lower that those seen in most BC herring spawning sites. This paper also examines the sources of egg mortality and reports that egg mortality was greatest in the shallow, intertidal zone and probably caused mainly by bird predation.

61. Rooper, C.N. and L.J. Haldorson. 2000. Consumption of Pacific herring (*Clupea pallasi*) eggs by greenling (Hexagrammidae) in Prince William Sound, Alaska. Fishery Bulletin 98(3):655-659. This paper is important and remarkable as the only paper dedicated to examination of fish predation on herring eggs. The study examined fish stomachs of six different species: two greenlings (Hexagrammidae*)*, two sculpins (Cottidae) a flounder (Pleuronectidae) and char (salmonidae). Only the greenling and char contained herring eggs but the sample sizes were small. The study estimated that the greenlings could consume between 2.3-and 3.7% of all herring eggs deposited in the study area, and this estimate was judged to be conservative. The implication of this paper is that fish predation could be overlooked and may be significant – and it has not been examined in most other areas of the Pacific coast.

62. Rounsfell, GA. 1930. Contribution to the biology of the Pacific herring, *Clupea pallasii*, and the condition of the fishery in Alaska. Bulletin of the U.S. Bureau of Commercial Fisheries 45:227-320. This report contains only incidental reference to predation on herring and herring eggs, noting predation in Kachemak Bay to occur by beluga whales, cormorants, murres, surf scoters, gulls and bald eagles.

63. Runnstrom, S. 1941. Quantitative investigations on herring spawning and its yearly fluctuations at the west coast of Norway. Fiskeridir. Skr. Ser. Havunders. 6(8):5-71.
This lengthy report contains a chapter titled: "The density of the herring roe on the spawning grounds and the mortality of eggs". This chapter points out that mortality increases with the thickness of the deposition, from 43-70% on roe that was 0.5 cm or greater and over 80% in roe that was greater than 2.5 cm. Such thickness was exceptional, however, and the average mortality during the study (from 1931 to 1937) was 12.1%.

64. Skaret, G., A. Fernö, L.Nøttestad, A. Johannessen and B.E. Axelsen. 2001. Impact of herring spawning behaviour on acoustic abundance estimates. ICES CM, Q22.
This paper is one of the few that comments on the reproductive advantages and disadvantages of egg density, of egg layers, as a short commentary in the Discussion – and comment that thick egg layers may attract predators. A quote from this paper is as follows:
"The ……… location selected for the small scale study on schooling dynamics had the densest herring concentrations during all surveys. However, within this location the layers of herring were not stationary, but moved in a south easterly direction from day to day. Similar directional horizontal spawning has been reported in North Sea herring……….. Thick egg layers might result in retarded development and high mortality rates for the deeper layers of the egg mat due to low oxygenation ……..but …. uppermost egg layer should not suffer from such an effect. Directional horizontal spawning could instead be a strategy to avoid eggs being consumed by predators, as thick egg layers should represent favourable areas for egg feeders (Høines et al., 1995).

65. Skaret, G., A. Fernö, L. Nøttestad, L.A. Johannessen and B.E. Axelsen. 2001. Impact of herring spawning behaviour on acoustic abundance estimates. ICES CM 2001/Q:22. 20 p. There is a brief comment in this paper that stomach analysis showed that pollock, haddock and saith contained herring eggs.

66. Stratoudakis, Y., Gallego, A., Morrison, J.A. 1998. Spatial distribution of developmental egg ages within a herring *Clupea harengus* spawning ground. Marine Ecology Progress Series, 174: 27-32. This is a short and novel approach to examination of spawn depositions by mapping development stages in incubating embryos. It may not be self-evident to some readers that the geographic scale of the spawning area examined in this paper is substantially greater than most herring spawn events in eastern Pacific populations. The paper provides evidence that dense egg layers result in retarded development and later hatching.

67. Sullivan, T.M., Butler, R.W., and Boyd, W.S. 2002. Seasonal distribution of waterbirds in relation to spawning Pacific herring, *Clupea pallasi*, in the Strait of Georgia, British Columbia. Can. Field-Nat. 116: 366–370. This short paper points out that 21 species of waterbirds prey on spawning herring or their eggs in the Strait of Georgia. Waterbirds move and congregate in the vicinity of spawning areas during the spawning season. The consequence is a sharp increase in density, from 66 to 616 birds/km^2. The paper advises that the available literature indicates that seabird predation on herring eggs is not considered to be significant but that the dependence of seabirds on herring as a post-winter food sources is undetermined.

68. Taylor, F.H.C. 1971. Variation in hatching success in Pacific herring (*Clupea harengus pallasi*) eggs with water depth, temperature, salinity, and egg mass thickness. Rapports et Procès-Verbaux des Réunions du Conseil International pour l`Exploration de la Mer, 160: 34-41. This is a widely cited paper but based on subsequent work the results seem questionable. The main concern is that the egg survival rates are all very low, and much lower than in many reports published subsequent to this work. The paper reports that egg survival was lowest at deepest depths (10m) but we now know that is well within the range for natural herring spawning in the eastern Pacific. In short, this paper does not provide any substantive information relative to the issue of egg loss.

69. Toom, M. M. 1958. "Experiments in the incubation of Baltic herring eggs." Trudy VNIRO, 34: 19-29. (In Russian, translation by Office of Technical Services. U.S. Dept. of Commerce, Washington 25, D.C.). This paper is unusual because it suggests that egg quality is related to egg survival. Presumably egg quality is related to female size, or age, on feeding conditions during the period of oogenesis. This is not the first or only paper to attempt to link egg or larval survival with maternal condition but may be the only one that suggests this may be important for herring.

70. Toresen, R. 1991. Predation on the eggs of Norwegian spring spawning herring (*Clupea harengus*) on a spawning ground on the west coast of Norway. ICES Journal of Marine Science, 48: 15-21. Field surveys that captured and examined stomach contents of haddock, combined with experimental tests of stomach evacuation rates were used to estimate consumption of herring eggs. These estimates were examined relative to acoustic estimates of total spawning biomass, from which total egg numbers were derived, to estimate the total rate of egg loss in the Buagrunnen area of the Norwegian coast, at about four percent of total egg production.

71. Wahl, T.R., S.M. Speich, D.A. Manuwal, K.V. Hirsch, and C. Miller. 1981. Marine bird populations of the Strait of Juan de Fuca, Strait of Georgia and adjacent waters in 1978 and 1979. U.S. Environmental Protection Agency, DOC/EPA Interagency Energy/Environment R&D Progr. Rep. EPA/600/f-81/156. This large report described the 1978-79 distribution and abundance of the marine birds in the southern Georgia Strait in the context of risk from oil spills. There is little information on the role of herring spawn as a food source but on page 67 there are comments on seabird distribution relative to herring spawning and the roe fishery.

72. Weathers, W.W., and J.P. Kelly. 2007. Energy Footprints on Tomales Bay. The Ardeid. 2007. pp7-9. This short article attempts to use some simple energetic calculations to estimate the actual and potential consumption of herring roe by the waterbirds of Tomales Bay. The preliminary estimates indicate that birds could consume most of the spawn in some years. The article extrapolates from estimates of spawning herring biomass (in short tons) to estimates of roe weight (and energy) but the basis for the conversions is not explained.

73. Wilcock, J.A., E.D. Brown, and E. Debevec. 1995. Herring spawn deposition and reproductive impairment, Exxon Valdez Oil Spill Restoration Project Annual Report (Restoration Project 94 166-I), Alaska Department of Fish and Game, Commercial Fisheries Management and Development Division, Cordova, Alaska. This report (plus Wlllete et al. 1997) provides the basis for two of the papers by Rooper et al. (1998 and 1999) and include draft versions of the analyses. These papers also include details about how herring spawn was sampled.

74. Willson, M.F., and Womble, J.N. 2006. Vertebrate exploitation of pulsed marine prey: a review and the example of spawning herring. Rev. Fish Biol. Fish. 16(2): 183–200. This review paper provides an interesting and useful overview of predators of Pacific herring and herring eggs. It points out that herring spawning is a substantial injection of energy into local environments but the variation in the timing and location of spawning makes access to the resource unpredictable to many predators. The paper does not provide explicit information on factors that might affect the numbers of egg layers but does make a case that predation rates could vary according to spawning locations and timing.

75. Willette, T.M., G.S. Carpenter, and K. Hyer. 1997. Herring spawn deposition and reproductive impairment. Exxon Valdez Oil Spill Restoration Project Annual Report (Restoration Project 96166),

Alaska Department of Fish and Game, Division of Commercial Fisheries Management and Development, Cordova, Alaska. See comment above for 'Wilcock et al. 1995.

76. Zydelis, R. and D. Esler. 2005. Response of wintering Steller's Eiders to herring spawn. Waterbirds 28: 344-350. This paper found that Steller's Eiders were more opportunistic than previously believed and were able to feed on herring spawn on the southern Baltic coast when it was available.