Spatial diversity of Pacific herring (*Clupea pallasi*) spawning areas

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Eastern Pacific herring spawn in intertidal and shallow subtidal areas. Spawning sites are conspicuous: milt turns coastal waters white, sometimes for distances of many kilometres. This attribute has enabled biologists to document spawning distributions for more than 70 years throughout the 29 500 km coastline of western Canada. Spawning distributions and spatial diversity have varied over time. When aggregated over 70 years (1938–2007), spawning occurred along 5574 km or ~20% of the total coastline. Cumulative annual spawn length ranges from 131 (in 1966) to 770 km (in 1992). We examined annual changes in spawn distribution using spatial units of variable size, ranging in area from a maximum of >1000 km^2 to a minimum of <0.1 km^2. Assessment of spatial diversity varied with the size of the spatial unit. Spatial diversity estimated from small spatial units (area <0.1 km^2) was significantly correlated with spawning-stock biomass (SSB). In contrast, there was no correlation, and sometimes opposite temporal trends, between SSB and all larger spatial units (mean area >0.3 km^2). The choice of spatial scale can affect the results from analyses of other factors, such as SSB, that could affect spatial diversity of spawning areas.

Keywords: Pacific herring, spatio-temporal variation, spawning distribution.

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Introduction

Much of the biological literature about spawning of Pacific herring (*Clupea pallasi*) has examined factors affecting the measurement of spawn ecology and distribution (Haegele *et al.*, 1981; Haegele and Schweigert, 1985), spawn measurement (Hay and Kronlund, 1987), and the timing of spawning (Hay, 1990). Less attention has been paid to annual variation in the spatial distribution of spawn or factors that affect these changes. Throughout their range in all northern-hemisphere oceans, herring spawn on bottom habitats (Blaxter, 1985). During mass spawning, females deposit adhesive eggs directly on the bottom or vegetative substrata (Haegele and Schweigert, 1985). The density of eggs can be assessed approximately by the number of egg layers, which rarely exceed ten (Hay, 1985). Based on many observations in the Northeast Pacific, the number of egg layers is usually less than five (Hay, 1985; Schweigert *et al.*, 1990).

In contrast to deeper-spawning herring in the Atlantic, Pacific herring spawn exclusively in shallow nearshore habitats (Haegele and Schweigert, 1985). Spawning activity is conspicuous: milt turns the water milky-white, and seabird and marine mammal predators often congregate at spawning sites. Comprehensive spawn surveys began in 1928 in southern British Columbia (BC) and expanded to the entire provincial coastline in the late 1930s (Hay and Kronlund, 1987). Annual quantitative assessments of spawn deposition provide an index of the relative abundance of spawning herring. This index is an essential component in age-structured analytical assessments (Schweigert and Haist, 2008). Spawn indices are also used to classify, monitor, and protect sensitive coastal habitats (Hay *et al.*, 1989; Hay and McCarter, 2008).

The assessment of temporal variation in the spatial diversity of Pacific herring spawning has received little direct attention in the biological literature. A measure of "spawning spatial diversity" is defined here as the number of potential sites utilized by spawners relative to the number known to be available. A key aspect of this definition is the spatial dimension of the "spawning site". References to the spatial dimensions of herring spawning sites vary widely in the literature, from relatively small sites (tens of metres) to large areas (hundreds of kilometres). We consider the implications of the spatial dimensions used to assess spawning sites for the estimation of annual spawning frequency at these sites. The spatial diversity of spawn depositions is also examined relative to the variation in spawning-stock biomass (SSB) and the size of spatial units used to assess the spawning sites.

Material and methods

The distribution of spawning sites in BC is based on 29 216 records collected since 1928, although early records were limited mainly to southern coastal areas. In all, 28 436 records have been collected since 1938, when spawn surveys were conducted in all areas of the coast, thereby establishing a relatively complete 70-year time-series. Spawning sites are dispersed throughout the BC coast (Figure 1) but are concentrated in relatively sheltered areas; there are virtually no spawning records in areas exposed to the open Pacific.

The BC coast has a cumulative length of more than 29 500 km. Between 1928 and 2007, spawning occurred on 5574 km or ~19% of the coastline (Figure 1). In a typical year, herring spawn on ~400–600 km (~1.8%) of the BC coastline (Hay and
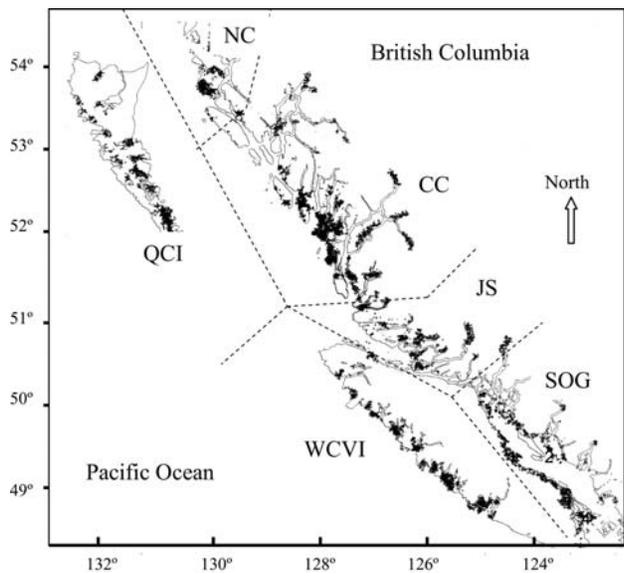
Figure 1. The coast of BC showing approximate areas where spawning has been observed in the past (black shading) and the six REGs distinguished: North Coast (NC), Queen Charlotte Islands (QCI), West Coast Vancouver Island (WCVI), Central Coast (CC), Johnstone Strait (JS), and Strait of Georgia (SG).

Figure 2. The geographically nested configuration of (a) 6 REGs, (b) 30 STATs, (c) 101 SECs, and (d) 282 SEPLs.

Kronlund, 1987). Some recorded lengths of spawn are <1 km, whereas others may extend over many contiguous kilometres of coastline.

Detailed records of herring spawn have been collected annually by fishery officers and diver teams (Hay and Kronlund, 1987). Usually, each record includes a location and an estimate of length, width, and density. We geo-referenced all spawn-location information and developed an electronic database using geographic names with unique numeric codes. The geographical areas represented by location names, however, can vary: from small islands or coves, measuring only 100 m in length or breadth, to bays or inlets, >50 km in length. In addition, spawning locations are frequently clustered, and different names have been used to describe the same general vicinity (i.e. they represent subsets of each other). To resolve these database problems, we developed a "shoreline km system" that provided a unique code for each kilometre of coastline (1 km segment, with latitude and longitude coordinates estimated from nautical charts; abbreviated to KSEG) where spawning has occurred one or more times since 1928.

For the purposes of research and management of marine fisheries, BC waters (Figure 2) have been subdivided into 6 regions (REGs), 30 statistical coastal areas (STATs), and 147 coastal subareas (Hay and Kronlund, 1987; Haist and Rosenfeld, 1988) Among the 147 subareas, only 101 have a history of spawning within their boundaries. These 101 sections (SECs) are further subdivided into section pools (SEPLs; Figure 2) that represent clusters of spawning sites that share similar physical attributes, especially with regard to spawn width. In all, 282 distinct SEPLs have been defined in BC waters (Hay and McCarter, 2008).

The coastal features of spawning areas vary considerably throughout the area, and the estimates of spawn width vary as a function of the subsurface slope of the shoreline (Haegele *et al.*, 1981). For quantifying local herring spawn, we developed a
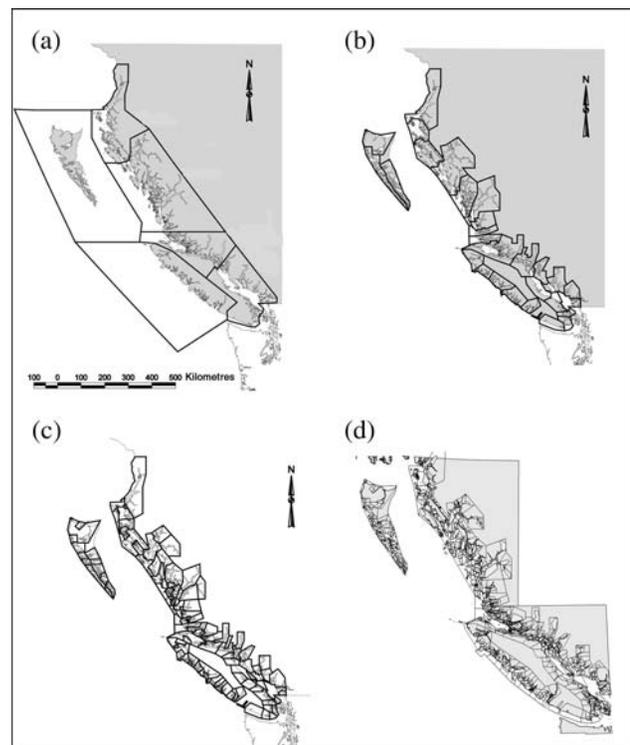
spawn index that uses detailed area-specific deposition coefficients based on observed measurements of spawn width and egg intensity at each SEPL (Hay and Kronlund, 1987; Hay and McCarter, 2008). The boundary lines for the entire nested geographical system (REGs, STATs, SECs, and SEPLs) were superimposed on digitized bathymetry charts to classify and quantify all subtidal habitats by depth strata (0–200 m) using geographic information software (Arcview©). Within these strata, the potential spawning habitat was defined as the spatial area between the 0 and 10 m depth contours. The total surface area (m^2) of each SEPL was estimated as the area between mean low tide (depth = 0 m) and a maximum depth of 10 m, using the following projection: Albers equal area conic; GRS80 spheroid; central meridian, 126°W; ref. latitude, 45°N; std parallel 1, 50°N, std parallel 2, 58.5°N; false easting, 1 000 000; and false northing, 0. Although herring spawn has been recorded at greater depths (especially on the west coast of Vancouver Island), such instances are infrequent and should have little impact on the estimates of suitable areas. Many nautical coastal charts lack adequate spatial resolution to delineate and measure the available spawning habitat within each KSEG, so this was not done.

SSB estimates were cited from the most recent annual assessment (Schweigert and Haist, 2008) presented to the Pacific Scientific Advice Review Committee (PSARC).

Results
Potential and utilized spawning habitat
The total area of the BC coastal waters, from 0 to 200 m shelf edge, is ~37 300 km^2. This estimate is slightly conservative because a few coastal areas lack bathymetric data and could not be included in the analysis. Table 1 shows the estimated mean

Table 1. Mean, s.e., and total potential spawning habitat (km²) for five different spatial units (*n*, number of units).

Spatial unit	*n*	Mean	s.e.	Total
REG	6	518.6	96.6	3 111
STAT	30	103.7	16.9	3 111
SEC	103	30.2	3.2	3 111
SEPL	375	8.3	0.8	3 112
KSEG	5 574	–	–	–

The estimated spatial areas within REGs, STATs, SECs, and SEPLs are shown as the sum of potential spawning habitat within the 1–10 m depth range, estimated from digitized bathymetric nautical charts. Estimated spawning areas within the KSEG units were not assessed.

and total area (km²) between 1 and 10 m depth for the four spatial units REG, STAT, SEC, and SEPL. The theoretical maximum spawning area, between 1 and 10 m depth, is 3111 km².

The potential width of spawning areas varies as a function of the slope (Haegele *et al.*, 1981). For all spawn records, the estimated mean spawn width is 34.7 m. If all habitat between 0 and 10 m depth for each of the 5574 KSEGs was suitable for spawning, then the total aggregated spawning habitat can be estimated as the product of the mean spawn width (34.7 m) and the number of KSEGs (5574) for an aggregated area of ~193 km². This estimate, which represents the area of all habitat ever used by herring in BC since 1928, is probably an overestimate because many spawning events do not occupy the entire length of the individual 1-km segments. For instance, within most KSEGs, there are areas without suitable spawning macrophytes, and macrophytes rarely cover all bottom areas of any KSEG. The main conclusion is that the cumulative area of coastal territory ever used for spawning may range up to a theoretical maximum of 193 km², which is much less than the 3111 km² available in the preferred 1–10 m depth stratum.

In any single year, the total cumulative area used for spawning ranges from ~5 to almost 30 km² (Figure 3). In this case, the area covered is estimated as the sum of products of the observed spawn length (not the sum of the KSEGs) and the mean spawn width (Hay and Kronlund, 1987; Hay and McCarter, 2008). The important observation is that, in any single year, there is a much greater potential spawning area than herring can utilize effectively. As an approximation, herring utilize a total area that ranges between 0.2 and 1.0% of the available area in the 0–10 m depth stratum, or from 10 to 20% of the aggregated spawning habitat defined as the 193 km² that has ever supported herring spawn.
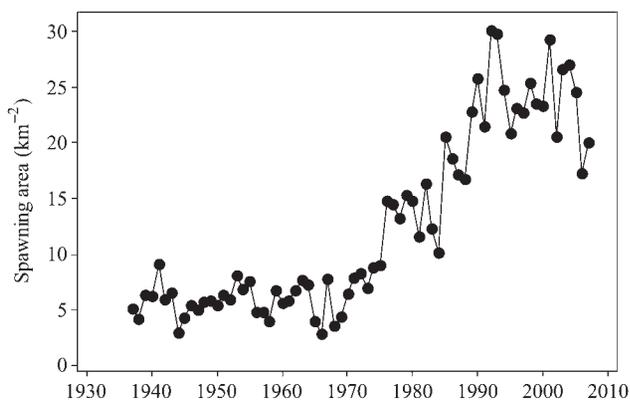
Figure 3. Estimated cumulative annual spawning area (km²) on the BC coast based on records by KSEG, 1938–2007.

Frequency of spawning and spatial diversity

The estimated frequency of spawning increases with the size of the spatial unit utilized to assess spawn (Figure 4). Figure 5a shows variation in the temporal pattern in spatial diversity for the entire BC coast. The trend lines show that from 1965 to 1985, the numbers of KSEGs where spawning events were recorded
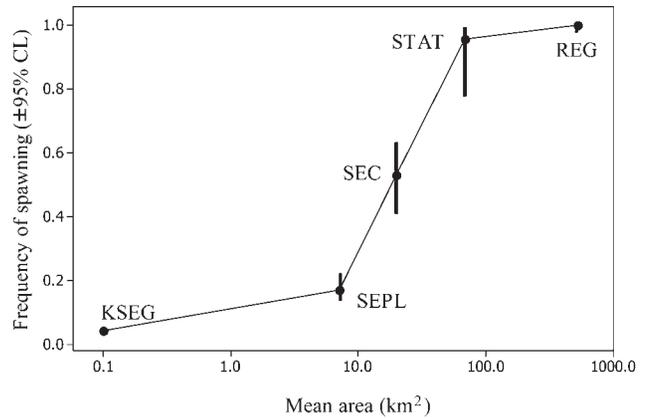
Figure 4. Frequency of spawning from 1938 to 2008 plotted against mean area (km²) of spatial units (SEPL, SEC, STAT, and REG); the short vertical lines show the 95% confidence limits (CL) about the median frequency.
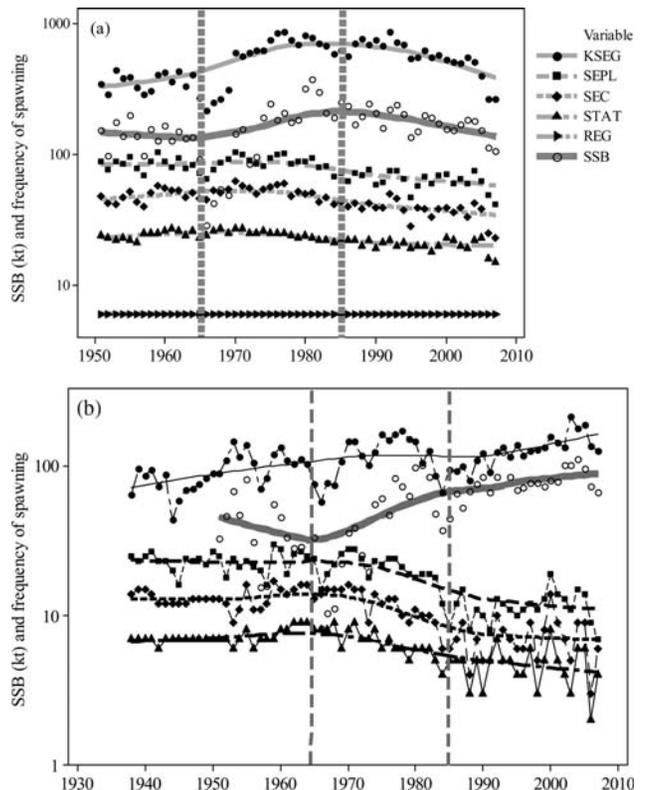
Figure 5. Annual variation (individual data points and Lowess-smoothed line) in frequency of spawning by spatial unit (KSEG, SEPL, SEC, and STAT) and in SSB (kt) for: (a) the entire BC coast, 1951–2007; and (b) the SOG, 1938–2007. The dashed vertical lines indicate approximate periods of change in SSB.

Table 2. Correlation coefficient matrix between the annual SSB and the numbers of spatial units (KSEG, SEPL, SEC, STAT, and REG) used as a measure of the spatial diversity of spawning, based on a 57-year time-series.

Spatial unit	SSB	KSEG	SEPL	SEC	STAT
KSEG	0.73*	−	−	−	−
SEPL	0.11	0.16	−	−	−
SEC	0.00	0.15	0.92*	−	−
STAT	− 0.21	− 0.09	0.78*	0.88*	−
REG	0.03	0.14	− 0.10	− 0.04	− 0.64

*$p < 0.001$.

increased, whereas the corresponding numbers of larger spatial units (STATs, SECs, and SEPLs) were stable initially and then decreased in more recent years. At the REG level, there was no trend at all: spawn occurred in all REGs in all years at approximately equal frequency.

In recent years, the temporal frequency of spawning has decreased in all spatial units (except REGs), indicating a decrease in spatial diversity. The SSB is positively correlated with KSEGs (Table 2) and is highly significant, but this is not the case for larger spatial units (SEPLs, SECs, STATs, and REGs). The negative correlation between SSB and STAT (Table 2) probably has no biological meaning, but it further illustrates the lack of correlation between spatial diversity and SSB. KSEGs are not significantly correlated with any of the larger spatial units.

These varying patterns of spatial diversity among spatial units are more clearly seen when the analyses are confined to the STATs representing the Strait of Georgia (SOG; Figure 5b). In this case, the trends at the KSEG level track the SSB more closely than for the whole BC coast, and trend lines plotted on both graphs deviate sharply from those observed for STAT, SEC, or SEPL.

Discussion
Size of spatial units and probability of spawning
The estimated frequency of spawning depends on the size of the area used to estimate probability (Figure 4). Our analyses indicate that the smallest geographic units (KSEGs) show different temporal trends from the larger spatial units (STATs, SECs, and SEPLs). In the SOG, spatial diversity of STATs, SECs, and SEPLs decreased, but the number of KSEGs increased. One explanation is that if spawning is concentrated in some areas, such as the northwest portions of the SOG, then the total amount of spawn in such areas may increase. This would lead to an increase in the number of KSEGs in the SOG, but not necessarily in the numbers of larger spatial units. Therefore, the effect of an increase in SSB could be an increase in the number of KSEGs that are concentrated in large spawning sites (i.e. longer cumulative spawn length), but not necessarily an increase in the number of larger spatial units (STATs, SECs, and SEPLs). At most, a very large SSB might result in long spawn lengths that might overlap between several SEPLs, two SECs, and sometimes even two STATs, if the spawning activity were close to the boundary between two STATs.

The implications of this are as follows: if spatial diversity is assessed as a proxy or corroborative measure of SSB, then small spatial scales (i.e. KSEGs) may be appropriate. Alternately, if spatial diversity of spawning is assessed to examine the geographic spread of spawning, then larger spatial scales (REGs, STATs, SECs,

and SEPLs) would be the most suitable. It could be misleading, however, to assume that a decline in spatial diversity, when assessed with large spatial units, is necessarily indicative of a decline in SSB.

The important observation from our analyses is that for Pacific herring, a low SSB is not necessarily related to a reduction in spatial diversity. Even during the population crash of the 1960s (Hourston, 1980), which followed several decades of intensive fishing, there was a relatively high spatial diversity of spawn, although the total estimated indices of spawn and SSB were low: in effect, a smaller amount of spawn was widely spread out.

A different concern about the loss of spatial diversity is that it may reflect a reduction in the number of reproductively isolated populations or distinct population segments. Such concerns make implicit assumptions that there is a degree of natal spawning/homing, so that the loss of spawning sites is related to the loss of unique stocks. In general, recent genetic studies of Pacific herring (Beacham *et al.*, 2001; Gustafson *et al.*, 2006) do not support this contention. Most Pacific herring populations appear to have little unique genetic variation, and tagging studies (Hay *et al.*, 2001) support the hypothesis of extensive genetic mixing, especially within each of the six BC REGs. There are, however, some small genetically distinct populations that are usually confined to local, isolated locations (Beacham *et al.*, 2001; Gustafson *et al.*, 2006). Such populations deserve special protection and are not subjected to commercial fisheries in BC.

Natural vs. fishery-induced changes in spawning distribution
There are significant management implications to changes in spawning distribution. The apparent cessation of spawning in some locations has led many observers to speculate that the cause is low SSB, and this in turn has led to concerns that the herring roe fishery has caused the serial depletion of local spawning populations. Hay *et al.* (2008) examined this issue by comparing geo-referenced fishing-location data with geo-referenced spawn data. In a detailed review of the spatial patterns of roe-herring fishing conducted since 1970, there was no evidence that the present roe fishery has led to local depletions of spawn, although it is clear that spawn abundance fluctuates widely in some areas. In most spatial areas (STATs, SECs, and SEPLs) where spawning activity ceased, there was no preceding fishery. In contrast, spawning appeared to increase in the STATs and SECs where fisheries occurred. Clearly, the fishery did not promote more spawning in certain areas; it was rather that the fishery was usually limited to very restricted areas of the coast, which tended to be in the areas where most spawning occurred. Therefore, it was the distribution of spawning that determined the location of the fishery, and not vice versa.

Spawn abundances (or SSBs) and spawning distributions change naturally, so it is probable that some observers of the herring fishery will, in the absence of other simple explanations, continue to hold the fishery responsible for such changes in spawn distribution. There are, however, other explanations, including instances of intense predation in specific locations by predators such as seabirds (Haegele, 1993a; Bishop and Green, 2001) and epibenthic predators, especially crabs (Haegele, 1993b).

Systematic changes in spawn distribution have been noted previously in BC (Hay and McCarter, 1997, 1999a, b). Changes in spawn distribution have also been described elsewhere in the eastern Pacific, including Washington State (Gustafson *et al.*,

2006), Alaska (Brown and Norcross, 2001), and California (Spratt, 1981). In other herring populations, changes in spawning locations have been related to changes in trophic conditions and feeding, as in the Baltic (Rajasilta et al., 1993) and the Norwegian Sea (Slotte, 1999). In the Sea of Okhotsk, spawning locations may change with ice conditions (Tyurnin, 1973). In most cases of changes in spawning distribution in other herring populations, such as those in Atlantic herring, the geographic range of the changes is considerably greater than many of the relatively fine-scale changes that occur in BC, where shifts, sometimes by only a few kilometres, can be interpreted by some observers as examples of depletion. In contrast, changes of spawning sites in the North Atlantic have been documented as occurring over hundreds and even thousands of kilometres (Hay et al., 2001). We do not have fully satisfactory explanations for the relatively small-scale changes in spawn distribution observed in BC, but we can tentatively conclude that such changes are not necessarily indicative of changes in SSB.

Acknowledgements

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