Measuring and modelling Pacific herring spawning-site fidelity and dispersal using tag-recovery dispersal curves

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Flostrand, L. A., Schweigert, J. F., Daniel, K. S., and Cleary, J. S. 2009. Measuring and modelling Pacific herring spawning-site fidelity and dispersal using tag-recovery dispersal curves. – ICES Journal of Marine Science, 66: 1754–1761.

An approach of relating Pacific herring (*Clupea pallasi*) tag-recovery data to dispersal distances is presented. Observations from coded wire tag sampling (1999–2006) were used to represent adult herring interannual spawning patterns on the British Columbia coast. Six datasets were applied, differing by number of years-at-liberty (1, 2, or 3) and gear type of recapture (purse-seine or gillnet). In total, 227 tag-recovery samples, consisting of 5687 tag recoveries, were used. Distances were approximated to the shortest paths through water between the release and recapture sites. Recovery rate and distance relationships suggest that exponential models fit the data reasonably well, with average rates of change in recovery rates (slopes) varying from approximately −0.009 to −0.005. A combined slope estimate of −0.007 is similar to four of the six estimates. Using these models, the intensity of movement among five stock-assessment regions was estimated by applying distances relative to their centres. Fidelity estimates range from 53 to 90% across all models and regions, which is consistent with previous findings and premises that influence resource management. Interpretation and application of the modelling exercise are discussed in terms of previous and future work.

Keywords: coded wire tag, dispersal distances, modelling, spawning-site fidelity, tag recovery.

Received 29 September 2008; accepted 14 March 2009; advance access publication 4 June 2009.

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Introduction

Observing and modelling movement patterns of a fish population may enhance stock assessment by permittting a better understanding of its population dynamics. Dispersal among populations is important because it contributes to colonization of vacant habitat and to gene flow, and therefore may increase overall species resilience. Tag-recovery studies on spawning populations of Atlantic herring (*Clupea harengus*) and Pacific herring (*Clupea pallasi*) have shown not only relatively high rates of interannual site fidelity but also dispersal tendencies that link spatially separated populations (Hourston, 1982; Wheeler and Winters, 1984; Schwarz *et al.*, 1993; Schweigert and Schwarz, 1993; Hay *et al.*, 2001). Because management decisions for Pacific herring fisheries have been based on the assumption of high spawning-site fidelity, there is merit in investigating whether high rates remain constant over time. Three tag-recovery studies on Pacific herring have been carried out in British Columbia (BC). Although they differ in experimental design, spatial resolution, and recovery methodology (Daniel *et al.*, 1999; Flostrand *et al.*, 2007), all datasets are amenable to investigating spawning-site fidelity and dispersal. The first study (1936–1967) employed internal belly tags, the second (1979–1992) external anchor tags, and the third (1999–2006) internal coded wire tags (CWTs). Here, we focus on the results from the CWT data.

The management and assessment of BC herring currently assumes that the resource is concentrated in five distinct stock-assessment regions (SARs), which collectively account for most of the spawning on the coast (Schweigert and Haist, 2007). These include: Queen Charlotte Islands (QCI), Prince Rupert District (PRD), Central Coast (CC), Strait of Georgia (SOG), and the west coast of Vancouver Island (WCVI). Smaller spatial units, known as statistical areas, have also been established for fishery management to delineate spawning sites (Figure 1). Information from annual stock assessments is used to set annual catch quotas for roe-herring fisheries, which generally occur in one or two of the statistical areas within a SAR. Among SARs, the exchange of individuals and the net movement from immigration and emigration is assumed to be negligible. These assumptions are associated with the estimates of average fidelity from belly- and anchor-tag-recovery data, which range from 54 to 97% for SARs and from 6 to 91% for statistical areas (Stevenson, 1954; Hourston, 1982; Ware *et al.*, 2000; Hay *et al.*, 2001).

Dispersal can be modelled either as a set of rates between discrete spatial strata or as a frequency "distribution of dispersal distances" (DDD) in a continuous space. The first approach has frequently been applied to tag-recovery data from herring and other pelagic fish (Hilborn, 1990; Schwarz and Arnason, 1990; Deriso *et al.*, 1991; Schweigert and Schwarz, 1993; Schwarz *et al.*, 1993; Hay *et al.*, 2001; McGarvey and Feenstra, 2002). However, the CWT-recovery data for Pacific herring are not particularly amenable to this type of modelling because sampling for release and recapture was patchy and irregular in terms of representing the different strata. Observations for DDD modelling do not need to be from a consistent set of locations but may come from a variety of distances over a variety of sources (Bullock and Clarke, 2000; Paradis *et al.*, 2002; Paris *et al.*, 2007). Ware *et al.* (2000) modelled interannual dispersal

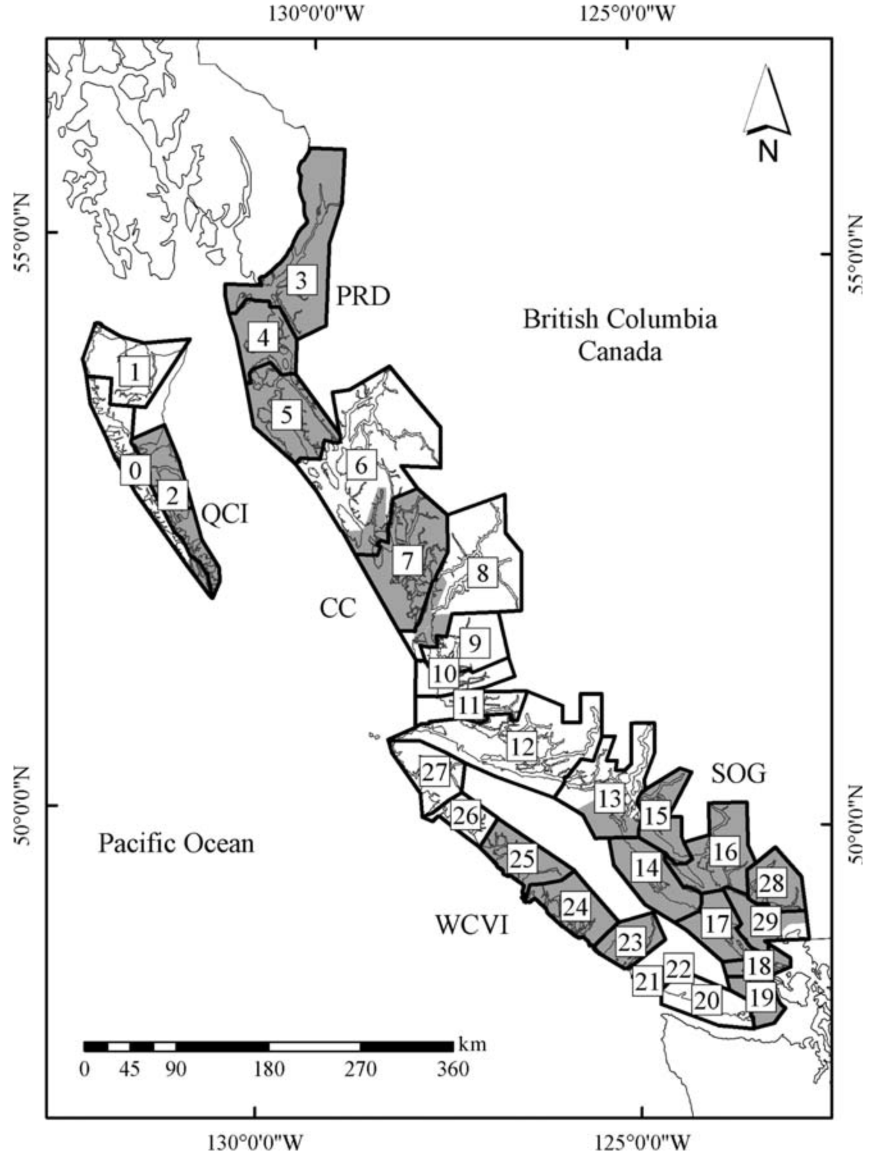

Figure 1. Fisheries and Oceans Canada SARs, as defined for Pacific herring (shaded) and for statistical areas associated with spawning and fishing off the coast of British Columbia (numbered 0–29). QCI, Queen Charlotte Islands; PRD, Prince Rupert District; CC, Central Coast; SOG, Strait of Georgia; WCVI, west coast of Vancouver Island.

of Pacific herring in the context of DDD by relating estimates of among-SAR dispersal rates from anchor tag data to approximate distances between release and recapture locations. Our main objective was to investigate the application of CWT-recovery data to DDD models. Tag-recovery data were grouped by gear type (purse-seine or gillnet) and years-at-liberty (1, 2, or 3), and adjusted by tag-release and catch-sampling intensities to compute recovery rates representing proportions of tag releases recovered per unit of catch searched. We fitted negative exponential DDD models to the datasets and discuss their application and interpretation in terms of previous and future work.

Methods

Tag release and recovery sampling

Using products from Northwest Marine Technology Inc., herring were tagged using Mark IV Automatic Coded Wire Tag Injectors, and catch sampling for recoveries was done using three R-9500 Rectangular Tunnel Detectors. Information on sampling methods and resulting datasets is given by Flostrand *et al.* (2007). In brief, tag and release sampling of sexually mature herring caught by purse-seine at or near spawning grounds was carried out from 1999 to 2004 during 2-month periods, starting in mid-February and ending in mid-April. In total, more than 1.3 million tagged fish were released throughout the coastal waters during 32 sampling events. The number of fish tagged by year and statistical area fluctuated widely, ranging from ~6000 to more than 180 000 fish (Table 1). Most herring tagged were 3 or 4 years of age, as determined through biological sampling.

Tag-recovery sampling was carried out at three fish-processing plants that received catches from purse-seine and gillnet roe-herring fisheries during the years 2000–2006. Spatial resolution of tag recoveries was based on the statistical areas in which the catches were taken. Here, the term “fishery” is used to identify a

Table 1. Number of herring released with CWTs by SAR, statistical area (sa), and year (for SAR codes, see Figure 1).

		Year					
SAR	**sa**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**
QCI	2	6 175	–	–	–	–	–
PRD	3	–	–	–	–	15 066	–
	4	–	–	65 809	48 960		–
	5	–	–	22 387	25 701	96 434	–
	5WI[a]	–	–	–	11 081	–	–
CC	6	–	–	–	18 168	–	52 049
	7	–	–	–	31 027	79 920	107 843
	8	–	–	–	9 463	27 453	44 614
	9[b]	–	–	–	–	13 660	17 770
SOG	14	23 187	180 229	60 558	83 528	89 247	–
	16	–	–	–	–	6 643	–
	14,17	5 815	6 471	–	–	–	–
	17	14 266	58 994	–	–	–	–
WCVI	23	–	–	–	–	–	33 608
	25	–	–	–	–	–	32 421
	25	–	–	–	–	–	38 601
	26[b]	–	–	–	–	–	27 181
Total	–	49 443	245 694	148 754	227 928	328 423	1 354 329

[a] 5WI refers to a remote location called Wilson Inlet, 70 km from where the other fish in statistical area 5 were tagged.
[b] Statistical areas near, but not within, a SAR.

Table 2. Estimates of catch (in tonnes) sampled for CWT recovery by gear, SAR, statistical area (sa), and year (for SAR codes, see Figure 1).

			Year						
Gear	**SAR**	**sa**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**
Purse-seine	QCI	2	136	–	99	–	–	–	–
	RD	5	152	72	207	192	132	347	246
	CC	6, 7	–	–	949	–	–	–	–
		7	1 713	2 202	–	1 123	1 181	1 072	607
	SOG	14	1 677	2 038	3 304	2 467	–	1 936	3 020
		17	–	–	–	–	1 446	–	–
	WCVI	23	–	–	–	961	–	–	–
		23, 24	246	–	–	–	–	–	–
		25	–	–	171	–	1 612	1 262	–
Gillnet	QCI	2	–	–	–	–	–	–	–
	PRD	3, 4	208	–	–	–	–	–	–
		4	–	206	897	344	441	499	264
	CC	6	–	–	–	62	–	–	–
		6, 7	–	–	69	–	–	–	–
		7	242	179	–	–	–	–	–
	SOG	14	1 249	2 151	–	–	–	2 058	–
		14, 17	–	–	2 722	1 854	1 210	–	1 934
	WCVI	25	57	–	41	40	84	274	–
Total	–	–	5 680	6 848	8 459	7 043	6 106	7 448	6 071

fishing activity that took place in a given year, at a particular location, and using one gear type (either purse-seine or gillnet). Samples of catch from 28 purse-seine fisheries and 23 gillnet fisheries were searched to recover tags. Quantities of catch searched were estimated by technicians while overseeing sample collection. Estimates varied by year, area, and gear type from 40 to 3304 t, largely reflecting the size of the fishery (Table 2).

Tag-recovery rates

Each sample of tag recoveries that could be spatially and temporally differentiated by its release and recapture sites was considered to be a unique "tag-recovery group" (TRG). We limited our analyses to include only TRGs with 1–3 years-at-liberty and with sample sizes >0, for a total of 227 TRGs representing 5687 tag recoveries.

A tag-recovery rate (v), defined as the fraction of releases recovered per tonne of catch searched, was derived for each TRG by scaling the number of fish in the TRG (U) by both the number of fish in the corresponding release sample (T; Table 1) and the size of the catch sample that it came from (C in tonnes; Table 2):

$$v = \frac{U}{(TC)}.$$

Modelling of DDD

Distances were represented as the shortest routes through water between the approximate centres of the statistical areas of release and recapture, consistent with the methods of Ware *et al.* (2000). A distance of 0 km was used to represent area fidelity, and distances representing area dispersal were derived using Nobeltec Visual Navigation Suite^{TM}. If the spatial resolution of a release or recapture location included two statistical areas, then an approximate centre of the combined areas was used as an endpoint.

The six sets of recovery rate and dispersal distance data, as determined by years-at-liberty (1, 2, or 3) and recapture gear (purse-seine or gillnet), were analysed separately and collectively as a combined dataset (with 227 TRGs). In the context of DDD modelling, recovery rates are treated as frequencies, and plotting them against dispersal distances provides guidance on the shape of the distribution to be considered in the analysis (Paradis *et al.*, 2002). Because negative exponential functions fit the data reasonably well ($r^2 = 0.45-0.67$), tag-recovery rates were log-transformed, and linear modelling was applied to estimate the average rates of change in recovery rate associated with changes in distance (slopes) and the average recovery rates representing fidelity (intercepts). Paradis *et al.* (2002) note that a probability function appropriately describes a DDD because such a function sums to 1 when integrated over space. Therefore, it is possible to compute a set of proportional probabilities for a given set of distances from a DDD-density function. A DDD-modelling approach was used to estimate interannual spawning-site fidelity and dispersal among SARs (Table 3) by assuming that (i) 100% of the herring on the coast spawn in the five SARs, (ii) distance is a determining factor, and (iii) a set of distances representing their degree of separation effectively represents their spatial linkages. The set of distances applied to the modelling was taken from Ware and Schweigert (2001), who used dispersal distances ranging from 197 to 776 km, and median and average distances from SARs ranging from 202 km (QCI) to 447 km (WCVI) and 323 km (QCI) to 421 km (SOG), respectively (Table 3). In association with this set of distances, the model fit to the combined CWT dataset was the DDD-density function used to compute proportional probabilities related to SAR fidelity and dispersal. To assist in explaining how sets of fidelity and dispersal rates were computed, Table 3 also shows sets of the average recovery rates that are required as an intermediate step for calculating fidelity and dispersal rates from each source. Standard errors were not computed because the estimates serve mainly to illustrate model behaviour.

Results

Figure 2 shows the observed and modelled log-transformed recovery rates as a function of dispersal distance by years-at-liberty and gear type. Information for the six datasets is summarized in Table 4, and Figure 3 illustrates trends between the slope and intercept estimates. Slope estimates for purse-seine models suggest a slight increase (decrease in steepness) as years-at-liberty increase, but the differences are not significant. For gillnet models, slopes are not significantly different from the purse-seine data, except for 3 years-at-liberty, where the slope is somewhat higher than other estimates. The estimated slope for the combined model is -0.0074 (s.e. $= 0.0004$, $p < 0.001$), which closely matches four of the six individual estimates, and which diverges most from the purse-seine model estimate for 1 year-at-liberty and the gillnet model estimate for 3 years-at-liberty. Intercept estimates for purse-seine models sequentially decrease as years-at-liberty increase, whereas estimates for gillnet models are not significantly different from each other and show a maximum at 2 years-at-liberty. Between gear types and years-at-liberty, intercepts are only significantly different for 1 year-at-liberty. The estimated intercept for the combined model is -14.14 (s.e. $= 0.12$), which is

Table 3. Information on approximate distances between SARs, estimated average recovery rates, and estimated average rates of interannual SAR fidelity/inter-SAR dispersal (error not accounted for), based on the combined log-transformed negative exponential model (slope= -0.0074, intercept= -14; for SAR codes, see Figure 1).

	Receiving SAR					D		
Source SAR	**QCI**	**PRD**	**CC**	**SOG**	**WCVI**	**Median**	**Average**	**Sum**
Distance (km)								
QCI	0	197	202	622	596	202	323	–
PRD	197	0	303	776	713	303	398	–
CC	202	303	0	434	447	303	277	–
SOG	622	776	434	0	274	434	421	–
WCVI	596	713	447	274	0	447	406	–
Recovery rate ($\times 10^8$)								
QCI	72.29	16.83	16.21	0.72	0.88	–	–	106.93
PRD	16.83	72.29	7.68	0.23	0.37	–	–	97.40
CC	16.21	7.68	72.29	2.91	2.65	–	–	101.74
SOG	0.72	0.23	2.91	72.29	9.52	–	–	85.68
WCVI	0.88	0.37	2.65	9.52	72.29	–	–	85.70
Fidelity (emboldened) or dispersal (%)								
QCI	**67.6**	15.7	15.2	0.7	0.8	–	–	–
PRD	17.3	**74.2**	7.9	0.2	0.4	–	–	–
CC	15.9	7.5	**71.1**	2.9	2.4	–	–	–
SOG	0.8	0.3	3.4	**84.4**	11.1	–	–	–
WVCI	1.0	0.4	3.1	11.1	**84.4**	–	–	–
Average fidelity across SARs								**76.3**

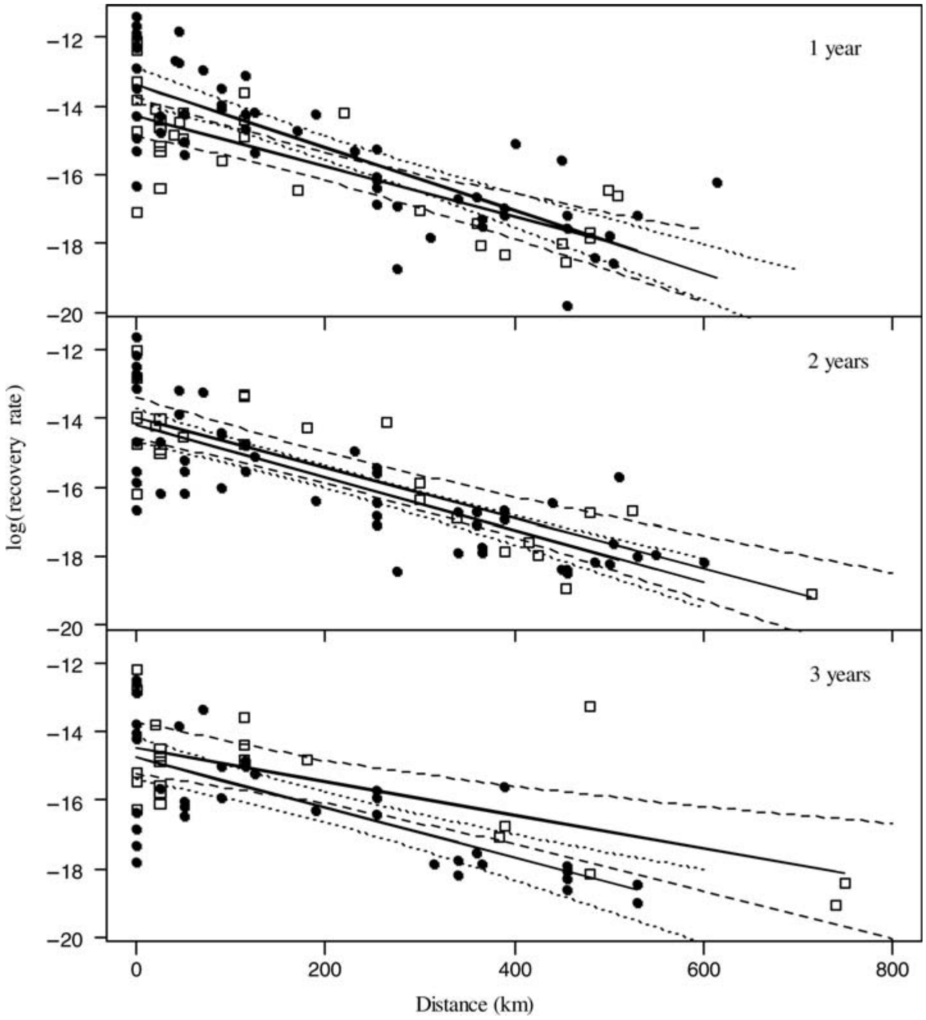

Figure 2. Observed and modelled log-transformed CWT-recovery rates plotted against dispersal distances by years-at-liberty (1–3, top to bottom) and gear type. Filled circles and open squares, observed purse-seine and gillnet tag-recovery rates, respectively; dotted lines and dashed lines, 95% confidence intervals of purse-seine and gillnet models, respectively.

only significantly different from the purse-seine model estimates for 1 and 3 years-at-liberty. Tables 3 and 4 summarize the estimated average rates of interannual fidelity and dispersal and show the ranges in SAR fidelity (expressed in %) across all models to be 53–75 (QCI), 60–81 (PRD), 54–79 (CC), and 68–90 (both SOG and WCVI), and the estimates of SAR fidelity from the combined model to be 68 (QCI), 74 (PRD), 71 (CC), 84 (SOG), and 84 (WCVI), with an overall average of 76.

Discussion

Recovery rate vs. distance relationships indicate declining dispersal with distance from a source, which is consistent with earlier conclusions (Stevenson, 1954; Taylor, 1964; Ware *et al.*, 2000). The similarity between the slope estimates across different years-at-liberty is remarkable, because it suggests that fidelity is fairly stable between consecutive years when herring survive to spawn again. We favour the slope estimates from purse-seine models over those from gillnet models because they are based on better geographic representation (five more recapture locations) and on larger sample sizes with lower s.e. (Tables 2 and 4). The increasing trend in slope values from 1 to 3 years-at-liberty suggests that fidelity may decrease with age, but observed differences are not significant (Figure 3, Table 4). The consistency in the slope estimates is reassuring because it suggests that modelling of DDD with CWT-recovery data yields robust results. Based on the simplified spatial representation of the composition of the spawning stock of Pacific herring among the five SARs, the models collectively predict a range in interannual spawning-site fidelity of 53–90%, entirely consistent with previous findings (Stevenson, 1954; Hourston, 1982; Ware *et al.*, 2000; Hay *et al.*, 2001; Ware and Schweigert, 2001) that have influenced the management of the resource for decades.

The variability in intercept values for the different models is of some interest. Purse-seine models indicate a significant decrease in intercepts as years-at-liberty increase, whereas the gillnet models do not. We suggest that the differences are related to the size selectivity of gillnet fishing gear, which would be expected to affect the scale of the recovery rates but not necessarily the DDD trends among them.

When comparing different slopes among datasets, a steeper negative slope would signify a lower rate of dispersal and a higher rate of fidelity (all else being equal). Ware *et al.* (2000)

Table 4. Parameter estimates for DDD modelling by gear type (purse-seine or gillnet) and years-at-liberty (1–3): *m*, total number of tagged fish recovered; average, median, and range in distributions of: *U*, recoveries per TRG, *v*, tag-recovery rate, and *D*, distance (in km); estimated be^{aD} relationship r^2 ($p < 0.001$ always) and degrees of freedom (d.f. = number of TRGs − 2); *a*, slope with s.e.; ln(*b*), intercept with s.e.; *F* (%), estimated rate of interannual spawning-site fidelity by SAR (for SAR codes, see Figure 1).

Parameter	**Purse-seine**			**Gillnet**		
Years-at-liberty	**1**	**2**	**3**	**1**	**2**	**3**
m	2 614	1 076	305	638	620	434
U						
Average/median (range)	46/5 (1–817)	21/4 (1–175)	8/3 (1–62)	20/5 (1–155)	23/7 (1–145)	20/8 (1–119)
v ($\times 10^{-6}$)						
Average/median (range)	1.32/0.25 (<0.01–11.35)	0.69/0.10 (<0.01–8.80)	0.47/0.09 (<0.01–3.70)	0.63/0.29 (<0.01–5.33)	0.69/0.34 (<0.01–5.92)	0.69/0.30 (<0.01–4.87)
D						
Average/median (range)	199/125 (0–615)	220/210 (0–600)	183/115 (0–530)	170/70 (0–510)	197/115 (0–715)	178/25 (0–750)
be^{aD}						
r^2 (d.f.)	0.64 (55)	0.63 (50)	0.52 (35)	0.60 (30)	0.67 (25)	0.45 (20)
a ($\times 10^{-4}$)						
Average (± s.e.)	−91 (±9)	−77 (±8)	−72 (±12)	−73 (±11)	−73 (±10)	−49 (±12)
ln(*b*)						
Average (± s.e.)	−13.40 (±0.25)	−14.19 (±0.24)	−14.78 (±0.30)	−14.30 (±0.27)	-13.99 (±0.29)	−14.49 (±0.36)
F						
QCI	75	69	67	67	66	53
PRD	81	75	73	74	73	60
CC	79	72	70	70	70	54
SOG	90	85	83	84	83	68
WCVI	90	85	83	84	83	68

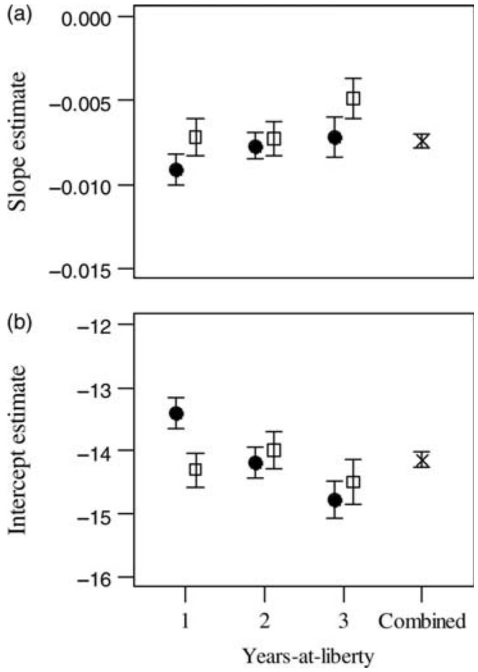

Figure 3. Estimates ($\pm$ s.e.) of (a) slope, and (b) intercept for purse-seine (filled circles) and gillnet (open squares) models by number of years-at-liberty and for the combined model (crosses) of log-transformed CWT-recovery rates vs. dispersal distances.

obtained a slope of -0.003 from a DDD model fitted to estimates of dispersal rates derived from 1 year-at-liberty anchor tag recaptures combined over the two gear types. Estimates of fidelity rate generated using a slope of -0.003 with the current modelling steps and inter-SAR distances ranged from 40 to 51%, whereas estimates generated using a slope of -0.009 from CWT purse-seine data for 1 year-at-liberty ranged from 75 to 90%. As the model reported by Ware *et al.* (2000) is based on just 20 data points representing 21 release samples and 310 tag recoveries, we surmise that the quality of the CWT-recovery data used here for DDD modelling offers more meaningful descriptions of dispersal parameters.

We have assumed that tagged fish mix evenly with non-tagged fish after release and that all processes other than movement affect all groups equally. Both assumptions greatly simplify modelling and are therefore commonly made in movement studies. However, evidence of non-random mixing of Pacific herring (based on observations on associations in fish schools) has been reported (Hay and McKinnell, 2002), and other processes (e.g. survival, tag loss, tag detection) may add considerable variability to recovery rates. We have also assumed that pooling data across sampling years and sampling sources randomly distributes extraneous sources of variability across each dataset, thereby limiting bias of parameter estimates.

Deductions from observations associated with either low sampling intensity or low movement intensity will be less accurate, less precise, and more prone to underestimating dispersal (Xiao, 1996; Bullock and Clarke, 2000). From Tables 1 and 2, it is clear that many combinations of the release and recapture samples might lead to small TRG sample sizes and thus to underestimation of movement intensity. In fact, of the 227 TRGs, 150 were characterized by sample sizes $\leq$10, and 58 TRGs had a sample size of 1. Furthermore, we excluded observations of zero tag recoveries, and their incorporation would have affected the resulting distributions and parameter estimates. However, this requires fitting different models and is left for future work.

Setting the number of SAR spawning sites and the relative distances between them to constants has been an oversimplification. Our estimates indicate that, because the QCI, CC and PRD are each relatively nearer other SARs, compared with the SOG and WCVI, herring from these three SARs have less site fidelity (Table 3). In contrast, previous studies have shown no evidence that northern stocks consistently have less fidelity than southern ones (Stevenson, 1954; Hourston, 1982; Ware *et al.*, 2000; Hay *et al.*, 2001). Alternative approaches to estimating fidelity and dispersal patterns could be adopted that represent a larger number of spawning locations and use different sets of distances between them, which might easily result in quite different trends in dispersal among SARs. A feature of the modelling approach is that, as more distances from each source are represented (e.g. by a decreasing spatial scale), all movement rates decrease accordingly. This feature is consistent with the trend in declining spawning-site fidelity with decreasing spatial scale reported by Hourston (1982) and Hay *et al.* (2001).

During the 20th century, the spatial distribution of the spawning sites and spawning population abundance of Pacific herring varied considerably (Schweigert and Haist, 2007; Hay *et al.*, 2007). The metapopulation concept of McQuinn (1997) is an attempt to explain changes in Atlantic herring spawning-site fidelity and dispersal patterns as behavioural responses to environmental conditions and social interactions of schooling fish. His description emphasizes that schools of repeat spawners may adopt strays from other spawning grounds, as well as virgin fish from nearby populations. His basic assumption is that herring represent a metapopulation consisting of components that vary in the extent of mixing. For our parameter estimates, CWT-recovery data were pooled across sampling events over several years, on the premise that herring belonging to one metapopulation were collectively sampled and that resulting dispersal curves measure the overall degree of the linkages among the different components. Further tests of the predictive power of the CWT modelling could be performed by examining annual spawning patterns over the CWT-sampling years and by examining outliers shown in Figure 2. It might be useful to fit similar models to the belly- and anchor-tagging recovery data collected earlier to compare resulting slopes. This should be relatively easy to do using either raw recovery rates or rates adjusted for catch sampling and by approximating distances to the best resolution possible. It would also be useful to fit models to tag-recovery data from individual SARs. The slope estimates obtained from dispersal-curve models may be incorporated into modelling biomass dynamics of metapopulations to characterize dispersal as well as colonization probabilities and to differentiate between emigration and natural mortality.

Acknowledgements

This work was funded by the Herring Conservation and Research Society in conjunction with Fisheries and Oceans Canada. We thank Streamline Consulting Services and J. O. Thomas and Associates for technical support in tag release and recovery sampling, respectively, crew members who assisted directly or indirectly in catch and release fieldwork on board the RV “Walker Rock”, FV “Lahaina Joye”, FV “Bernice C”, FV “Royal Mariner”, FV “Ocean Venture”, FV “My Lady Jane”, and FV

"Ocean Marauder", and fish-plant staff at Canadian Fishing Company Ltd, Bella Coola Fisheries Ltd, and Delta Pacific Seafoods Ltd (formerly Icicle Seafoods Inc.) for cooperating in tag-recovery sampling.

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doi:10.1093/icesjms/fsp151