Tagging of Pacific herring *Clupea pallasi* from 1936–1992: a review with comments on homing, geographic fidelity, and straying

D.E. Hay, P.B. McCarter, and K.S. Daniel

Abstract: Nearly 1.6 million tagged herring (*Clupea pallasi*) were released in two separate programs (1936–1967 and 1979–1992) in British Columbia. Several thousand tags were released in each of 955 release sessions. Over 85% of the release sessions had subsequent recoveries. Almost 43 000 tags were recovered over all years. We re-assembled the tagging data into an electronic database, geo-referenced all tag release and recovery data, analysed spatial movements, and estimated straying and fidelity rates. The analyses do not wholly support the conclusions of previous work indicating high homing rates to local coastal areas. Estimates of fidelity, defined as the proportion of tags recovered in the same area as released, varied with the size of the geographic area used in the analyses. Fidelity rates are high for large areas, such as the Strait of Georgia (~10 000 km^2), but lower for small geographical areas, such as inlets or bays (~100 km^2). High fidelity is not necessarily evidence for "homing." Homing and fidelity are different biological processes and tagging cannot necessarily distinguish between them. Although fidelity rates for small areas are generally low, there are exceptions that may be evidence for the existence of biologically distinct populations in certain areas.

Résumé : Près de 1,6 million de harengs (*Clupea pallasi*) ont été marqués et relâchés dans le cadre de deux programmes de marquage de 1936 à 1967 et de 1979 à 1992 en Colombie-Britannique. Dans chacune des 955 opérations, des milliers de poissons marqués ont été remis à la mer. Plus de 85% de ces opérations ont donné lieu à des recaptures subséquentes. Au cours de ces années, près de 43 000 poissons marqués ont été repris. Nous avons réuni toutes ces informations dans une base de données électronique et nous avons relié toutes les données de marquage et de recapture à des coordonnées géographiques, ce qui a permis d'analyser les déplacements et d'estimer les taux d'errance et de fidélité. Les résultats de ces analyses n'appuient pas les conclusions de travaux antérieurs qui indiquent un fort taux de homing vers les régions côtières locales. Les estimations de fidélité, définies comme la proportion des poissons marqués recapturés dans la région où ils ont été relâchés, varient avec la surface géographique analysée. La fidélité est élevée pour les grands espaces géographiques, tels que le détroit de Georgie (~10 000 km^2), mais plus faible pour les espaces plus restreints, tels que les anses et les baies (~100 km^2). Une haute fidélité n'indique pas nécessairement un comportement de homing; la fidélité et le homing sont des processus biologiques différents et le marquage ne permet pas nécessairement de les distinguer. Bien que les taux de fidélité soient généralement faibles pour les régions restreintes, il y a néanmoins des exceptions qui peuvent laisser croire à l'existence de populations biologiquement distinctes à certains endroits.

[Traduit par la Rédaction]

Introduction

The issue of homing is a key part of an ongoing debate and dialogue about herring (*Clupea*) stock structure (e.g., Iles and Sinclair 1982; Stephenson and Kornfield 1990; Hay and McCarter 1997). A view held by most participants in this debate is that herring stock structure is related in some way to the geographical location of spawning areas. It is not clear, however, if some herring "home" in the same way that many salmonids species home by returning to natal spawning areas (Hasler 1966). "Natal homing"— the return to natal spawning areas—is a commonly understood use of the term "homing" and requires the fish to have the ability to memorize a natal area through imprinting or some other form of geographic memory developed during the early life stage.

The term homing also is used more broadly and, as discussed by McQuinn (1997), can be taken to mean a return of a spawning fish to the same spawning area used in previous years but not necessarily the one in which the fish lived as an egg or larvae or juvenile. This usage, perhaps better called "sexual" homing to distinguish it from "natal" homing, would apply to the way it was used by Wheeler and Winters (1984), who commented on homing in Atlantic herring (*Clupea harengus*). This type of homing requires that a herring develop a memory of its first spawning area or in some way develop associations with other individuals that will exhibit sexual homing. This usage also is seen in essays describing theories of herring population such as the member–vagrant hypothesis (Sinclair 1988) and the adopted-migrant hypothesis (McQuinn 1997). Repetitive interannual

Received April 28, 2000. Accepted March 16, 2001.
Published on the NRC Research Press Web site at http://cjfas.nrc.ca on June 4, 2001.
J15741

D.E. Hay,[1] P.B. McCarter, and K.S. Daniel. Fisheries and Oceans Canada, Biological Sciences Branch, 3190 Hammond Bay Road, Nanaimo, BC V9R 5K6, Canada.

[1]Corresponding author (e-mail: hayd@pac.dfo-mpo.gc.ca).

 DOI: 10.1139/cjfas-58-7-1356 © 2001 NRC Canada

use of the same summer feeding areas or overwintering areas by herring that spawn in many different locations may also represent a form of homing, but not to spawning areas, and is not considered in the present paper. Implicit in these definitions, however, is the assumption that herring move or migrate because to home a fish must first move away; therefore, any usage of the term homing must involve some form of movement or migration. We suggest that this assumption often may not be warranted and may lead to incorrect conclusions about the prevalence and specificity of homing in herring.

This paper reports results on tagging experiments conducted from 1936 to 1992 in British Columbia (B.C.). We describe interannual changes in herring distribution to measure and describe "reproductive" homing behaviour. We show that estimates of homing are affected by assumptions about the geographic area (km^2) of release and recapture sites: estimates of homing are high, or inflated, if the geographical areas are large, and vice versa. We distinguish between homing and "geographic fidelity" and point out that recapture of nonmigratory herring in the same location as their release, which they may never leave, is not evidence of homing but could be misinterpreted as homing. Rather, recapture of tagged nonmigratory herring is evidence of geographic retention or fidelity.

Although herring tagging experiments have been conducted in B.C. for over six decades, it is only the most recent experiments (1979–1992), with external Floy© tags, that have specific dates of recapture. From 1936 to 1967, herring were tagged with internal "belly" tags. Although there were many recoveries, few had specific information on the date of recovery (Hourston 1982). Therefore, only anchor-tagging recoveries can be used to comment on the specific issue of homing to specific spawning sites during the spawning season, although much of the older tagging data provide reliable estimates of fidelity. We use anchor-tagging data to comment on the specific issues of (*i*) geographic fidelity and (*ii*) homing to previously used spawning sites.

Herring tagging data are organized according to geographical divisions of the B.C. coast based on spawning areas. We begin with a brief description of the major spawning locations and a description of the geographical divisions.

Materials and methods

Distribution of spawning sites in B.C. herring

The intertidal and shallow subtidal spawning areas of Pacific herring (*Clupea pallasi*) have been documented on the B.C. coast since the 1930s. Data on spawning sites are maintained in an electronic database that is updated annually at the Pacific Biological Station. Each year the cumulative length of spawning events is about 400–600 km (Hay and Kronlund 1987). Since the 1930s, herring have spawned on about 20% of the total B.C. coastline, but most spawning activity is clustered into a few key areas in each of the six main geographical regions of the B.C. coast (Fig. 1). Hay and Kronlund (1987) described a simple quantitative index of spawning that can be used to compare the relative spawn deposition among different areas of the B.C. coast (Fig. 1).

Description of herring tagging projects in B.C.

The earliest tagging programs (1936–1967) used metallic belly tags that were inserted into the body cavity and recovered with magnetic detectors in reduction plants. Release of belly tags stopped in 1967 with the closure of the reduction fishery. The development of the roe fishery in the early 1970s led to a renewal of a new herring tagging program in 1979 that used external anchor tags. Pilot studies examined recovery rates from fish plants and the tag retention and survival of tagged fish in captivity (Hay 1981). A description of all previous herring tagging programs in B.C. is presented in Daniel et al. (1999).

The tags

Most belly tags used from 1936 to 1967 were nickel-plated iron rectangles with rounded ends (approximately 19 mm long, 4 mm wide, and 1.6 mm thick) that were inserted into the body cavity through a small incision (Hart and Tester 1937). The Floy© anchor tags used from 1979 to 1992 were made of a plastic tube attached to a monofilament T-shaped end that was inserted into the dorsal musculature (Daniel et al. 1999). Both the belly tags and anchor tags had individual coding numbers so that recoveries could be traced back to the date and location of release.

Tagging data records

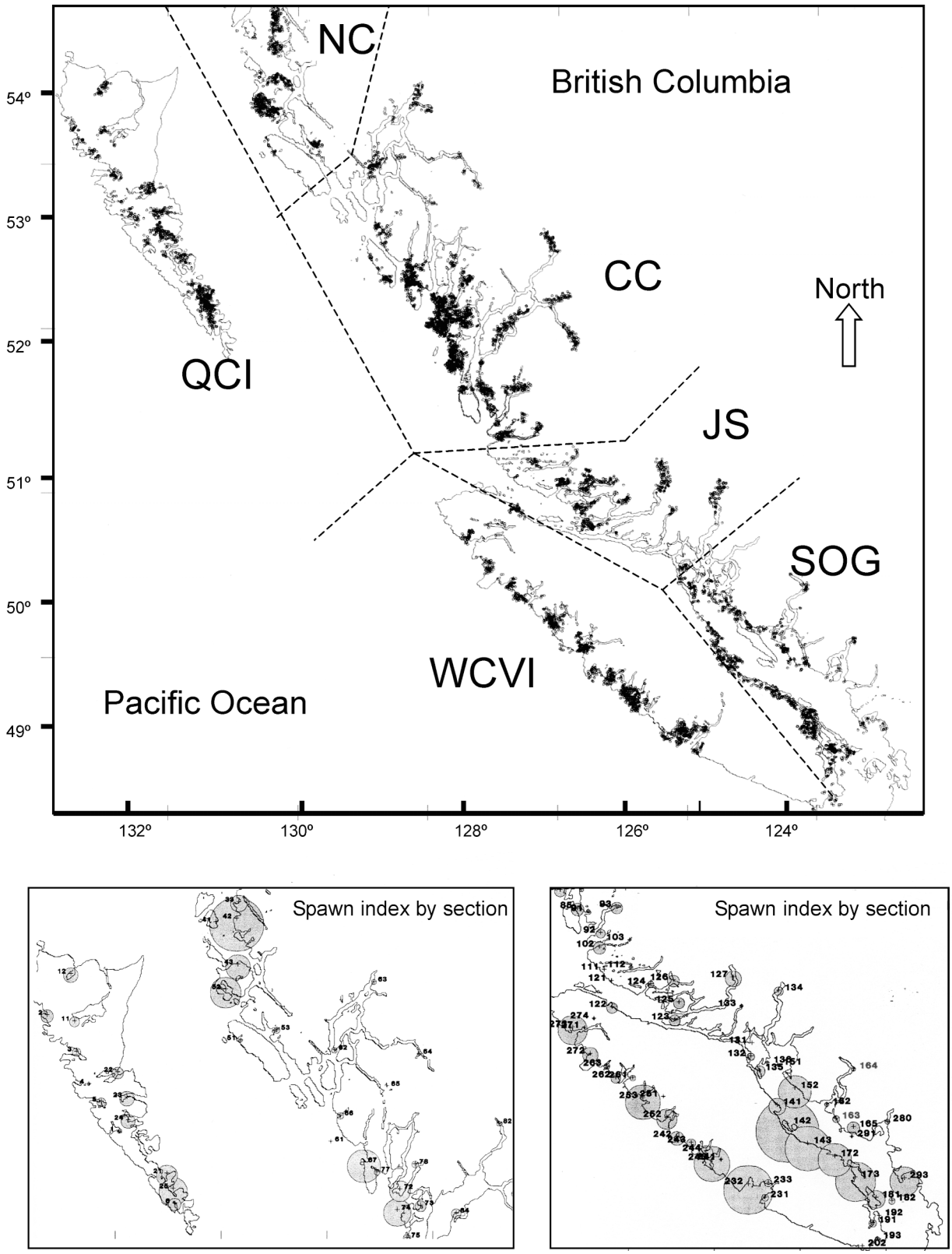
Almost 1.6 million tags were released from 1936 to 1991 (Appendix 1). Most tag recovery data from 1936 to 1957 were published annually in Provincial (B.C.) Government reports that are listed in detail in Daniel et al. (1999), which also lists sources of more recent results data, mainly manuscript reports from Fisheries and Oceans Canada Pacific Stock Assessment Review Committee (PSARC) working papers. There are different levels of precision about tag recovery information, particularly with respect to exact date and location of the recovery. The exact location and date of release is known for all tag releases but the accuracy and precision of tag recovery data varies. For nearly all belly-tagging data, we know only the "season" or year of recovery, although from review of historical catch data, it is clear that most fisheries, hence tag recaptures, were made between November and March. In the reduction fishery, the metal tags accumulated in the reduction chambers in processing plants and were not necessarily recovered for individual catches; therefore, such recovered belly tags may have come from several different statistical areas or many different sections, although for most the region was known. In contrast, exact recovery dates were recorded for most anchor tags.

Estimating the number of years-at-large

Although all tag release dates were recorded to the nearest day, recovery dates were recorded to the nearest day only for anchor tags (1979–1992). Recovery dates for most belly tags, released from 1936 to 1967, were recorded only to the nearest year. To estimate the approximate number of years-at-large for belly tags, we assumed that all belly tags with unknown recovery dates (day or month) but with a known recovery year were recovered at midyear (July 1) of the same year they were recovered. Therefore for belly tags released in July of the previous year, the estimate of years-at-large would be about 1 year. For tags released in October, the estimated time-at-large would be only 8 months or 0.66 years-at-large. For tags released in March, the estimated time-at-large would be 16 months or 1.33 years. Over 75% of all belly tags were released between mid-January to April (Appendix 2), so the estimated time-at-large for these tags, captured in the next calendar year after release, would range from about 1.25 (late April releases) to about 1.49 years (for very early January releases), and for our analyses, all would be rounded to represent 1 year at large. The time-at-large for tags recovered in two or more years was estimated in the same way. When rounded, all tags released between January and April and recovered in the same calendar year would be estimated to have been at large for a period of less than 1 year and be classified as zero (0) years-at-large.

© 2001 NRC Canada

Fig. 1. The British Columbia coast showing all herring spawning areas (dark areas) and the six major regions identified as QCI (Queen Charlotte Islands), NC (North Coast), CC (Central Coast), JS (Johnstone Straits), SOG (Strait of Georgia), and WCVI (West Coast of Vancouver Island). The dark areas indicate all recorded spawning locations from 1936–2000 but do not differentiate the relative size or importance of spawning areas. This is indicated in the panels below by the shaded circles that show a relative index of spawn (Hay and Kronlund 1987) representing the approximate locations of major spawning areas.



© 2001 NRC Canada

Estimating the geographic precision of recovery

The basic geographical unit for Fisheries and Oceans management of all species is a "statistical area," and about 30 are applicable to herring in coastal waters of B.C. (Fig. 2). Each statistical area is subdivided into "sections," designed specifically for herring management (Haist and Rosenfeld 1988). There are over 100 sections included in either tag release or recovery data (Table 1). In general, many of these sections comprise the smallest geographical unit that could define a "spawning ground," although in some instances, single spawning areas will overlap two or three different sections. In contrast, large sections, particularly some that include long fjords, may include two or more separate spawning areas. The smallest or most precise geographical unit used is a "location" or geographical name. There are about 536 locations used in the herring data release and recovery database (Table 1).

Statistical areas can be pooled into six larger areas called regions (Table 1), which correspond to large natural geographic groupings. The approximate sea surface area (km^2) for each section was estimated using Sigmascan© image analysis software. The areas of the larger geographical domains, statistical areas and regions, were then estimated as the sums of the areas of the component sections. Locations were only points on a chart, so sea surface areas for locations were not estimated.

Tag recovery information

During the reduction fishery tagging (1936–1967), processing plants sometimes were able to identify the tag origins according to the statistical area of the fishery, but the specificity of geographic recovery location varied. For many tags, the plants could determine only that recovered tags were from a potential group of statistical areas, such as between Statistical Areas 14 and 18. This range of statistical areas falls within the Strait of Georgia, one of six regions of the B.C. coast; therefore, in such instances, the Strait of Georgia (region) would be the most precise return information available. The six regions are Queen Charlotte Islands (QCI), North Coast Rupert District (NC), Central Coast (CC), Johnstone Strait (JS), Strait of Georgia (SOG), and West Coast of Vancouver Island (WCVI) (Fig. 2). For other tags, we could name the statistical area of recovery with certainty, but not the section or location. For many tags, no geographic recovery information was available. (Subsequent reference to statistical areas and sections are made by number corresponding to Fig. 2.)

Estimating rates of tag recovery

The location of each tag recovery was compared to the area of release at each of the four different geographic scales or domains: region, statistical area, section, and location. For each recovery, we estimated the number of years-at-large or the estimated mean number of years between release and recapture. Most belly tag recovery information was incomplete, with either the recovery date or exact location missing. Usually, however, there was at least partial information on the geographical region of recovery and the calendar year of recovery was known. Therefore, for any group of tag releases within 1 year, the rates of recovery in each of the following years can be estimated as the ratio N_y/N_{y-1}, where N is the number of recaptures after y and $y - 1$ years of release.

Estimating fidelity (*F*), straying (*S*), and immigration (*I*) rates

Estimates of fidelity are made for a specific time period (1 or more years) and are based on the geographic distribution of tag recoveries relative to the area of release. To estimate fidelity for a specific geographical domain d (i.e., a section, statistical area, section, or location), we let n_d represent the number of tags released and recovered within domain d, n_o equal the number released in domain d but recovered in all other domains (o), and t_d equal the total number of tags recovered from tag releases within domain d but recovered in all domains so that $t_d = n_d + n_o$. We let i_d represent the numbers of tags recovered in domain d but released in other domains. The ratio n_d/t_d is an estimate of area-specific fidelity (F) rate, which will be between zero and one, or between zero and 100 when shown as a percentage. F represents herring that were retained within domain d or that left and returned to domain d before recapture. The ratio n_o/t_d is an estimate of straying (S) from domain d (or emigration), and the ratio $i_d/(n_d + i_d)$ is an estimate of immigration (I), or the proportion of fish in domain d that are immigrants from other domains. Rates of F, S, and I can be estimated for different geographical scales or domains including locations, sections, statistical areas, or regions. Further, F, S, and I can be estimated for different combination of years of release, or estimated according to the years that tags were at large. We show rates of F, S, and I for herring that have been at large for 1 year or more and compare F among different geographic scales (domains). For analyses of homing, we examine a subset of the data that restricted tag release and recovery to March or April, corresponding to the spawning times, and to tags that had been at large for 1 year or more. All but a few of the data in this subset consisted of anchor tags, released and recovered in the roe fishery.

Results

Area of geographical divisions

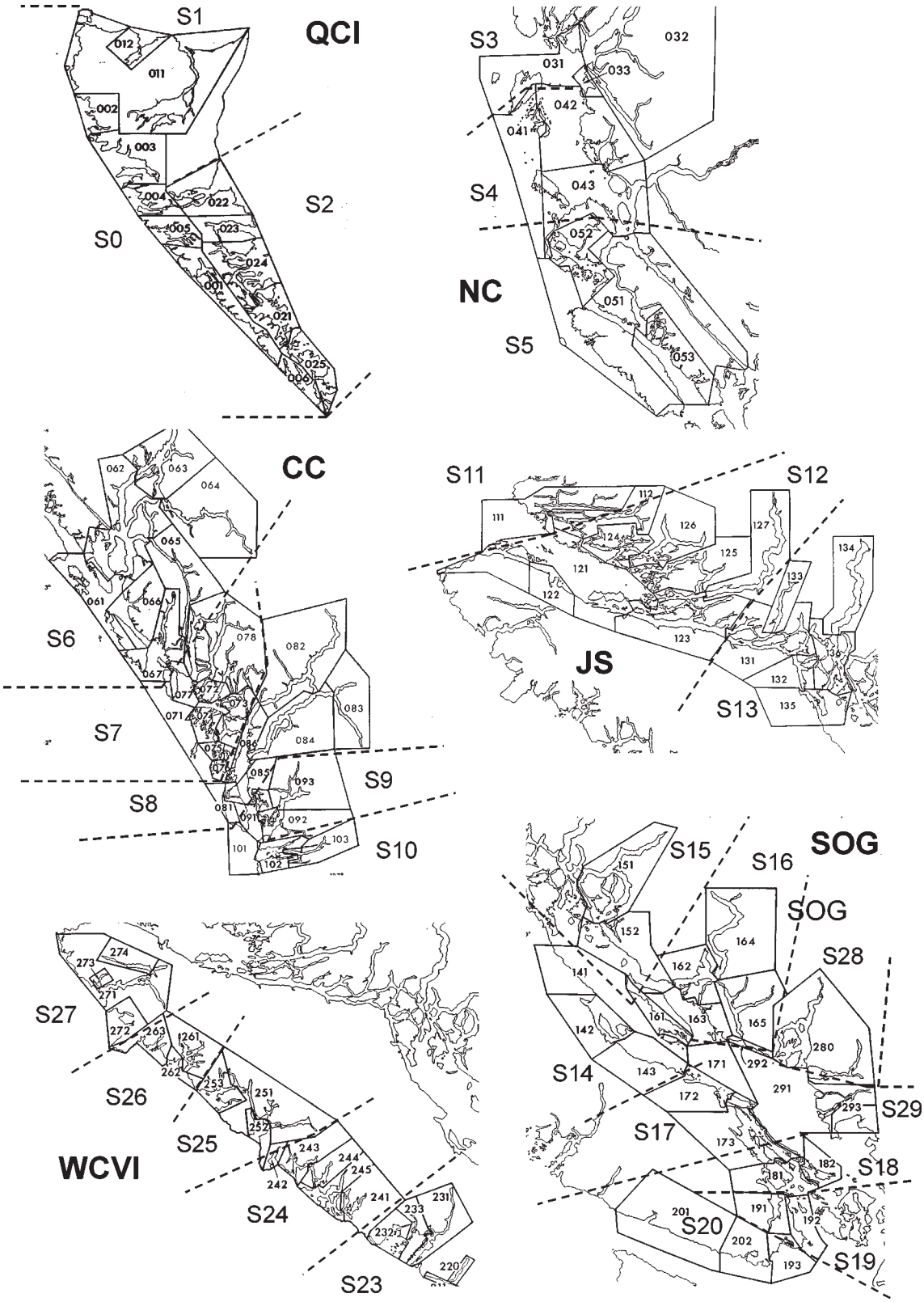
Table 1 shows approximate area (km^2) for each region, statistical area, and section. The regions vary from about 3000 km^2 to 10 000 km^2. Most statistical areas are between 500 and 2500 km^2, and most sections are less than 300 km^2. There is overlap in sizes among the respective geographical divisions, with some statistical areas being larger than regions, and some sections larger than statistical areas. Also, these estimates of area (km^2) are approximate, particularly because the position of lines separating the many divisions from open water is arbitrary (Fig. 2). The sums of area for the sections are used to estimate the areas of statistical areas. The areas of the regions shown in Table 1 refer only to the areas in proximity to spawning areas (i.e., sections). The actual area (km^2) for all regions except the Strait of Georgia is larger than indicated here and includes areas of open water in Hecate Strait, or the open Pacific off the west coast of Vancouver Island.

Recovery numbers and spatial and temporal distribution of released and recovered tags

Between 1936 and 1991, tags were released in a total of 955 different capture and release sessions (Appendix 1). A total of 1 595 249 herring tags were released, including over one million belly tags released from 1936 to 1967 and over 500 000 anchor tags released between 1978 and 1991. Approximately 85% of the 955 tag release sessions resulted in some eventual tag returns and the overall mean recovery rate of the 1.6 million was 2.68%, but this varied annually from a low of about 0.5% to a maximum of over 11% (Appendix 1). For both belly and anchor tags, about 76% were released between February and April, during the spawning season (Appendix 2), and about 15% of the belly tags were released in the summer months. The year of recapture is known for nearly all belly tags returns but the month and day are unknown for most. Most anchor tags (>85%) were recovered in March and April (Appendix 2). A total of 42 767 tags were recaptured, including 37 326 belly tags and 5441 anchor

© 2001 NRC Canada

Fig. 2. The British Columbia coast showing two levels of geographical divisions called regions and sections. Each of the six regions is shown in detail in separate panels: (*a*) Queen Charlotte Islands, (*b*) North Coast, (*c*) Central Coast, (*d*) Johnstone Straits, (*e*) West Coast of Vancouver Island, and (*f*) the Strait of Georgia. Three-digit-numbered subdivisions within each region indicate different herring sections. Intermediate-sized statistical areas (see Table 1) consist of one or more sections and can be identified as the first two digits in the numbers shown for each section. Not shown are the 500 different locations that were recorded as tag release or recovery sites.



© 2001 NRC Canada

Table 1. The relationship between regions, statistical areas, sections, and locations.

Region	Area (km^2)	Statistical areas			Area of sections (km^2)		Number of locations
		Code	Area (km^2)	No. of sections	Minimum	Maximum	
QCI	4 361	S0	1 409	6	138	380	15
		S1	1 169	2	326	843	1
		S2	1 783	5	162	535	31
NC	5 230	S3	1 267	3	54	647	17
		S4	2 210	3	706	765	25
		S5	1 753	3	316	1 108	23
CC	11 123	S6	3 822	7	246	1 007	25
		S7	3 159	8	113	1 212	56
		S8	1 594	6	62	407	5
		S9	600	3	155	238	5
		S10	856	3	115	561	3
		S11	1 092	2	213	879	0
JS	5 105	S12	3 634	7	207	1 591	26
		S13	1 471	6	83	363	45
SOG	9 490	S14	1 597	3	272	953	33
		S15	1 029	2	465	564	13
		S16	1 168	5	150	403	7
		S17	1 130	3	180	554	56
		S18	581	2	289	292	20
		S19	762	3	73	350	9
		S20	968	2	310	658	4
		S21	70	1	70	—	4
		S28	494	1	494	—	2
		S29	1 691	3	55	1 525	1
WCVI	3 192	S22	38	1	38	—	0
		S23	653	5	196	255	41
		S24	663	1	50	246	21
		S25	600	3	130	252	24
		S26	476	3	145	183	12
		S27	762	4	30	428	12

Note: The six major regions are QCI (Queen Charlotte Islands), NC (North Coast), CC (Central Coast), JS (Johnstone Straits), SOG (Strait of Georgia), and WCVI (West Coast of Vancouver Island). The areas of the regions and statistical areas (under column Code, corresponding to Fig. 2) and minimum and maximum sea surface areas of sections within each statistical area are expressed in km^2. The numbers of different sections and locations, applicable to release of recovery of tags, is shown in far right.

tags. Of these recaptures, however, about 9400 were made within the same year as the release.

Rates of recovery: recoveries versus releases

For each year, the annual recovery rate represents tags released in a single year but recovered from over a number of different years. Table 2 shows the numbers of returns by the year of release and the number of years between the release and recapture. Most belly tags were recovered after 1 year at large but many were recovered over several years and a few were at large for 10 years. We cannot rule out, however, the possibility of some delays between date of the actual recovery of a tag from a plant and the date that it was forwarded to the laboratory. For releases with a single year, recovery rates can be estimated from the number of recaptures (N) after y years of release (N_y), divided by the number of recaptures a year later (N_{y-1}) after $y - 1$ years of release. The estimate of N_y/N_{y-1} is consistent with an approximate rate of 0.32 for belly tags the first 3 years (Table 3). This estimate would be affected by several factors, including annual fishing rates, the numbers and locations of tags released, natural mortality, tag retention, and tag detection. The rate of anchor tags recovery after the first year was lower than belly tags. A total of 81 anchor-tagged fish were recaptured after 2 years, or about 17% of the number (482) captured in the previous year. The lower rates of capture in the anchor-tagged fish could reflect (*i*) lower fishing rates during the roe fishery of the 1980s and 1990s; (*ii*) higher mortality rates of tagged fish (some tags were returned from salmon anglers who found the tags in salmon guts); and (*iii*) shedding of tags (Hay 1981) and incomplete reporting (Haegele 1990).

Geographic fidelity

Table 4 shows the release and recovery of all tags, for all times at large (1 day to 10 years). Herring movements were extensive: tags released in each region were recovered in nearly all other regions, but most tags were recovered in the same region in which they were released. Table 4 also shows some release and recovery sites in U.S. waters, although the numbers are low and are not included in the subsequent analyses. Table 5 shows a subset of the data restricting tag recoveries to those at large for 1 or more years and (similar to the subset used by Hourston 1982) limits the period of tag releases to the months of January to April. Table 5 shows es-

© 2001 NRC Canada

Table 2. Total number of tag recoveries shown by the numbers of years between release and recapture.

Year of Release	Years between release and recapture											Total
	0	1	2	3	4	5	6	7	8	9	10	
1936	43	3	5	2	0	0	0	0	0	0	0	53
1937	152	770	29	1	1	0	0	0	0	0	0	953
1938	0	352	108	7	2	0	0	0	0	0	0	469
1939	570	540	112	19	2	0	0	0	0	0	0	1 243
1940	65	664	161	39	20	2	1	0	0	0	0	952
1941	0	288	111	50	9	1	2	0	1	0	0	462
1942	0	112	130	16	23	0	2	1	0	0	0	284
1943	0	516	79	20	5	8	0	1	0	0	**0**	629
1944	0	352	75	45	23	11	4	1	1	**0**	2	514
1945	0	528	117	125	97	20	24	12	**0**	2	1	926
1946	0	564	295	102	16	5	7	**0**	0	1	0	990
1947	0	1 779	766	129	26	20	**0**	0	0	0	0	2 720
1948	0	2 184	287	82	68	**0**	6	2	1	0	0	2 630
1949	0	688	261	140	**0**	16	1	1	0	0	0	1 107
1950	0	1 919	1 096	**0**	113	20	8	5	0	0	0	3 161
1951	0	3 401	**2**	525	55	38	19	0	1	3	0	4 044
1952	1	**4**	1 216	123	165	59	2	4	0	0	0	1 574
1953	**1**	2 687	409	497	154	3	12	2	0	0	0	3 765
1954	0	1 696	1 109	211	4	31	2	4	0	0	0	3 057
1955	0	879	305	24	7	0	0	0	0	0	0	1 215
1956	218	945	91	25	5	0	0	0	0	0	0	1 284
1957	0	68	108	22	24	0	0	0	0	0	0	222
1958	0	30	6	0	0	0	0	0	0	0	0	36
1959	0	0	0	0	0	0	0	0	0	0	0	0
1964	242	2 310	911	307	0	0	0	0	0	0	0	3 770
1965	0	1 091	107	0	0	0	0	0	0	0	0	1 198
1966	21	0	8	0	0	0	0	0	0	0	0	29
1967	0	0	0	0	0	0	0	0	0	0	0	0
1979	29	4	0	0	0	0	0	0	0	0	0	33
1980	79	38	23	2	2	1	0	0	0	0	0	145
1981	622	135	14	8	3	0	0	0	0	0	0	782
1982	570	47	7	0	0	0	0	0	0	0	0	624
1983	234	9	0	0	0	0	0	0	0	0	0	243
1985	73	3	0	0	0	0	0	0	0	0	0	76
1986	300	0	0	0	0	0	0	0	0	0	0	300
1988	264	12	4	0	0	0	0	0	0	0	0	280
1989	505	71	26	0	0	0	0	0	0	0	0	602
1990	1 402	141	7	0	0	0	0	0	0	0	0	1 550
1991	780	22	0	0	0	0	0	0	0	0	0	802
All	6 171	24 852	7 985	2 521	824	235	90	33	4	6	3	42 724

Note: The second column "0" indicates that less than 1 year transpired between release and recapture. The column "Total" shows all recoveries for each release year. In 1953, an industry strike reduced catches to nearly zero. The effect of that low catch is seen as a low return of tags released in previous years (in bold). The period of anchor-tag release is 1979–1991. The total is slightly lower than in Table 1 and Appendix 2 because the return years for some tags are unknown.

timates of *F*, *S*, and *I* as percentages. Based on 25 147 recoveries, most regions have approximately similar estimates of *F* and *I*. The estimates of fidelity within regions are high, with an $F > 90\%$ in three regions. These estimates for regions are similar to those presented by Hourston (1982).

The relationship between fidelity and geographic size of the domain used for analysis (areas of release or recovery (in km^2)) is shown in Fig. 3. Regions have the highest mean fidelity, followed by statistical areas and sections. Fidelity for nearly all locations is low and *F* estimates can be examined according to the sea surface area of each geographical domain (Fig. 4). Regions, with the largest sea surface area, have the highest mean fidelities. Locations, with the smallest sea surface areas, have the lowest mean fidelities. There is some overlap, however between the smallest and largest domains in each category. Estimates of fidelity do not appear to be affected by the numbers of years at large (Fig. 5), although there may be a decline in fidelity with time in some statistical areas. Some statistical areas and sections have high (>50%) fidelity estimates, but in some of these instances, the estimate may be based on very few recoveries. Figure 6 shows the relationship between mean fidelity and

© 2001 NRC Canada

Table 3. Summary of the number of tags recovered after 0–10 years at large.

	All tags		Belly tags		Anchor tags	
Years free	Number recovered	Frequency n_y/n_{y-1}	Number recovered	Frequency n_y/n_{y-1}	Number recovered	Frequency n_y/n_{y-1}
0	6 171	—	1 313	—	4 858	—
1	24 852	—	24 370	—	482	(0.099)
2	7 985	0.321	7 904	0.324	81	0.168
3	2 521	0.316	2 511	0.324	10	0.123
4	824	0.326	819	0.326	5	
5	235	0.286	234	0.286	1	
6	90	0.383	90	0.385		
7	33	0.367	33	0.367		
8	4		4			
9	6		6			
10	3		3			
Totals	42 724		37 297		5 437	

Note: Data are shown for both tag types combined and belly and anchor tags separately. The frequency is the number of tags recovered in 1 year as a proportion of the number of tags recovered in the previous year. Note that the totals are slightly smaller than in Appendix 1 because of uncertainties about the recovery year for some tags.

Table 4. The number of recaptures of all tags shown by region.

Release region	Recovery region								
	UNK	QCI	NC	CC	JS	SOG	WCVI	USA	All
QCI	747	**2 885**	146	104	0	9	12	0	3 903
NC	679	204	**3 098**	220	18	15	11	3	4 248
CC	1 767	118	551	**8 249**	52	37	80	1	10 855
JS	536	0	4	369	**801**	142	22	0	1 874
SOG	2 922	7	12	64	282	**3 494**	287	4	7 072
WCVI	1 644	26	16	175	18	458	**12 398**	10	14 745
OFFS	16	0	0	0	0	45	9	0	70
All	8 311	3 240	3 827	9 181	1 171	4 200	12 819	18	42 767

Note: Columns indicate regions of recovery and rows indicate regions of release. The recovery location of 8311 tags was unknown (shown under column "UNK"). Release region "OFFS" refers to offshore releases. Region USA refers to a few recoveries from Washington State or Alaska. Tags recovered in the same area as the release are shown in bold. Regions: Queen Charlotte Islands (QCI), North Coast Rupert District (NC), Central Coast (CC), Johnstone Strait (JS), Strait of Georgia (SOG), West Coast of Vancouver Island (WCVI).

the number of tag returns for statistical areas (Fig. 6*a*) and sections (Fig. 6*b*). The total numbers of tag returns (defined as n_t in Methods and materials) to some areas smaller than regions (statistical areas, sections, and locations) are low and fidelity estimates could be misleading in these instances.

Herring movements, area-specific fidelity, and homing to spawning areas

Fidelity rate varies with geographical scale. After 1 or more years at large, between 4 and 39% of herring released between January and April strayed to different regions (Table 5). Straying rates were higher for smaller domains with about 40% among statistical areas, 83% among sections, and almost 99% among locations (Fig. 3). These estimates are means, however, and a few sections had relatively high fidelity rates, which indicates that some individuals were recovered in nearly the exact place of tagging and release, even after a period of years.

High fidelity does not necessarily indicate high homing. From surveys made in the summer, we know that some herring are widely distributed in nearshore shallow waters as well as on the continental shelf. Perhaps some herring do not migrate far, if at all, from their natal spawning areas. If so, we cannot use tag returns to distinguish between fidelity rates associated with homing and those that reflect a sedentary (nonmigratory) life history, and we suggest that such a distinction is not possible in some other areas, unless there were unequivocal evidence that all herring were migratory.

The most restrictive data of our analyses of the tag returns were obtained by selecting only tag recoveries that were at large for 1 or more years and released and recovered during a 2-month period corresponding to the spawning season (March and April). Only 285 tag recoveries fit these criteria, and all are from the anchor-tagging records, where information on exact dates and location of some tag recoveries was available (Table 6). Because most of these herring were captured on the spawning grounds or in the immediate vicinity, *F* could be interpreted as the best estimates of homing available from any of the tagging data from B.C. For most statistical areas, there is independent evidence that herring migrate to and away from spawning areas, probably to and from offshore feeding areas or overwintering areas (Table 6).

© 2001 NRC Canada

Table 5. The number and percentage of releases and recoveries for each region for herring released between January and April and at large for 1 year or longer.

	Recovery						
Release area	QCI	NC	CC	JS	SOG	WCVI	All releases
QCI	**1 582**	49	61	0	2	4	1 698
%	**93.17** (*F*)	2.89	3.59	0.00	0.12	0.24	100.00
S	**6.83**						
I	**11.96**						
NC	121	**1 864**	172	14	12	5	2 188
%	5.53	**89.19** (*F*)	7.86	0.64	0.55	0.23	100.00
S		**10.81**					
I		**20.78**					
CC	86	425	7 188	34	25	49	7 807
%	1.10	5.44	**92.07** (*F*)	0.44	0.32	0.63	100.00
S			**7.93**				
I			**9.33**				
JS	0	1	367	**711**	60	15	1 154
%	0.00	0.09	31.80	**61.61** (*F*)	5.20	1.30	100.00
S				**38.39**			
I				**32.16**			
SOG	0	5	45	272	**1 807**	192	2 321
%	0.00	0.22	1.94	11.72	**77.85** (*F*)	8.27	100.00
S					**22.15**		
I					**16.11**		
WCVI	8	9	95	17	248	**9 602**	9 979
%	0.08	0.09	0.95	0.17	2.49	**96.22** (*F*)	100.00
S						**3.78**	
I						**2.69**	
All recoveries	1 797	2 353	7 928	1 048	2 154	9 867	25 147

Note: The two rows show the numbers and percentage of tags recovered in each region. Tags recovered in the same area as the release are shown in bold. The estimates of *F* (fidelity), *S* (straying), and (*I*) immigration are shown for each region. Regions: Queen Charlotte Islands (QCI), North Coast Rupert District (NC), Central Coast (CC), Johnstone Strait (JS), Strait of Georgia (SOG), West Coast of Vancouver Island (WCVI).

Fig. 3. Comparison of fidelity rates. The symbols show the mean fidelity for regions (solid circles), statistical areas (open circles), sections (solid squares), and locations (open squares). The overall mean for each geographic category is shown by the largest symbols, which connect the different geographical categories. Within each group, the array of points is jittered horizontally to reduce overlap but there is considerable overlap of symbols among sections and locations with low fidelity (lower right corner).

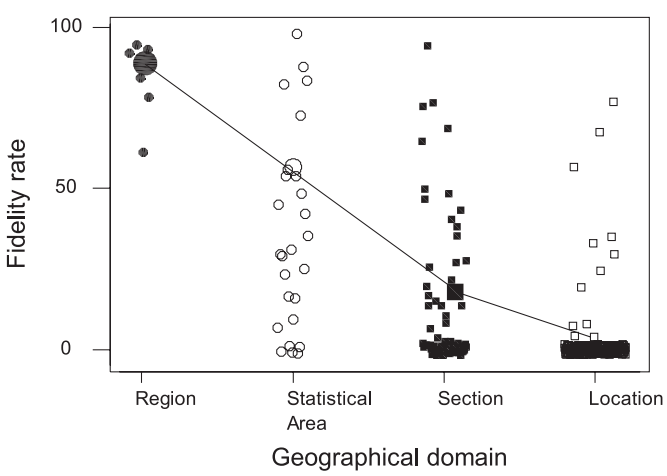
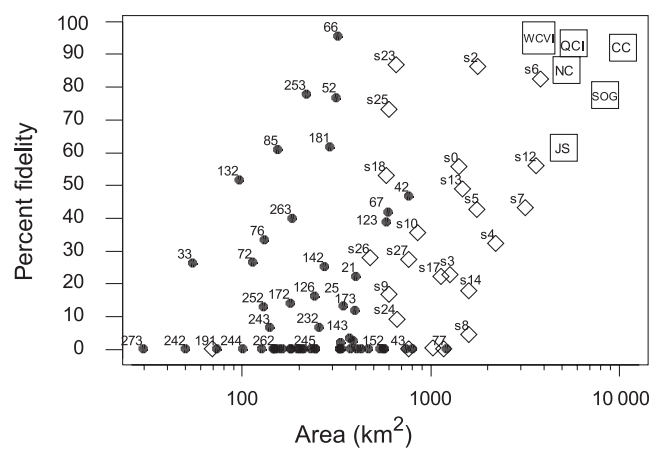


Fig. 4. Tag fidelity rates arrayed by the sea surface area (km^2) for regions (open rectangles), statistical areas (open diamonds), and sections (solid circles). The numbers beside each symbol represent the region, statistical area, or section as shown in Fig. 2.



For instance, in SOG, many years of summer surveys have failed to find many adult herring present, although juvenile herring abundance in SOG is high (Haegele 1997). Table 6 shows that five statistical areas (2, 5, 7, 14, and 23) all have high (>70%) homing estimates, although the sample size for Area 14 is low. A concern with these estimates, however, is that the same statistical areas that have high fidelity rates also are the main areas where closely regulated commercial

© 2001 NRC Canada

Fig. 5. Mean fidelity for regions (open circles), statistical area (solid circles), sections (open triangles), and locations (solid squares) shown according to the number of years at large. The numbers at the top of the panel show the number of tag recoveries used for each estimate.

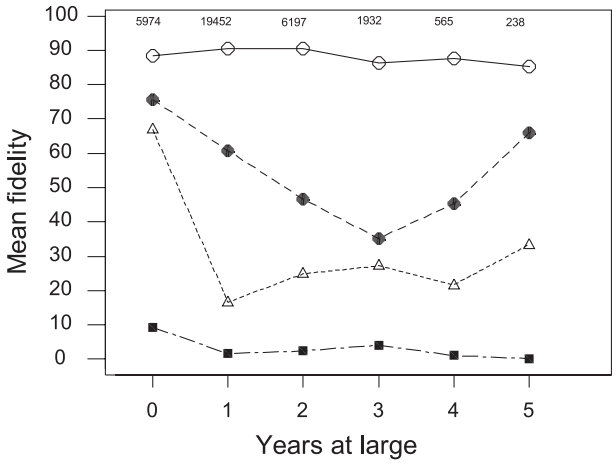
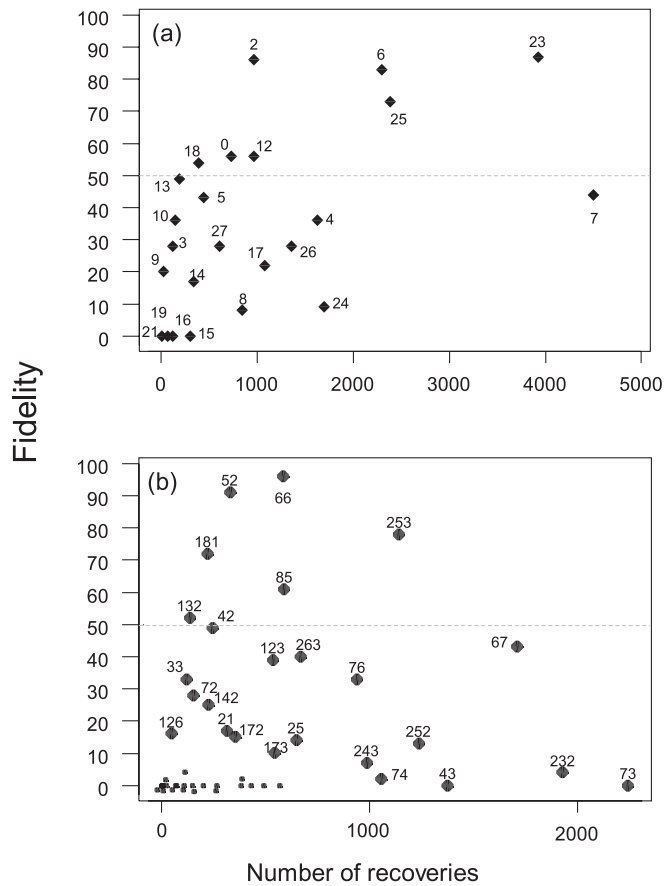


Fig. 6. Mean fidelity for statistical areas and sections by number of recaptures. These estimates represent tags released during March and April and recovered 1 or more years later. The broken lines indicate fidelity estimates above and below 50%. (*a*) Statistical areas. The numbers beside each symbol (solid diamonds) indicate the statistical area as shown in Fig. 2. Several overlapping symbols in the lower left corner indicate areas with low fidelity and recoveries. (*b*) Sections. The numbers beside each symbol (solid circles) indicate the individual section as shown in Fig. 2. Sections with low fidelity and recoveries are shown in the lower left corner where the size of the symbol is small to reduce overlap.



roe fisheries occur, and no fisheries occur in most of the statistical areas with low fidelity estimates; therefore, these fidelity rates estimates may be inflated. There is indirect evidence of this in the form of relatively high immigration rates for many statistical areas, many exceeding 50% (shown at the bottom of Table 6). Therefore, we see a pattern of high fidelity and immigration rates in statistical areas with fisheries, and lower rates (but few tag recoveries) in areas with little fishing activity (Table 6). We suspect that this pattern may be explained by the fact that anchor tags were released over a broad geographic area that included many statistical areas but tag recoveries were confined to relatively limited number of areas where roe fisheries were conducted. The probable effect of this is an overestimate of fidelity for statistical areas with fisheries and an underestimate for those without, or with only small fisheries. The probable bias in Table 6 that applies to statistical areas probably is less of a concern when estimating for regions. Throughout nearly all years of anchor tagging, roe fisheries occurred in each region and with a similar catch rate in all, estimated at about 20% (Schweigert 1993).

In spite of these limitations, the results make a convincing case that some herring do indeed home to previously occupied spawning grounds and that the homing is made with the geographical precision of the approximate size (sea surface area) of statistical areas (Table 1). Table 6 shows that many herring do not home with such precision and presumably change spawning areas between years: over 20% moved to different spawning areas between regions. Some may argue, however, that there are other explanations for the apparent interannual changes in spawning areas. One alternate explanation is that some herring may make fast migrations immediately before spawning, so that the 2-month period (March–April) used to select the data from Table 6 is too broad and it is unreasonable to assume that all herring will be confined to spawning areas during this time. To this we would reply that based on past observation of roe fisheries, spent Pacific herring appear to leave spawning areas quite rapidly after spawning. Although we are uncertain about the migration routes or immediate destinations, we do not believe that spent herring travel to other spawning areas, and roe fisheries occur only in the immediate vicinity of spawning areas. Therefore, we think it is reasonable to conclude that Table 6 shows evidence that some Pacific herring change spawning areas among years. Such a conclusion also is consistent with other observations of spawning and we have noted frequent occurrences of spawning on "new" grounds in some years, as well as abandonment of long-used spawning grounds (Hay et al. 1989).

Discussion

Homing and fidelity: implications of geographic scales on analysis

Fidelity rates depend on geographic scale used in the analysis: large areas have high fidelity rates and vice versa. Fidelity in exceptionally large areas, such as the entire B.C.

© 2001 NRC Canada

Table 6. Estimates of homing to statistical areas of release and recovery during the spawning period, March–April, after 1 year or more at large.

Releases (region and statistical area)		Recoveries (region and statistical area)																
		QCI		NC			CC		SOG				WCVI				% *F*	% *F*
		0	2	3	4	5	6	7	14	15	17	28	23	24	25	All	(statistical area)	(region)
QCI	0	**10**	13	1	—	—	—	3	1	—	—	—	1	—	—	29	**34.4**	**77.3**
	2	2	**33**	3	—	3	—	3	1	—	—	—	1	—	—	46	**71.1**	
NC	3	—	—	**5**	3	6	—	2	—	—	—	—	1	—	—	17	**29.4**	**91.7**
	4	—	—	3	**3**	2	—	—	—	—	—	—	—	—	—	8	**37.5***	
	5	—	—	—	1	**10**	—	—	—	—	—	—	—	—	—	11	**90.9**	
CC	6	1	1	—	—	—	—	8	—	—	—	—	1	—	—	11	**0**	**80.7**
	7	4	4	—	—	1	1	**76**	1	—	1	—	5	—	1	94	**80.8**	
	8	1	1	—	—	—	—	7	—	—	—	—	—	—	—	9	**0***	
	9	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1	**0***	
JS	13	—	—	—	—	—	—	—	1	1	—	—	—	—	—	2	**0***	**0***
SOG	14	—	—	—	—	—	—	—	**5**	—	1	1	—	—	—	7	**71.4***	**83.3**
	15	—	—	—	—	—	—	—	1	—	1	—	1	—	—	3	**0***	
	16	—	—	—	—	—	—	—	1	—	—	—	—	—	—	1	**0***	
	17	—	—	—	—	—	—	1	4	—	—	—	1	—	—	6	**0***	
	18	—	—	—	—	—	—	—	1	—	—	—	—	—	—	1	**0***	
WC	23	—	1	—	—	—	—	—	—	—	—	—	**13**	—	2	16	**81.2**	**87.2**
	24	1	1	—	—	—	—	1	—	—	—	—	11	**1**	3	18	**5.5**	
	25	—	—	—	—	—	—	—	—	1	—	—	3	—	—	4	**0***	
	27	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	**0***	
All		19	54	12	7	22	1	102	16	2	3	1	39	1	6	285	**57.5**	**81.7**
% *I* (statistical area)		47.3	**38.8**	**58.3**	**57.1**	**54.5**	—	**25.4**	**68.7**	—	—	—	**66.6**	—	—			
% *I* (region)		**20.5**		**19.5**			**8.8**		**31.8**				**26.1**					

Note: Underlined numbers show regions and bold numbers show numbers recovered in the statistical area as release. In this table, the estimate of fidelity also is an estimate of homing. Fidelity (*F*) is shown on the far right for statistical areas and regions. Immigration rates (*I*) to recovery areas and regions are shown at the bottom for statistical areas (where $F > 0$) and regions. Asterisks indicate small (<10) numbers. The overall homing rate is 81.7% for regions and 57.5% for statistical areas. Regions: Queen Charlotte Islands (QCI), North Coast Rupert District (NC), Central Coast (CC), Johnstone Strait (JS), Strait of Georgia (SOG), West Coast of Vancouver Island (WC/WCVI).

© 2001 NRC Canada

coast or the Gulf of Alaska, as areas of release and recovery, would always approach one (1). At other extremes, fidelity of small geographic units (e.g., locations or smaller) will approach zero (0). The question of biological interest is the spatial scale at which fidelity begins to increase above 0 and when it approaches 1. From this study, it is clear that regions, with an approximate area of 5000 – 10 000 km^2, have an *F* of about 80–90%. At the other extremes, there are almost no sections, except Section 33 with a low number of returns, with areas <100 km^2 that have detectable fidelity above 0. There are, however, a number of sections with fidelity estimates between 10% and 80% that are approximately 200–500 km^2 in sea surface area. At about 1000 km^2, there are a number of sections and statistical areas that have *F* estimates in the range of 20% to 60%. Wheeler and Winters (1984) showed estimates of homing rates from 65% to 93% (mean = 81%) based on returns to coastal areas ranging in length from 100 km to 500 km (mean = 276). There are several ways these estimates can be compared to B.C. fidelity estimates. The entire province has a total coastline of about 25 000 km, so the linear coastline of each of the six regions would then be about 4000 linear km and each statistical area would be about 800–1000 linear km. These linear lengths, however, do not provide a reasonable basis for comparison because we recognize that the total spawning areas are only a fraction of the total sea surface area. In general, herring have spawned on about 5000 km or 20–25% of the total B.C. coastline. Therefore, if we adjust the linear coastlines to reflect this, each region and statistical area would consist of about 400 and 100 linear km of spawning area, respectively. Viewed in this way, the geographical dimensions of Newfoundland coastline required to support fidelity rates of 80% are approximately similar to those of B.C. herring and would have about 80–100 linear km of spawning coastline.

Presently there are concerns that there may be distinct stock units within some of the major assessment areas (regions) used to manage the B.C. herring roe fishery. Our results do not address that issue but point to additional information requirements. For example, the tag recovery data indicate that about 10–20% of herring move between regions each year. These movements may be episodic (Hay et al. 1999) and more extensive in some years than in others. Future short-term tagging programs may not detect episodic movements, but such movements may have significant impacts on some aspects of population dynamics and differentiation. In particular, there appears to be a net direction of fish moving northwards in some years (Hay et al. 1999), particularly from CC to NC, with about 20% of the tagged herring recovered in NC released in other regions.

Implications for genetic analyses

Spawning biomass estimates in the last decade are high for most areas (Schweigert et al. 1998) but spawning has declined in some local areas (Hay and McCarter 1998). There are suggestions that declines in local spawning are caused by the reduction of local, nonmigratory, genetically distinct local populations from fishing or other causes. O'Connell et al. (1998), reporting on genetic structure of herring populations in Prince William Sound (PWS), Alaska, concluded that herring were genetically differentiated and reproductively isolated among three areas within PWS, which is approximately the same size as SOG at about 10 000 km^2. These putatively distinct Alaskan populations are not geographically isolated in remote inlets or fjords but are described as occupying different parts of PWS. O'Connell et al. (1998) acknowledge that there may be exchange of individuals among these populations but suggest that only a fraction of the strays that intermingle among the populations represent "genetically effective migrants." In support of their argument, O'Connell et al. (1998) cite Hourston's (1982) estimate of the B.C. herring homing rate of 83.6% as an estimate that may apply to PWS. Probably a better geographic comparison for PWS would have been an estimate of fidelity for statistical areas within regions because these correspond more closely in size and topography with the subdistricts within PWS described by O'Connell. Using statistical areas as the basis for comparison, it is probable that *F* would not exceed 60%. Also, our estimates of *I* for many statistical areas, estimated independently of *F*, may exceed 40%. If these estimates of *F* are roughly correct, it would be surprising if herring populations could maintain genetic differences when the annual exchange rate may reach 40% or higher.

Limitations and strengths of the present data and analysis

We acknowledge that the estimates of *F* in this paper, as well as Hourston's (1982) estimate of homing, may be biased and could be overestimated in areas with the greatest catches and lowest in areas with the smallest catches. For instance, if herring were only tagged and released in, for example, two different areas A and B, but if the fishery (hence recaptures) were limited to one area (A), then the estimate of fidelity in A would be 100%, even if the herring mixed completely among both areas. (In part, this type of bias is a concern for the numbers in Table 6.) The opposite also holds: if there were a high (>90%) fidelity to B, with the remainder (10%) straying to A, a low catch rate in B and a large catch rate in A would underestimate fidelity or homing to area B. To correct for this potential bias, analysis of tagging data should be made with reference to catch data. Like previous analyses (Hourston 1982), we do not attempt to adjust tag recoveries according to area-specific catch data or fishing rates but acknowledge that this is a required step for further analyses. Further analysis will require that the tagging data be examined in the context of several independent area-specific databases on annual catches, biological samples, and spawn escapement. Detailed cross-referencing and linkages between independent databases was not possible until recent years, with the advent of relational databases and spreadsheets. Even with these new tools, the task is enormous because the databases are large and complex. On the other hand, although further analyses will improve our understanding about biological factors affecting herring fidelity and homing, such further analyses are unlikely to change the basic conclusions of this paper.

In spite of the limitations of these data and analyses, we can make some firm observations and conclusions. First, there appears to be a number of different herring spawning areas in B.C. that have high fidelity rates. Often associated with these areas are differences in spawning times (Hay and McCarter 1997), growth rates, and demographics and populations dynamics (Schweigert et al. 1998). Fidelity rates

© 2001 NRC Canada

seem to be roughly related to the size of the area under consideration, about 500 km^2 being an approximate minimum size to support high fidelity. In general, results from tagging experiments indicate that there is considerable mixing of individuals among small geographic domains but also show that some herring home to spawning areas used in previous years. An interesting observation is that the geographic scale associated with fidelity rates of 60–80% in Pacific herring in B.C. (~1000 linear km of coastline or a sea surface area of about 4000 km^2) is roughly similar to that described for Atlantic herring in Newfoundland (Wheeler and Winters 1984). From the literature, we note that the genetic status of many herring populations remains uncertain, with few, if any, genetic differences observed over broad geographical ranges (Grant and Utter 1984). We also note that within the ranges for which no apparent genetic differences are described, we may see substantial variation in biology, including variation in spawning times, growth rates, and demographic composition of populations. Further genetic analyses may reveal differences among herring populations. If not, we suggest that the interpopulation mixing (straying and immigration) observed from tagging may be sufficient to preclude neutral genetic differentiation among populations but perhaps not sufficient to prevent local adaptation that results in unique demographics, growth rates, and spawning times.

Acknowledgements

The authors thank Ivan Winther, Dennis Chalmers, Sue Farlinger, and Greg Thomas for their efforts in recovering unpublished anchor-tagging data for inclusion in the herring tagging database. Parts of the paper reflect discussions about fish populations with Chris Wood and others at the Pacific Biological Station. Matt Thompson estimated the sea surface areas of herring sections. The Herring Conservation and Research Society provided the financial support for the work.

References

Daniel, K., McCarter, P.B., and Hay, D. 1999. The construction of a database for Pacific herring tagged and recovered in British Columbia from 1936 to 1992. Can. Tech. Rep. Fish. Aquat. Sci. No. 2280.

Grant, W.S., and Utter, F.M. 1984. Biochemical population genetics of Pacific herring *Clupea pallasi*. Can. J. Fish. Aquat. Sci. **41**: 856–864.

Haegele, C.W. 1990. Anchor tag return rates for Pacific herring in British Columbia. Am. Fish. Soc. Symp. **7**: 127–133.

Haegele, C.W. 1997. The occurrence, abundance and food of juvenile herring and salmon in the Strait of Georgia, British Columbia, in 1990 to 1994. Can. Manuscr. Rep. Fish. Aquat. Sci. No. 2390.

Haist, V., and Rosenfeld, L. 1988. Definitions and codings of localities, sections, and assessment regions for British Columbia herring data. Can. Manuscr. Rep. Fish. Aquat. Sci. No. 1994.

Hart, J.L., and Tester, A.L. 1937. The tagging of herring (*Clupea pallasii*) in British Columbia: methods, apparatus, insertions, and recoveries during 1936–37. Report, British Columbia Department of Fisheries for 1936. pp. 55–67.

Hasler, A.D. 1966. Underwater guidepost: homing of salmon. University of Wisconsin Press, Madison, Wis.

Hay, D.E. 1981. Retention of tags and survival of tagged Pacific herring held in captivity. Can. Tech. Rep. Fish. Aquat. Sci. No. 1050.

Hay, D.E., and Kronlund, A.R. 1987. Factors affecting the distribution, abundance, and measurement of Pacific herring (*Clupea harengus pallasi*) spawn. Can. J. Fish. Aquat. Sci. **44**: 1181–1194.

Hay, D.E., and McCarter, P.B. 1997. Larval retention and stock structure of British Columbia herring. J. Fish. Biol. **51**: 155–175.

Hay, D.E., and McCarter, P.B. 1998. Distribution and timing of herring spawning in British Columbia. Can. Stock Assess. Sec. Res. Doc. 99/14.

Hay, D.E., Kronlund, R., McCarter, P.B., and Roy, C. 1989. Spawning areas of British Columbia herring. A review, geographical analysis and classification. Vols. I–VI. Can. Manuscr. Rep. Fish. Aquat. Sci. No. 2019.

Hay, D.E., McCarter, P.B., and Daniel, K. 1999. Pacific herring tagging from 1936–1992: a re-evaluation of homing based on additional data. Can. Stock Assess. Sec. Res. Doc. 99/176.

Hourston, A.S. 1982. Homing by Canada's west coast herring to management units and divisions as indicated by tag recoveries. Can. J. Fish. Aquat. Sci. **39**: 1414–1422.

Iles, T.D., and Sinclair, M. 1982. Atlantic herring: stock discreteness and abundance. Science (Washington, D.C.), **215**: 627–633.

McQuinn, I.H. 1997. Metapopulations and the Atlantic herring. Rev. Fish Biol. Fish. **7**: 297–329.

O'Connell, M., Dillon, M.C., Wright, J.M., Bentzen, P., Merouris, S., and Seeb, J. 1998. Genetic structuring among Alaskan Pacific herring populations identified using microsatellite variation. J. Fish Biol. **53**: 150–163.

Schweigert, J.F. 1993. Evaluation of harvesting policies for the management of Pacific herring stocks, *Clupea pallasi*, in British Columbia. *In* Proceedings of the International Symposium on Management Strategies of Exploited Fish Populations. *Edited by* G. Kruse, D.M. Eggers, R.J. Marasco, C. Pautzke, and T.J. Quinn. Alaska Sea Grant College Program Rep. No. 93-02. University of Alaska, Fairbanks. pp. 167–190.

Schweigert, J.F., Fort, C., and Hamer, L. 1998. Stock assessment for British Columbia herring in 1997 and forecasts of the potential catch in 1998. Can. Tech. Rep. Fish. Aquat. Sci. No. 2217.

Sinclair, M. 1988. Marine populations: an essay on population regulation and speciation. University of Washington Sea grant, Seattle, Wash. University of Washington Press, Seattle. Wash.

Stephenson, R.L., and Kornfield, L. 1990. Reappearence of spawning Atlantic herring *Clupea harengus harengus* on Georges Bank: population resurgence not recolonization. Can. J. Fish. Aquat. Sci. **47**: 1060–1064.

Wheeler, J. P., and Winters, G. H. 1984. Homing of Atlantic herring (*Clupea harengus harengus*) in Newfoundland waters as indicated by tagging data. Can. J. Fish. Aquat. Sci. **41**: 108–117.

© 2001 NRC Canada

Appendix 1. The number of release sessions per year, sessions with no subsequent tag recoveries, numbers of returned tags, and the recovery rates are shown by year of release. The total return number of 42 767 tags includes some for which recovery information is incomplete.

Year	Release sessions	Releases with no recovery	Number of tags released	Number of tags recovered	Percent recovery
1936	4	0	8 590	53	0.6170
1937	15	0	15 673	955	6.0933
1938	18	0	17 436	469	2.6898
1939	25	2	24 355	1 243	5.1037
1940	29	4	29 502	952	3.2269
1941	21	0	23 870	462	1.9355
1942	19	5	23 209	284	1.2237
1943	13	1	30 131	629	2.0876
1944	15	4	47 374	514	1.0850
1945	16	0	47 579	926	1.9462
1946	18	0	51 531	990	1.9212
1947	22	0	41 551	2 720	6.5462
1948	22	1	45 577	2 630	5.7705
1949	17	0	34 874	1 107	3.1743
1950	29	0	56 435	3 161	5.6011
1951	31	2	69 106	4 044	5.8519
1952	40	1	88 820	1 574	1.7721
1953	53	9	111 693	3 765	3.3708
1954	21	1	42 465	3 057	7.1989
1955	25	9	51 711	1 215	2.3496
1956	28	13	64 978	1 284	1.9761
1957	9	1	28 258	258	0.9130
1958	1	0	10 412	36	0.3458
1959	2	2	7 664	0	10.0000
1964	18	0	33 568	3 771	11.2339
1965	8	0	11 928	1 198	0.0436
1966	4	0	482	29	16.0166
1967	3	3	4 099	0	0.0000
1979	4	0	3 554	33	0.9285
1980	68	23	75 233	147	0.1954
1981	99	30	114 099	783	0.6862
1982	37	3	72 097	625	0.8669
1983	27	6	56 748	243	0.4282
1985	7	1	8 900	76	0.8539
1986	6	0	8 969	300	3.3449
1988	10	0	10 741	280	2.6068
1989	54	7	68 844	602	0.8744
1990	71	8	96 671	1 550	1.6034
1991	46	10	56 522	802	1.4189
All	955	146	1 595 249	42 767	2.6808

© 2001 NRC Canada

Appendix 2. Monthly summary of numbers and percentages of (*a*) tag releases, (*b*) tag recoveries, and (*c*) tag recoveries from tags at large for one or more years. Numbers of belly and anchor tags are shown separately. The column "Unknown" indicates that the month of recovery was not known.

Tag type (years)		Unknown	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	All
(*a*) **All tag releases**															
All belly tags	*n**	44.8	45.9	66.1	620.1	91.1	4.8	1.8	17.1	35.3	80.2	38.1	17.4	1.4	1 022 871
(1937–1967)	%	4.38	0.45	6.47	60.63	8.91	0.47	0.18	1.67	3.45	7.84	3.73	1.70	0.14	100.00
All anchor tags	*n*														572 378
(1979–1991)	%	0.00	1.00	19.35	51.26	5.20	0.35	0.60	0.00	0.00	3.56	0.00	12.37	6.31	100.00
All tags	*n*														1 595 249
	%	2.81	0.65	11.09	57.26	7.58	0.42	0.33	1.07	2.21	6.31	2.39	5.53	2.35	100.00
(*b*) **All tag recovery**															
All belly tags	*n*	37 026	47	1	1	1	0	0	0	1	0	31	181	37	37 326
(1936–1967)	%	99.20	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.48	0.10	100.00
All anchor tags	*n*	13	96	64	3707	1001	18	18	13	4	6	0	415	86	5 441
(1979–1991)	%	0.24	1.76	1.18	68.13	18.40	0.33	0.33	0.24	0.07	0.11	0.00	7.63	1.58	100.00
All tags	*n*	37 039	143	65	3708	1002	18	18	13	5	6	31	596	123	42 767
	%	86.61	0.33	0.15	8.67	2.34	0.04	0.04	0.03	0.01	0.01	0.07	1.39	0.29	100.00
(*c*) **Tags at large for >1 year**															
All belly tags	*n*	33 309	5	1	1	1	0	0	0	0	0	5	18	28	33 368
(1936–1967)	%	99.82	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.05	0.08	100.00
All anchor tags	*n*	1	2	15	409	28	1	0	1	1	2	0	7	8	475
(1979–1991)	%	0.21	0.42	3.16	86.11	5.89	0.21	0.00	0.21	0.21	0.42	0.00	1.47	1.68	100.00
All tags	*n*	33 310	7	16	410	29	1	0	1	1	2	5	25	36	33 843
	%	98.43	0.02	0.05	1.21	0.09	0.00	0.00	0.00	0.00	0.01	0.01	0.07	0.11	100.00

*All *n* values except those in the final column "All" are $\times 10^3$.

© 2001 NRC Canada