

# Tagging along: association among individual Pacific herring (*Clupea pallasii*) revealed by tagging<sup>1</sup>

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**Abstract:** More than 570 000 Pacific herring (*Clupea pallasii*) were tagged with external anchor tags during 429 tag release sessions between 1979 and 1992. Individually numbered tags were released in quantities of 1000–2000 at a time and recovered from commercial fisheries. Often several tags were recovered at the same time and place, and some recoveries occurred as “matches”, where two or more tags from a single release session were recovered together. We tested the hypothesis that the frequency of matching tag recoveries occurred by chance through random mixing of tagged herring before their recapture during fishing operations. The alternative is nonrandom, positive association among tagged individuals that persisted through time and during migrations. We used a statistical method developed to address a similar question in steelhead trout (*Oncorhynchus mykiss*). In separate tests, we examined tag recovery data from migratory stocks in five major regions of the British Columbia. The results indicate nonrandom association of herring for periods of 6 months to several years and through migrations over considerable distances.

**Résumé :** Plus de 570 000 harengs du Pacifique (*Clupea pallasii*) ont été marqués à l'aide d'étiquettes-ancres externes au cours de 429 sessions de marquage de 1979 à 1992. Les poissons marqués individuellement ont été libérés en groupes de 1000–2000 à la fois et recapturés au cours de la pêche commerciale. Souvent, plusieurs étiquettes étaient récupérées simultanément au même endroit et quelquefois il y avait des “appariements” lorsque deux étiquettes ou plus provenant de la même session de libération étaient récupérées en même temps. Nous avons éprouvé l'hypothèse selon laquelle la fréquence de récupération de ces étiquettes appariées se fait au hasard, le résultat d'un mélange aléatoire des poissons marqués avant leur capture durant la pêche. L'hypothèse de rechange est qu'il existe une association positive non aléatoire entre les individus marqués qui persiste dans le temps et se maintient durant les migrations. Nous avons utilisé une méthode statistique mise au point pour résoudre un problème semblable chez la truite arc-en-ciel anadrome (*Oncorhynchus mykiss*). Des tests séparés nous ont permis d'examiner les données de recapture des stocks migrateurs provenant de cinq régions majeures de la Colombie-Britannique. Nos résultats confirment l'existence d'une association non aléatoire des harengs qui dure pour des périodes de 6 mois à plusieurs années et qui persiste au cours de migrations sur de grandes distances.

[Traduit par la Rédaction]

## Introduction

There is a substantial scientific literature on the subject of the biology of schooling and aggregations of herring (*Clupea* sp.) and other fishes. This literature covers an array of subjects such as observations and measurements of school density or aggregations, polarization of schools and shoals, stratification with depth and effect of fish size, and ecological significance of schools (e.g., general review of clupeid

biology by Blaxter and Hunter 1982). In this paper, we present another perspective on herring schooling that has implications for understanding stock structure. This perspective is based on evidence from tagging data from Pacific herring (*Clupea pallasii*). First, we emphasize that a fundamental characteristic of herring is that they are schooling fish and spend most of their lives in schools, “shoals”, or aggregations. There may be some important biological distinctions between these terms but such distinctions are not required for this paper (see Blaxter and Hunter (1982) or Pitcher (1986) for a discussion of terminology). Instead, we present evidence that herring, tagged together and released from specific locations, have an affinity for each other and that they do not mix randomly with tagged herring released from other locations. From cursory analysis of the spatial and temporal patterns of tag recoveries, we observed that most tagged herring were recovered in groups of two or more, often originating from the same tagging release date and site. Sometimes two or more tagged fish were recovered at the same date and location, after having been tagged and released in the same operation some months or years earlier. This raises the question of whether the event was simply a coincidence or whether there might be some aspect of fish

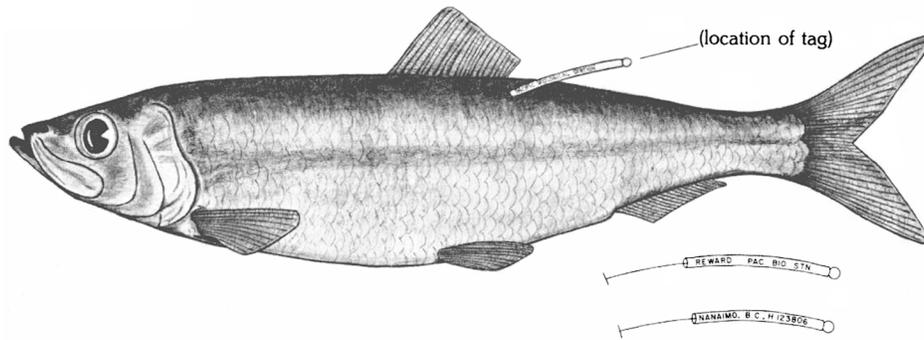
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**Fig. 1.** Drawing of a herring (*Clupea pallasii*) showing the anchor tags and the position of insertion in the dorsal musculature.**Table 1.** Summary of the year and month of tag releases showing that most tags were released in March and that few tags were released in the fall months from 1985 to 1991.

Year	January	February	March	April	May	June	September	November	December	All
1979								3 554		3 554
1980	978		41 703	8 212			10 758	8 617	4 965	75 233
1981	2 958		64 968	14 878	1 998		9 641	9 171	10 485	114 099
1982	1 496	11 636	20 990	2 677		2 479		29 844	2 975	72 097
1983	296	8 828	9 372			976		19 596	17 680	56 748
1985			8 900							8 900
1986			6 969	2 000						8 969
1988			10 741							10 741
1989		31 429	37 415							68 844
1990		45 130	50 042	1 499						96 671
1991		13 744	42 278	500						56 522
All	5 728	110 767	293 378	29 766	1 998	3 455	20 399	70 782	36 105	572 378

**Note:** Empty cells indicate months of no releases.

behaviour that could be responsible for their identical proximity in time and space at release and at recovery.

After finding a high incidence of matching tags (animals tagged at the same time and location and subsequently recaptured together) recovered in high seas fishing for Pacific salmon and steelhead trout (*Oncorhynchus mykiss*) in the North Pacific Ocean, McKinnell et al. (1997) developed a method to determine the probability that an observed frequency of matching tag recoveries might have occurred if these tagged fish had been randomly mixing with other similarly tagged fish. Our objective in this paper is to describe the occurrence of matching tag recoveries and test a null hypothesis that "all herring recovered from a release event occurred with no more coordination among their recovered members than with members of other release events". The alternative hypothesis is that at least some of the recovered members of the release event traveled in a coordinated manner and associated with herring from the same release site.

## Methods and materials

### Tagging data

A fishery for herring roe was started in British Columbia (B.C.) in the early 1970s. In 1979, a new tagging program that used external Floy<sup>®</sup> anchor tags (Floy Tag Inc., Seattle, Wash.) accompanied this developing fishery. Individually numbered tags could be traced back to the date and location of release. Each tag consisted of a plastic tube attached to a

monofilament T-shaped end that was inserted into the dorsal musculature (Fig. 1). Full descriptions of previous herring tagging programs in B.C. are provided in Haegele (1990), Daniel et al. (1999), and Hay et al. (2001).

Our analysis of tagging data used Microsoft Excel<sup>®</sup> and Access software, and quantitative analyses were made with SYSTAT<sup>®</sup> and Minitab<sup>®</sup> (Minitab Inc., State College, Pa.) statistical software and custom software developed by McKinnell to test the hypothesis of random mixing. Most tags were released in the early 1980s during the spawning and fishing seasons (Table 1). Most releases occurred during two distinct periods: (i) a spring roe fishery (February–April) when herring migrate to nearshore waters to spawn, and (ii) a fall fishery (November–December) for whole herring that occurs as herring migrate from summer feeding areas to overwinter areas (Hay and McCarter 1997a).

### Tag recoveries

Roe fisheries usually occur in the spring in the immediate proximity of spawning areas. Two types of fishing gear are used: purse seines and gillnets. In general, there are separate fisheries for each type of gear (Stocker 1993). The objective of the fishery is mature roe, and therefore, fishery openings are very short: usually no longer than a day or two for gillnets and often only a few hours for purse seines. Sometimes tags were recovered onboard vessels, but most were recovered in processing lines where individual fish were handled to excise the roe. In one season, there were usually only

a few fisheries open in any single region, and openings were restricted to relatively small geographic areas, usually within a single statistical area and often with single sections or parts thereof. The price of roe varies according to the type of fishing gear and location of the catch. For these reasons, the exact origin and date of a tagged fish recovered in the plants was known, even when the fish were on the processing line. Some recoveries also occurred during much smaller fall "food" fisheries when purse seiners captured herring, usually from the North Coast or Strait of Georgia, for small specialized markets for fresh, pickled, or smoked herring. Again, tag recoveries were made mainly in processing plants and the exact recovery date and geographical origin could be determined. It was not possible, however, to determine the vessel that recovered each tag.

### **Spatial analysis: geographical definitions and temporal and spatial precision**

Management of herring in coastal waters of B.C. (by Fisheries and Oceans Canada) relies on nested geographical groupings, the largest of which are called "regions", that correspond to natural geographic groupings. The six regions are the 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. 2a). Regions are polygons that are subdivided, for management purposes, into about 30 smaller polygons called "statistical areas" (Fig. 2b) or 108 "sections" (Fig. 2c). Each statistical area is an aggregation of several smaller sections (Fig. 2). Regions vary in size from 3000 to 10 000 km<sup>2</sup>, statistical areas from 500 to 2500 km<sup>2</sup>, and most sections are less than 300 km<sup>2</sup> (Hay et al. 2001). An even finer geographic category is a "location", which is a specific geographical entity, but not a polygon. There are about 1800 location names used for various aspects of herring management in B.C. (Haist and Rosenfeld 1988) and usually many locations per section. Although locations have no "area" (i.e., km<sup>2</sup>), they represent geographic categories that usually are considerably smaller than sections.

For analyses we defined three different events, each with specific dates and locations: (i) a tag "release" event was the release of tagged fish at a specific location on a specific day; (ii) a tag "recovery" event was the recovery, at a specific location, of one or more tags originating from one or more release events; and (iii) a "release-recovery" event was the number of unique combinations of release and recovery events. For instance, single recovery events often recovered two or more tags from several release events. Tag recoveries were considered to be matching if two or more tags from the same release event were caught in the same recovery event.

### **Tag selection criteria**

Only anchor-tag data collected from 1979 to 1992 were used. Earlier tagging data, collected from 1936 to 1969 using internal belly tags collected in reduction plants, provided only approximate information on dates and locations of recovery (Hay et al. 2001). In contrast, most anchor-tag data had included the date of recovery and location but the precision varied. Some tags had no information on the location or date of capture, and some had only partial information such as the date to the nearest month or only general information

on recovery location. Therefore, we restricted the data for this analysis to include only those recovery records for which we knew the exact location and date (day). For analysis of the probability of matches, we further restricted the data to include only tags that had been at large for a minimum of 6 months. This restriction ensured that the release-recovery duration was sufficiently long that all herring underwent some degree of migration: either from the spawning areas to summer feeding areas, and then back to overwintering areas, or from wintering areas to spawning areas. Finally, we restricted the analyses to two distinct time periods: a 4-year period between 1981 and 1984 and a second period from 1989 to 1991. Because most herring were tagged when they were sexually mature and because the age of maturity in B.C. herring is about 3 years of age (Hay 1985), most tagged herring would be age 3 or older. Therefore this restriction allowed for a biologically reasonable period for tagged herring, released 2–3 years apart, to either disassociate and mix or, alternatively, retain associations over long periods of time and space.

### **Estimating geographical position and distances traveled**

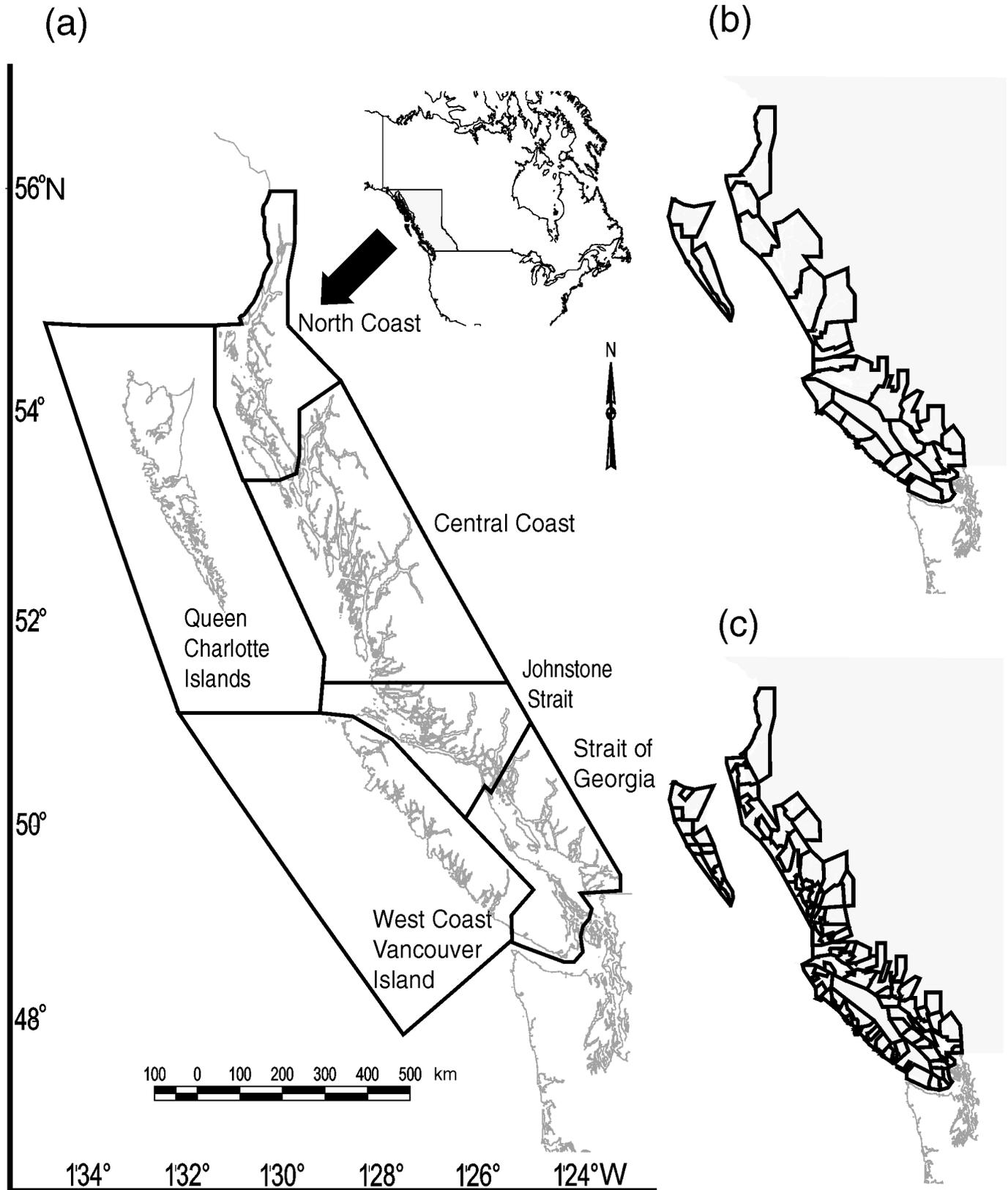
We calculated the duration of time at large in days and estimated the distance between release and recovery for each release-recovery event. Estimates of distance traveled were made by comparing geographical coordinates (latitude and longitude) of central positions of the sections for each release and recovery record. Simple triangulation was used to estimate the approximate distance traveled (nautical miles (n.mi.)) between release and recovery. We did not adjust for additional distances required to migrate around complex coast lines; therefore, the actual distances moved by herring are underestimated by our approach, especially between the Strait of Georgia and other regions. The estimates were intended only to be approximations.

### **Match analyses—estimating probability of nonrandom tag aggregations**

To quantify the rarity of the observed numbers of matching recoveries, we used the probability distribution when the null hypothesis was true (the null distribution), i.e., how many matches are expected if tagged herring from release events did not associate with each other and traveled in an uncoordinated manner? Temporal stratification of tags to early and late periods facilitated a spatial-temporal framework where the null hypothesis of uncoordinated movement might apply. For example, herring from two release events separated by 10 years probably would not have the opportunity to travel together, and therefore, temporal stratification is required. As was done for steelhead trout (McKinnell et al. 1997), the geographic or regional stratification was based on prior knowledge of herring behavior that most tagged herring (~80–90%) are recovered within the region of release (Hay et al. 2001). As only six tag recoveries had been released in Johnstone Strait, no analysis was possible for that region.

For each stratum, we determined the unique null distribution resulting from the number and size of successful recovery events and their matching recoveries. If the null hypothesis of random mixing were true, then the observed matches were taken from an unorganized mixture of release events and could be viewed as one realization from all possible ran-

**Fig. 2.** Map of the coast of British Columbia, Canada, indicating (a) the six geographical regions, (b) statistical areas, and (c) sections.



dom shuffles of the recoveries among the successful recovery events without regard to release event. The numerical values for the probabilities of matches among recovery events,

which compose each null distribution, were evaluated from 10 000 Monte Carlo trials. For each simulation, the stratum tag recoveries were shuffled randomly and independently,

without reference to release event membership, among the total successful recovery events so that the observed numbers and sizes of recovery events were preserved. For each simulation, the total number of tags involved in matching recoveries was recorded.

Compared with the null distribution, the probability distribution of matches when the alternative hypothesis was true (the alternative distribution) would have its probability mass shifted toward outcomes with greater numbers of matches. Therefore, the probability ( $P$ ) associated with the statistical test of the null hypothesis was computed from the null distribution as the sum of probabilities of outcomes with equal or more matching tags than was observed. The probability of the test was called the tail probability because the sum included all outcomes in the right-hand tail of the null distribution. The same hypothesis was tested from data of each stratum.

## Results

### The frequency of matches

Over 572 000 tags were released between 1979 and 1991 (Table 1). Of these, 5400 (about 1%) were eventually recovered, although most were recovered within a short time after release. A total of 3537 tags met the precise criteria for date and location (Table 2). Of these, 767 tags were recovered singly and 2870 tags (81%) were recovered with at least one other tag from the same release. Sample sizes of the latter ranged from 2 tags to a maximum of 165 matching tags. Most occurrences of large matched recovery events, however, involved tags that were at large for relatively short periods, some as short as a single day, but most for 10–15 days. These generally represent instances where tagging operations occurred several weeks before fisheries. In some instances, however, large numbers of matched tags were recovered several months after release.

A total of 330 tags were at large for more than 6 months, or 183 days (Table 2). This subset of the data includes tags released and recovered from all regions of the B.C. coast (Table 3). By limiting our analyses to tags that had been at large for a minimum of 6 months, we ensured that there was ample opportunity for mixing to occur and that all recoveries were from herring that had undergone some form of seasonal movements: either movement or migration to or from spawning areas or overwintering areas or to feeding areas in late spring and summer. The subset of data includes tags that were released and recovered in all regions. Over 70% were at large for a year or more. The 330 recoveries that met all criteria for inclusion consisted of 208 tags that were recovered as single tags and 122 tags that occurred as matches of two or more tags (Table 2). Most of the latter were “pairs”, but there were instances of matching recoveries of up to 10 tags.

### Probability of cohesion occurring by chance

The Monte Carlo tests of hypothesis (Table 4) indicated that four of the six tests were significant at the 0.05 probability level (for three of these,  $p \ll 0.01$ ). For instance, of 37 tags recovered in the NC, there were 15 tags from matched recoveries. The probability of this number of matching tags (15) occurring by chance was  $<0.0005$ . The results for three

of the other region–period strata indicated that the probability of the observed numbers of matching tags occurring by chance was unlikely. No matches occurred among the 12 tags in the stratum with the least number of tags recovered (CC early), so no test was possible. Of the two remaining strata, the NC early had a tail probability of 0.099 of occurring randomly and the WCVI test was not significant.

### Geographical movements and time at large of matched tags

Thirteen of the 122 matched tag recoveries were made in regions other than their release, for a mean distance between the release and recovery site of 80 n.mi. and a mean time at large of 1.12 years (Table 5). Similarly, 28 matched recoveries changed statistical areas (mean distance and time of 48 n.mi. and 1.1 years, respectively) and 58 changed sections (mean distance and time of 20 n.mi. and 1.4 years, respectively). Only 23 matched tags were captured in the same section as their release.

## Discussion

### A perspective of the occurrence of matches and the significance of the tests

Although the overall recovery rate of anchor tags was only about 1% (Hay et al. 2001), most were recovered in matches of two or more tags; therefore, such matched recoveries appear to represent the norm and not the exception. Viewed in this way, we suggest that the results of our analyses, which show significant nonrandom associations of individual herring, are not surprising or precariously dependent on a specific subset of the data as the basis for statistically significant outcomes. Rather, the same results, with even higher levels of significance, would have been achieved had we used a larger subset of the data, say, allowing for only 3 months at large instead of 6 months. Therefore, we think that our stringent selection criteria and analyses would have failed to show significant nonrandom associations if such nonrandom associations were weak. Instead, because of the strict selection criteria of the subset of data used, our results would tend to err on the conservative side in the sense that the significance of the tests may tend to underestimate the strength of positive association among tagged herring.

### Biological explanations of the results

The analyses do not support the hypothesis that the frequency of matched tags would occur as a coincidence through random, uncoordinated movements of herring. Instead, the results indicate that there is positive association among tagged individuals released at the same site. For simplicity and clarification in subsequent discussion, we call this a “conspecific” association—meaning that there is some form of cohesion among groups of similar origins—or conspecifics. A direct explanation of the results requires that tagged herring from single release sites continue to associate with each other as they undergo seasonal movements throughout the B.C. coast and that such associations persist through time, for at least 6 months but probably for years. An alternate explanation for these results is that herring tagged and released together do not necessarily associate at all, but rather mix randomly and then home to spawning sites. If so, the incidence of

**Table 2.** Summary of anchor-tag recovery data.

Category of matched tags	Frequency	Total number	Number at large >6 months	Days at large		
				Minimum	Mean	Maximum
1 (unmatched)	767	767	208	1	171.6	1817
2 (pairs)	146	292	52	1	105.4	1084
3 (triplets)	78	234	42	4	92.7	751
4	41	164		4	41.3	177
5	21	105	10	4	54.7	387
6	17	102		1	23.9	122
7	17	119		1	18.1	98
8	7	56	8	2	74.7	383
9	4	36		14	35.0	96
10	6	60	10	11	79.0	376
11	3	33		10	41.0	98
12	4	48		9	60.7	111
13	2	26		98	104.5	111
14	2	28		16	19.0	22
15	1	15		10	10.0	10
16	1	16		13	13.0	13
17	3	51		17	46.3	98
18	2	36		22	22.0	22
19	1	19		20	20.0	20
22	2	44		13	13.5	14
23	1	23		21	21.0	21
25	1	25		21	21.0	21
29	1	29		13	13.0	13
30	1	30		18	18.0	18
32	1	32		8	8.0	8
35	1	35		14	14.0	14
37	1	37		15	15.0	15
38	1	38		14	14.0	14
39	1	39		16	16.0	16
40	1	40		8	8.0	8
41	1	41		9	9.0	9
43	1	43		15	15.0	15
44	1	44		18	18.0	18
46	1	46		15	15.0	15
49	1	49		10	10.0	10
55	1	55		13	13.0	13
84	1	84		18	18.0	18
89	1	89		7	7.0	7
95	1	95		20	20.0	20
108	1	108		13	13.0	13
139	1	139		3	3.0	3
165	1	165		12	12.0	12
All	1147	3537	330	1	139.6	1817

**Note:** The first column shows the category or number of matched tags in recovery events. The frequency of all occurrences of unmatched and matching tags and the total number of tags (category  $\times$  frequency) is indicated in the second and third columns. Tags used for hypothesis testing (>6 months at large) are shown in the fourth column, where no entry indicates zero. Columns on the right show the minimum, mean, and maximum duration of tags at large (in days). There were only single occurrences of all matches exceeding 22 tags.

matched tags could be a consequence of a reassociation of tagged herring homing to spawning sites. A problem with this explanation, however, is that degree of homing (fidelity) to specific locations is low (Hay et al. 2001). Also, matched tags were released or recovered at times other than the spawning season, during late fall, or 1–2 months before spawning.

Further, most matched tags were recovered in areas different than their release. Therefore, the combination of uncoordinated movement combined with homing to spawning areas is not a satisfactory explanation for our results. Instead, the results suggest that there must be some form of cohesion among conspecific herring allowing them to remain to-

**Table 3.** The subset of tag recovery data used for the Monte Carlo hypothesis test.

Release region	Recovery region					Total
	QCI	NC	CC	SOG	WCVI	
QCI	24	9	5	0	0	38
NC	3	46	2	0	0	51
CC	0	1	94	1	2	98
JS	0	0	0	5	1	6
SOG	0	1	3	60	1	65
WCVI	3	1	5	23	40	72
Total	30	58	109	89	44	330

**Note:** Only tags with precise recovery information (location and day) recovered within two periods (1981–1984 or 1989–1991) and at large for 6 months or longer were used. The regions include the Queen Charlotte Islands (QCI), North Coast (NC), Central Coast (CC), Johnstone Strait (JS), Strait of Georgia (SOG), and the West Coast of Vancouver Island (WCVI). None of the recoveries in JS met the selection criteria.

**Table 4.** Results of tests of association, stratified by region and period (early, 1981–1984; late, 1989–1991).

Recovery region	Period	Total number of tags	Observed number of matches	Probability of random mixing
QCI	Early	30	6	0.0990 ns
NC	Early	21	5	0.0036 *
NC	Late	37	15	0.0005 **
CC	Early	12	0	na
CC	Late	97	66	0.0000 **
SOG	Early	89	22	0.0002 **
WCVI	Early	44	8	0.3240 ns

**Note:** The matching tags are those with the same “release–recovery” event. The asterisks indicate the levels of significance at probability levels of 0.05 (\*) and 0.01 (\*\*); ns, not significant; na, not available. The regions include the Queen Charlotte Islands (QCI), North Coast (NC), Central Coast (CC), Johnstone Strait (JS), Strait of Georgia (SOG), and the West Coast of Vancouver Island (WCVI).

**Table 5.** Release and recovery statistics of 122 matches from 44 release–recovery events.

	Number of release–recovery events (matches)	Number of release events	Sum of tags recovered	Mean years at large	Mean distance traveled (n.mi.)
Region change	6	5	13	1.12	80
Statistical area change	12	11	28	1.10	48
Section change	17	17	58	1.42	20
No change (same sections)	9	9	23	1.15	7
All matches	44	42	122	1.24	33

**Note:** The list is ordered according to the degree of geographic change, indicated by three rows showing movements of matching recoveries among regions, statistical areas, and sections and one row showing matches with no change in geographical area. The column on the left shows the “release–recovery” events associated with specific release event. For each category, the three columns on the right show sum of all matched tags, the mean time (years) at large, and distance traveled (in nautical miles, n.mi.) between release and recovery.

gether within aggregations that move over considerable distances and endure for considerable periods: years or more and perhaps most of their lives.

### Biological mechanisms of social cohesion in herring

If cohesion of conspecific herring occurs, it is unclear whether there are distinct signals that allow herring to recognize other members of their group. If individual herring “stick together” over long periods and broad spatial scales, then they might benefit from some mechanism for conspecific recognition or social cohesion and “membership”. The phenomenon of cohesion has been described for other pelagic fishes such as yellowfin tuna (*Thunnus albacares*; Klimley and Holloway 1999). Klimley and Holloway also provide a brief review of the literature, showing that there are a few reports of such occurrences of “social cohesion” in other species, but they are mainly without comment on the biological mechanisms involved. Although we have no further information on this topic, we point out that the biological mechanisms required to maintain social cohesion would, presumably, involve some or all sensory systems, including visual recognition. If vision were involved, it is difficult to understand how this would operate at great depths (often greater than 100 m) when herring aggregate close to bottom, or at night when herring form broad, loose spatial aggrega-

tions near the surface (Hay and McCarter 1995). Other sensory systems that could maintain these associations might involve the acoustic lateral system, which is well developed in herring (Blaxter and Holliday 1963). Conceivably, herring might emit and detect sounds with could enable recognition of fellow members in a group, although this would seem to be unlikely in view of the dynamic changes in swim bladder gas volume (Ona et al. 2001). The remaining sensory system would involve olfaction. There is evidence that olfaction may be used to detect sexual readiness in herring (Carolsfeld et al. 1992), but this occurs during periods when milt concentrations are extremely high. The detection and distinction of different “groups” of herring would require sensitivity of much lower concentrations of material. Although such detection seems intuitively improbable, especially when there is no basis for assuming that there would be any differences in scent among herring, olfactory detection is used by salmonids to navigate to natal spawning areas (Hasler 1966) and perhaps even to recognize conspecifics (Groot et al. 1986).

The issue of possible conspecific recognition and how it might occur is not understood but may be fundamental to understanding issues related to assessment and conservation of herring and other fish species. On the other hand, perhaps the issue of biological linkages among conspecifics is a “red

herring” and not required to explain these results. Instead our initial dichotomous hypotheses of random mixing or panmixis (the null hypothesis) versus positive association of conspecifics (the alternative hypothesis) may be an oversimplification. Perhaps some random mixing among individuals occurs in large shoals or conglomerations, but this may be the exception and not the rule. Instead, herring, like other social fishes, may rarely segregate as individuals, but smaller groups may remain together in a level or organization between an individual and a large school. If so, then the social behaviour that binds individuals together may operate without any requirement for biological recognition of conspecifics. Rather, the mechanisms that promote tight schooling may be so strong that many individuals in a group (such as those released from a tagging operation) may be expected to retain membership in that unit only through the strength of mutual attraction from schooling behaviour and not necessarily because of population-specific recognition signals. This is speculation, however, and perhaps the only conclusion that we may draw from our analyses is that tagged herring stick together, but we do not know how they do it.

### Implications for research and management

If conspecifics associate together, it follows from the results that there may be a level of structure, perhaps dynamic and subtle, that occurs in large aggregations of herring that prevents thorough mixing. If so, large aggregations of herring typical of summer feeding concentrations could represent conglomerations of different populations, with different biological origins, destinations, and other characteristics. In B.C. and most other areas inhabited by herring, dense aggregations also form during the overwintering period. In general, these aggregations appear to be larger but fewer in number and spatial scale than aggregations observed at other times of the year, particularly during spawning periods (Hay and McCarter 1997b). This indicates that when these aggregations break up, herring move into smaller components and move away, perhaps to spawning or feeding areas. Therefore, we think that it is reasonable to assume that herring from different origins could merge or “appear” to merge into large loose aggregations. Subsequently they might dissociate into smaller units that retain some or much of the original membership. This would explain the patterns of matched tag recoveries observed after considerable periods (>200 days) and spatial ranges (>100 n.mi.). This interpretation supports the view that smaller aggregations may consist of fish with some common heritage, although not necessarily genetic. If so, when such small aggregations of relatively homogeneous fish (conspecifics) join with others to form larger conglomerations, they may not mix thoroughly. If so, conglomerations may confound attempts to take representative biological samples random from such mixtures. Instead such conglomerations of herring may contain components that exhibit a range of different biological attributes, such as different sizes and ages, nutritional states and conditions, and maturation schedules, and perhaps even some form of spatial imprinting for approximate spawning sites (McQuinn 1997; Hay et al. 2001). It follows that fisheries directed on such mixed groups would have uncertain consequences, with the risk of relatively higher mortality among the smaller components.

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