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Review of tagging studies on Atlantic herring (*Clupea harengus*) in relation to transboundary movement in the Bay of Fundy/Gulf of Maine/Scotian Shelf region of the Northwest Atlantic

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Abstract

The management of Atlantic herring in the Bay of Fundy/Gulf of Maine/Scotian Shelf region of the Northwest Atlantic (NAFO areas 4WX5YZ) assumes separate stocks in Canadian and US waters; however, herring landed in the weir fishery in southwest New Brunswick (SWNB) are assumed to be of US origin for management purposes. The present study is a review of tagging studies that have been conducted on herring since the 1950s in NAFO areas 4WX5YZ. The tagging data show consistent patterns over time. Juvenile herring in the coastal Gulf of Maine and SWNB nursery areas generally show only movements between these two areas. These nursery areas are believed to include herring that hatched from the US and Canadian spawning grounds, contrary to the current management assumption for the weir fishery in SWNB. As herring mature, they are understood to primarily return to their natal spawning area. The tagging data show mixing of adults from different spawning grounds (including transboundary mixing) during the summer feeding and overwintering seasons. Canadian spawners have been observed to overwinter in New England and US spawners have been observed to overwinter in Nova Scotia. Herring tagged on Canadian spawning grounds have been recaptured in the SWNB weir fishery, refuting the assumption that all herring landed in this fishery are of US origin. The tagging data suggest that the weir fishery comprises a mix of herring hatched from spawning grounds in Canada and the US. The biases associated with recapture data from tagging programs precludes estimation of any proportions of stock mixing. Alternative methods for evaluating stock structure in NAFO areas 4WX5YZ are recommended.

Keywords: juvenile herring; migration; overwintering; stock structure; weir fishery

Introduction

Stock structure of Atlantic herring (*Clupea harengus*; hereafter, herring) is complex and stocks have generally been defined in the Western Atlantic based on Northwest Atlantic Fisheries Organization (NAFO) divisions (Melvin *et al.,* 2009). Stock in this context refers to a group of fish sufficiently isolated from other groups so as to allow for fisheries management. Each stock has multiple spawning areas that result in reproductively isolated subpopulations and there is mixing among adjacent stocks during feeding and overwintering migrations (McQuinn, 1997; Stephenson *et al.,* 2009). Each stock spawns in specific locations at known times (Geffen, 2009; Melvin *et al.,* 2009). The assumption that herring exhibit spawning-area fidelity (Stobo, 1982; McQuinn, 1997) has been

the basis of the definition of herring stocks and fisheries management (Stephenson *et al.,* 1993), but the degree of natal homing versus genetic exchange among spawning assemblages within a metapopulation remains a source of uncertainty (Brophy *et al.,* 2006; Stephenson *et al.,* 2009). Herring stock structure for fisheries management in the Bay of Fundy/Gulf of Maine/Scotian Shelf region of the Northwest Atlantic (NAFO areas 4WX5YZ) is complicated by the life history of herring, where annual long distance migrations occur to adult feeding and overwintering areas where there is overlap of multiple sub-populations from different spawning areas (Stephenson *et al.,* 2009). In NAFO areas 4WX5YZ, at least seven major spawning areas have been characterized (Fig. 1). The timing of spawning varies from May to November with the degree of spring spawning increasing with latitude, but the majority of spawning (~90%) occurs in autumn (Wuenschel and Deroba, 2019). These spawning time differences (spring vs. autumn) provide a further basis for reproductive stock separation (Melvin *et al.,* 2009).

The Canadian herring fishery in NAFO areas 4VWX5YZ is managed as five different units: Southwest Nova Scotia/Bay of Fundy (SWNS/BoF), offshore Scotian Shelf, coastal Nova Scotia (NS), Southwest New Brunswick (SWNB) "migrant juveniles" (nearshore fishery), and Georges Bank. The SWNS/BoF management area makes up the majority (75% over the last 10 years) of the 4VWX landings (DFO, 2020a). The SWNS/BoF herring fishery is managed by an annual total allowable catch (TAC). The SWNB "migrant juvenile" fishery (hereafter, "SWNB weir fishery") overlaps spatially with the SWNS/BoF management unit, but consists only of nearshore landings by weir, trap nets, and shut-offs in SWNB. The SWNB weir fishery is effort controlled and the landings are not included towards the TAC for the SWNB/BoF management unit (DFO, 2020b).

The SWNB weir fishery landings are primarily juveniles and for decades have been assumed for management purposes to be dominated by "migrant juveniles" from the Gulf of Maine (GoM) and Georges Bank spawning

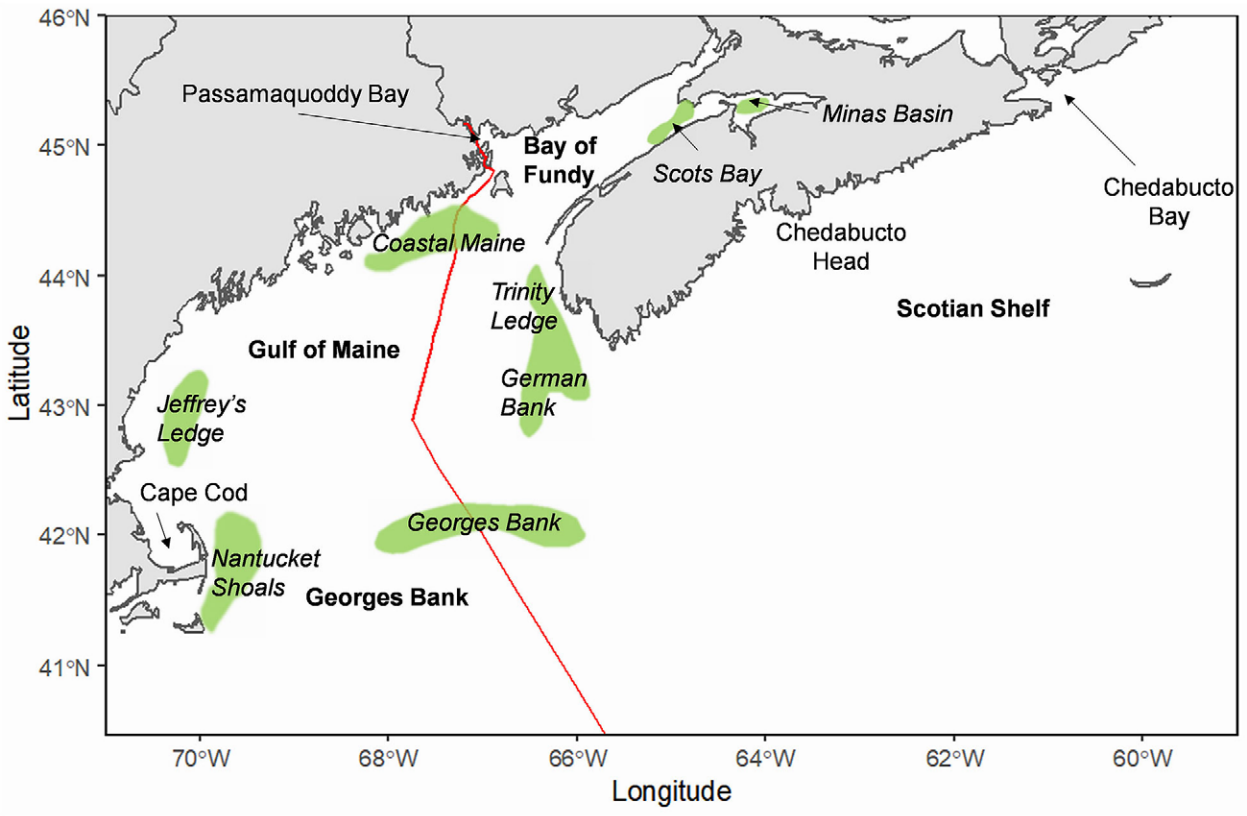

Fig. 1. Map of the study area showing the Bay of Fundy, Gulf of Maine, Scotian Shelf and areas referenced in this review. Major spawning areas in green based on Stephenson *et al.* (1993) although there are spatial variations in the spawning areas reported in other studies (*e.g.*, Waring 1981; Tupper *et al.* 1998; Overholtz *et al.* 2004; Stephenson *et al.* 2009). The Canada/US border is in red.

components of the US stock (Stephenson *et al.,* 1993; DFO, 1999, 2000; NFSC, 2012). This assumption dates back to at least the 1970s when it was hypothesized that juvenile abundance in SWNB may indicate future recruitment to the Georges Bank fishery (ICNAF, 1973). The assumption listed in the 1999 Fisheries and Oceans Canada (DFO) stock status report for NAFO areas 4VWX5Z herring was that all juvenile herring from the SWNB weir fishery originate from the US coastal complex which at the time was considered at high abundance (DFO, 1999). In the most recent 4VWX assessment, all juvenile and adult herring landed in the SWNB weir fishery are excluded from the SWNS/BoF TAC and assumed, although not explicitly stated, to originate from the US spawning components (DFO, 2020a).

The US herring fishery in NAFO areas 5YZ is managed as four different units. Quota management begins with the specification of a stock-wide, annual, overfishing limit (OFL) that corresponds to the catch that would result from applying the fishing mortality rate associated with maximum sustainable yield or a proxy. The OFL is then reduced to account for scientific uncertainty, which results in the annual, allowable biological catch (ABC). The ABC is further reduced to account for management uncertainty, which results in the stock-wide, annual catch limit (ACL). The SWNB weir catches are assumed to be fish from the US stock, but the effort controls used to manage the SWNB weir fishery can create fluctuations in catch that are difficult to anticipate. To account for these fluctuations during US quota setting, a recent (usually 10 year) average of the SWNB weir catches is subtracted from the ABC as part of management uncertainty, resulting in the ACL. The stock-wide ACL is then subdivided into four management areas with the intention of avoiding overfishing in each sub-stock. The biomass of the US stock has decreased in recent years and the ABC has been reduced such that the SWNB weir catches have approached 50% of the ABC. The assumption of the SWNB weir catches being US fish now has a strong influence on ACLs.

The scientific characterization of herring stocks and management units in NAFO areas 4WX5YZ has been almost exclusively examined through tagging studies for the past several decades (*e.g.*, ICNAF, 1976; Stephenson *et al.,* 1993; DFO, 2007; NFSC, 2012). The number of herring tagged in NAFO areas 4WX5YZ exceeds 750 000 individuals. Tagging studies have focused on both nearshore juvenile herring, overwintering herring, and spawning adults. Tagging studies have used a wide variety of gear and fisheries for capture and recovery and an equally diverse array of timing and duration of study. The present study is a synthesis of all data to date on tagging studies in NAFO areas 4WX5YZ to address two main objectives related to the management of herring fisheries: 1) evaluate the assumption that herring landed in the Canadian weir fishery in SWNB are of US origin, and 2) evaluate transboundary movement and the degree of movement of herring among management units in NAFO areas 4WX5YZ.

Materials and Methods

Data from tagging studies in NAFO areas 4WX5YZ were assembled and synthesized. The studies consisted of peer-reviewed publications, government reports, and unpublished data. The synthesis of tagging study data presented a number of challenges due to the age/life-stage tagged, varying geographic resolution, duration of each study, capture methods, inconsistencies in return collection, and inconsistencies in calculation of the reporting metrics. In order to provide an interpretable synthesis of these data, all tagging and recapture locations were reassigned to consistent geographic zones. Spawning areas are distinct and given the importance of spawning areas in defining populations, these were included in the geographic resolution (each tag return area typically held a distinct spawning area). Wherever possible, the boundaries of the NAFO areas were used as the initial basis of tagging zones (Fig. 2). One of the objectives of this study relates to transboundary movement so the Canada-US border was used to define tagging area boundaries (Fig. 2, shown in red). The exception to this is in the area of the disputed "gray zone" were the 4X5Y NAFO boundary was used to delineate zones and the Canadian portion of Georges Bank was included in the Georges Bank zone. As NAFO area 4X encompasses a number of distinct herring spawning areas, the tagging boundary designations IX and X agreed upon by the US National Marine Fisheries Service and DFO (Stobo, 1982, Creaser *et al.,* 1984) were used to distinguish SWNB (X), the upper BoF (IX) from the remainder of NAFO area 4X. While scientists have agreed upon 14 tagging zones (Creaser *et al.,* 1984), six of which are in the GoM, these were largely aggregated within the NAFO areas to simplify results for the purposes of this review. Given the geographic scope of this review and the rarity of far northern and eastern tag recoveries, NAFO areas 4VW were considered as one zone. The resultant divisions provide seven geographic zones for evaluation of tagging data. These geographic zones are referred to as New England, encompassing the area to the southwest of 5Z (5Zw and 6), Georges Bank (5Z) which encompasses both Georges Bank and Nantucket Shoals spawning zones, GoM (5Y), which encompasses the Jeffery's Ledge and Coastal Maine spawning areas, SWNB (4X-X) into which the Coastal Maine spawning area extends and includes

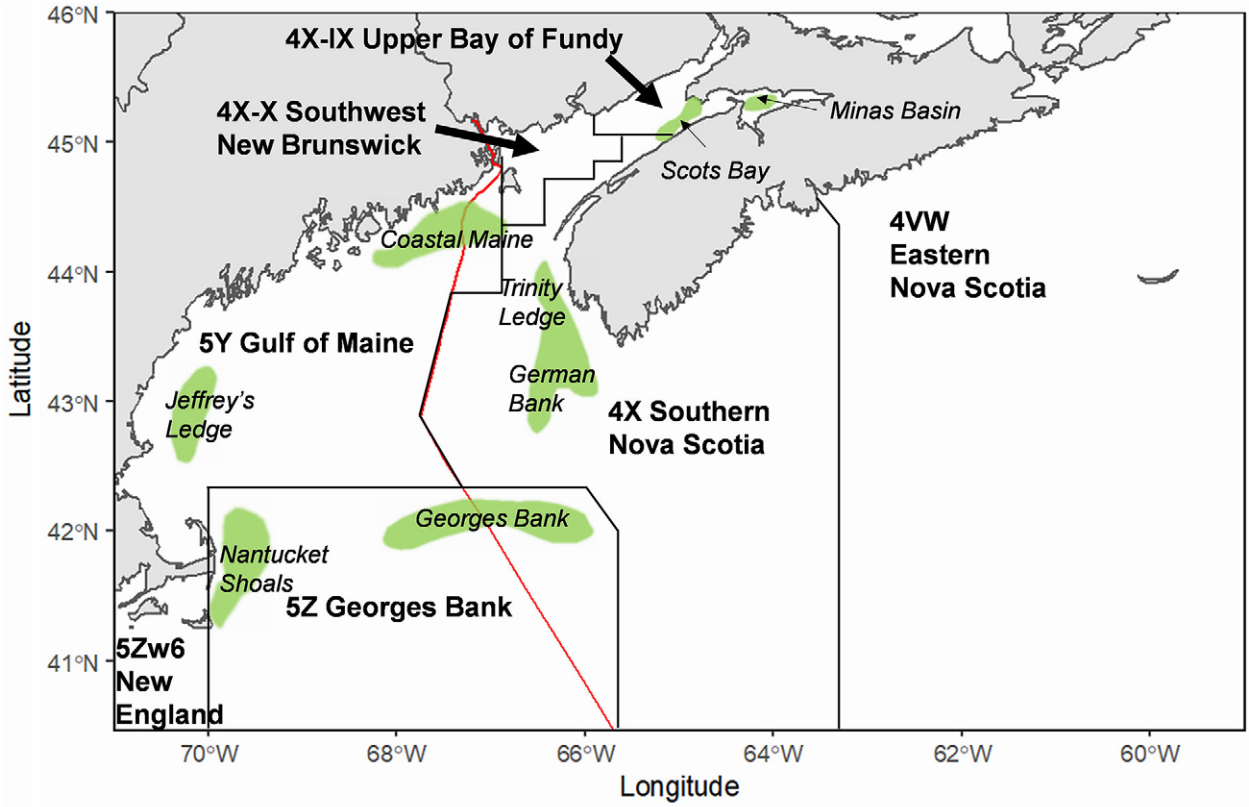

Fig. 2. Map showing the seven tagging zone delineations based on NAFO area divisions. The Canada/US border is in red. Major spawning areas in green based on Stephenson *et al*. (1993) although there are spatial variations in the spawning areas reported in other studies (*e.g.*, Waring 1981; Tupper *et al*. 1998; Overholtz *et al*. 2004; Stephenson *et al*. 2009).

the SWNB weir fishery, upper BoF (4X-IX) that has the Scots Bay and Minas Basin spawning areas, Southern NS (remainder of 4X) with the German Bank and Trinity Ledge spawning areas, and Eastern NS (4VW; Fig. 2).

Although tagging studies included multiple tagging locations within a geographic zone, the tagging locations were aggregated to one of the seven geographic zones. Each study is reported by the zone for which the tags were applied. Dates of recapture and time at large are important in the evaluation of individual studies, these vary substantially from study to study and are reported for each study to aid in interpretation of the tag return data. Tagging studies often use an effective recovery time period (*e.g.*, number of days) when presenting results because tagging efforts are likely to recapture tagged individuals within short periods after tagging. The effective recovery time period reported for each study is the initial period of time during which recaptures are ignored in the results. For the studies in this review, this varied from 0 to 14 days and could not be adjusted to a consistent value. The percentage of tag recoveries reported in the results are the effective recoveries and ignore the recaptures before the effective recovery time period.

Results

Herring movement in the Bay of Fundy and Gulf of Maine 1957 and 1958

The movement of immature herring was examined in the southern part of the BoF and the western part of the GoM in 1957 and 1958 (McKenzie and Tibbo, 1961). Results of the 1957 tagging studies were also reported in McKenzie and Scud (1958) and McKenzie and Tibbo (1958) but are reported for the combined study (McKenzie and Tibbo, 1961). All herring were obtained from nearshore weirs and seines and were implanted with opercular tags. The overall mean length of herring tagged in 1958 was 14.1 cm and was thought to represent age 1 to 3 (juvenile) herring.

Herring were tagged at 42 locations and more than half of those locations were located in SWNB. Two sampling locations (Loring Cove and Gleason Cove) were in

US waters but within Passamaquoddy Bay (Fig. 1), so were considered in the SWNB zone, consistent with the geographic zones defined in other tagging studies in the GoM (*e.g.*, Creaser and Libby, 1988). Effective recovery time was not applied to recapture data, so a significant proportion of recaptures were in the initial weeks after tagging. Tagging was conducted between March and October in each year and more than 95% of recaptures were within eight weeks of tag deployment. The total duration of recapture efforts was approximately six months. Herring were also tagged at two locations in Southern NS. Of the 1 126 herring tagged in NS, none were recovered. Of 73 188 tags applied in SWNB, 2 644 (3.6% recovery) tags were recovered with 99.8% of recaptures in SWNB and only 0.2% in GoM (Table 1). Of the 26 786 herring tagged south of the US-Canadian border, 146 (0.55% recovery) tags were recovered with 91.1% in GoM and only 8.9% in SWNB (Table 1). In both Maine and New Brunswick, a general northerly pattern of movement was observed and herring were typically recaptured in locations in close proximity to initial capture (approximately one-third recaptured within 20 km).

Juvenile herring movement along Coastal Maine 1960

Watson (1963) tagged 8 303 juvenile herring between May and October 1960 along the Maine coast (GoM) using spaghetti tags. The average time to recovery was 18 days, and no effective recovery time was used. Recaptures were reported up to September 1962 and 109 tag returns (94% of recoveries) were in GoM and 7 tag returns (6.0% of recoveries) in SWNB (Table 1). The longest distance between mark and recapture was approximately 90 km and the longest recovery time was 391 days.

Movements of mixed (juvenile/adult) herring tagged in the Bay of Fundy 1973–1974

A total of 24 140 herring were tagged near Grand Manan (November to December 1973 and June 1974) and Campobello Island (July 1974) using T-bar anchor tags or dart tags (Stobo *et al.,* 1975; Stobo, 1976). Fish tagged in 1973 were from the purse seine fishery and in 1974 from the weir fishery. The length range was 13 to 30 cm and included juvenile and adults. An effective recovery time of 14 days was used and tagging returns

Table 1. Summary of tag returns (percentage of returns by zone) from studies that tagged only juvenile herring. Tagging zones are abbreviated as NE: New England, GB: Georges Bank, GoM: Gulf of Maine, SWNB: Southwest New Brunswick, UBoF: Upper Bay of Fundy, SNS: Southern Nova Scotia, and ENS: Eastern Nova Scotia. Returns from the zone of tagging are shaded.

Reference	Tagging Dates	Recovery Dates	N Tagged	N Returned	Effective Recovery (%)	Effective Recovery (days)	NE	GB	GoM	SWNB	UBoF	SNS	ENS
1	1957–58	1957–58	73 188	2 644	3.6	0			0.2	99.8			
1	1957–58	1957–58	26 786	146	0.55	0			91.1	8.9			
1	1957–58	1957–58	1 126	0	0	0						0	
2	1960	1960–62	8 303	116	1.4	0			94.0	6.0			
3	1976–78	1976–80	4 463	17	0.38	14			82.4	17.6			
4	1976–78	1976–81	37 664	1 642	4.4	14		0.3	96.5	3.0		0.2	
4	1976–78	1976–81	3 700	107	2.9	14	1.0			98.1	1.0		
5	1980–82	1980–84	48 324	1 973	4.1	14			98.5	1.4		0.1	
5	1981–82	1981–84	9 635	260	2.7	14			3.7	95.5		0.8	
6	1982	1983–85	7 161	97	1.4	14				100			
6	1983	1983–85	7 923	61	0.77	14			92.3	7.7			
7	1999	1999–03	1 389	4	0.28	Unknown			75.0	25.0			
7	1999–02	1999–03	27 818	389	0.95	Unknown		0.4	1.5	89.1	0.4	7.9	0.8
8	2002–04	2002–04	76 957	1 986	2.6	4	0.2	0.1	1.3	93.1	1.2	4.2	
8	2003–04	2003–04	1 230	4	0.33	4				25.0		75.0	

[1]McKenzie and Tibbo 1961, [2]Watson 1963, [3]Waring 1981, [4]Creaser *et al.* 1984, [5]Creaser and Libby 1988, [6]Creaser and Libby 1986, [7]Mouland *et al.* 2003, [8]Waters and Clark 2005.

were reported until March 1976. The return rate was 4.2% (1 020 tags) with 94.1% in SWNB, just under 3% in each of GoM and Southern NS, and 0.3% in each of Eastern NS (overwintering in Chedabucto Bay) and Georges Bank (Table 2).

Herring movement of spawning and overwintering life stages in the Gulf of Maine and Georges Bank 1976–1978.

From 1976 to 1978 adult herring collected from fixed gears were tagged in US waters in both the GoM and Georges Bank and juveniles were tagged in coastal Maine area using T-bar anchor tags (Waring, 1981). Tagging was primarily conducted from September to November for spawning adults, May for migrating/overwintering fish, and February or August for juveniles and tag returns were recorded in all months of the year. Tags were recovered in fish processing plants in Canada, the US, and Europe and tagging results were combined across years. Recoveries were reported after 14 days (effective recovery time) after tagging until the end of 1980.

Herring tagged in spawning condition were recaptured in adjacent areas, although recaptures from Georges Bank were low due to a fishery closure at the time making estimates unreliable (Table 3). Of 29 693 tags applied to GoM spawning herring, there were 302 recaptures (~1% recovery) with 97.3 % of the recaptures in GoM and less than 1.7% migrating north to SWNB, and 1% south to New England (Table 3). For Georges Bank tags, the effective recovery was 0.05% of 30 346 tags with returns from only Georges Bank (82.4%) and GoM (17.6%).

Herring tagged in May that were assumed by Waring (1981) to be migrating/overwintering showed a substantially different pattern of movement than herring tagged in spawning condition. Of the 10 973 herring tagged in the GoM, there were 509 recaptures (4.6% recovery rat e) with approximately half of the recaptures in GoM with the next highest percentage (35.4%) captured in SWNB and the remaining recaptures were in New England or NS, as far north as Chedabucto Bay, NS (an overwintering area) (Table 2). No herring tagged in the Georges Bank zone in May (tagged in the Great South Channel and assumed by Waring (1981) to be migrating/overwintering) were recaptured on Georges Bank, likely due to the absence of a fishery at the time. Most of the recaptures from the Georges Bank tagging were in the GoM zone, though there were recaptures in SWNB, Southern NS, and New England.

Of 4 463 juvenile herring tagged in Coastal Maine, the effective recovery was 0.38% with 82.4% of recoveries in GoM and 17.6% in SWNB (Table 1).

Table 2. Summary of tag returns (percentage of returns by zone) from studies that tagged mixed (adult/juvenile) herring or herring identified as overwintering (OW), summer feeding adults (A–Feed), or autumn migrating adults (Mig). Tagging zones are abbreviated as NE: New England, GB: Georges Bank, GoM: Gulf of Maine, SWNB: Southwest New Brunswick, UBoF: Upper Bay of Fundy, SNS: Southern Nova Scotia, and ENS: Eastern Nova Scotia. Returns from the zone of tagging are shaded.

Reference	Group	Tagging Dates	Recovery Dates	N Tagged	N Returned	Effective Recovery (%)	Effective Recovery (days)	NE	GB	GoM	SWNB	UBoF	SNS	ENS
1	Mixed	1973–74	1973–76	24 140	1 020	4.2	14		0.3	2.5	94.1		2.8	0.3
2	OW	1976–78	1976–80	10 973	509	4.6	14	0.8		50.5	35.4		12.8	0.6
2	Mixed	1976–78	1976–80	22 882	268	1.2	14	5.2	0	84.3	8.2		2.2	
3	Mixed	1976–78	1976–81	4 800	177	3.7	14	0.7		93.3	5.9			
3	A–Feed	1976–78	1976–81	11 723	475	4.1	14	2.7		67.4	26.1	0.2	3.2	0.4
4	A–Feed/Mig	1980–82	1980–84	22 033	711	3.2	14	0.3		81.6	13.8		4.4	
5	OW	1999–02	1999–03	46 152	389	0.84	Unknown	0.5			8.2	4.1	37.5	49.6
6	OW	2003–06	2003–07	45 411	144	0.32	0	23.6		37.5	6.9	3.5	28.5	

[1]Stobo *et al.* 1975 with updates from Stobo 1976, [2]Waring 1981, [3]Creaser *et al.* 1984, [4]Creaser and Libby 1986, [5]Mouland *et al.* 2003, [6]Kanwit 2006.

Table 3. Summary of tag returns (percentage of returns by zone) from studies that tagged only spawning herring. Tagging zones are abbreviated as NE: New England, GB: Georges Bank, GoM: Gulf of Maine, SWNB: Southwest New Brunswick, UBoF: Upper Bay of Fundy, SNS: Southern Nova Scotia, and ENS: Eastern Nova Scotia. Returns from the zone of tagging are shaded. Tagging areas are abbreviated as "E Shore" = Eastern Shore Nova Scotia, "Ger Bank" = German Bank, GB: Georges Bank, GoM: Gulf of Maine. Returns from the zone of tagging are shaded.

Reference	Tagging Area	Tagging Dates	Recovery Dates	N Tagged	N Returned	Effective Recovery (%)	Effective Recovery (days)	NE	GB	GoM	SWNB	UBoF	SNS	ENS
1	GoM	1976–78	1976–80	29 693	302	1.0	14	1.0		97.3	1.7			
2	GB	1976–78	1976–80	30 346	14	0.05	14		82.4	17.6				
2	Ger Bank	1974	1974–81	23 938	393	1.6	14		0.8	13.2	16.5	5.3	48.6	15.5
2	Ger Bank	1977	1977–81	54 266	750	1.4	14		0.3	5.7	5.9	3.3	43.9	40.9
3	GoM	1980	1980–82	990	11	1.1	14			100				
3	SWNB	1980	1980–80	692	21	3.0	14			19.0	81.0			
4	E Shore	1998–01	1998–03	1 941	3	0.15	Unknown						33.3	66.6
4	SNS	1998–01	1998–03	24 175	107	0.45	Unknown			3.7	1.9		90.7	3.7
4	Scots Bay	1998–01	1998–03	4 908	31	0.63	Unknown				6.4	71.0	19.4	3.2
5	GoM	2003–06	2003–07	40 150	139	0.35	0	8.6	4.3	72.7	3.6	1.4	9.4	
5	GB	2005	2005–07	10 325	9	0.09	0	66.7	0	22.2				11.1
6	Scots Bay	2005	2005	5 047	151	3.0	2			3.1	31.0	60.5	5.4	
6	Ger Bank	2005	2005	8 580	52	0.61	2				17.0		80.9	2.1
7	Ger Bank	2009	2009–11	10 334	86	0.83	2			1.2	1.2		96.4	1.2
8	Ger Bank	2010	2010–11	6 036	36	0.60	2						80.6	19.4
8	Ger Bank	2011	2011–12	6 623	57	0.86	2			1.8			98.2	

[1]Waring 1981, [2]Stobo 1982, [3]Creaser and Libby 1988, [4]Mouland *et al.* 2003, [5]Kanwit 2006, [6]Clark 2006, [7]Maxner *et al.* 2010 with updates from DFO unpublished data,[8]Melvin *et al.* 2014 with updates from DFO unpublished data.

Herring movement from the German Bank spawning area 1974 and 1977.

Herring collected by purse seine and fixed gears were tagged using T-bar anchor tags on German Bank (off southwest NS) in two separate events in August 1974 and August to September 1977 (Stobo, 1982). The intent of the study was to tag ripe and running herring on the spawning area, but the 1974 component of the study captured and tagged substantial numbers of ripe herring that were not running. Recapture efforts focused on all potential fisheries including weir, gillnet, and purse seines. Recovery efforts were reported up to 7 years after tagging and the effective recovery time used was 14 days. Recaptures were reported by season (summer or winter). The 1974 and 1977 studies are examined independently as they were separate efforts. Of the 23 938 herring tagged in 1974, the effective recovery was 1.6% with approximately half of the recaptures in Southern NS, approximately 15% were captured in each of Eastern NS, GoM, and SWNB, 5.3% in the upper BoF, and less than 1% in Georges Bank (Table 3). The 1977 study differed from the 1974 tagging effort in that of the 54 266 herring tagged (1.4% effective recovery), 40.9% of the recaptures were in Eastern NS (Table 3) and small number of recaptures (3 to 6%) were documented in the upper BoF, SWNB, and the GoM, while Georges Bank recaptures were again less than 1% of the total (Table 3).

Herring tagging in Gulf of Maine coastal waters 1976–1978

A tagging study in the GoM was divided into and summarized according to 1-year-old juveniles, summer feeding adults, or mixed (adult/juveniles) (Creaser *et al.,* 1984). Tagging was conducted using T-bar anchor tags. Recoveries were reported by quarter of the year and were observed in all quarters and an effective recovery time of 14 days was applied to the recapture data.

Of 34 664 juvenile herring tagged in GoM, the effective recovery was 4.4% with 96.5% of recoveries in GoM, 3.0% in SWNB, and 0.3% in Georges Bank (Table 1). In SWNB, 3 700 juvenile herring were tagged and the effective recovery was 2.6% with 98.1% of recoveries in SWNB, 1.0% in each of the upper BoF and New England (Table 1).

A total of 4 800 summer feeding adult herring (Table 2) were tagged in GoM and the effective recovery was 3.7% with 93.3 of recaptured in GoM, 5.9% in SWNB, and 0.7% in New England (Table 2). Tagging of summer feeding adult herring (11 723 tags) demonstrated that fish had a much higher probability of leaving the GoM as more than one quarter of the 475 recoveries were from SWNB, approximately 3% from each of New England and Southern NS, and a single fish (0.2%) from the upper BoF, and two fish (0.4%) from Eastern NS near Cape Breton (Table 2).

Herring tagging in Gulf of Maine coastal waters 1980–1982

The tagging study by Creaser *et al.* (1984) in the GoM was repeated in 1980–1982 (Creaser and Libby, 1988). Results were summarized according to 1-year-old juveniles and summer feeding adults (Creaser and Libby, 1988). The authors expressed tag recoveries as a ratio of tags to 1000 metric tons (mt) of catch per geographic area. In order to provide comparable numbers for comparison to other studies in this review, the actual number of tags recovered in each geographic area was calculated using the total catch and tag ratio data provided. Tag ratios reported as < 0.05 tags/1000 mt were substituted with 0.025 tags/mt (*i.e.*, half the reporting limit) for estimation of counts, resulting in counts of either 1 or 2 recaptures. Tagging was conducted in the summer months using T-bar anchor tags. Recoveries were reported by quarter of the year and were observed in all quarters and an effective recovery time period of 14 days was used.

Tagging of summer feeding juvenile herring (48 324 tags; 4.1% effective recovery) revealed that while the vast majority (98.5%) were recaptured in GoM waters, there was movement to SWNB (1.4%) and Southern NS (0.1%) (Table 1). A smaller tagging effort (9 635 tags; 2.7% effective recovery) targeted juveniles in the SWNB weir fishery, and the only recoveries outside of SWNB were from the GoM (Table 1).

Consistent with the 1976–78 tagging study, summer feeding and autumn migrating adult herring demonstrated that fish had a much higher probability of leaving the GoM compared to juveniles. Of 22 033 tags, 711 were recovered (3.2%) with 13.8% from SWNB, 4.4% from Southern NS, and 0.3% from New England (Table 2). A small number of adult herring in spawning condition were tagged in GoM (990 tags) and SWNB (692 tags) in 1980. A total of 11 GoM tags (1.1%) were recovered, all in GoM, and a total of 21 SWNB tags (3.0%) were recovered with 81% in SWNB and 19% in GoM (Table 3).

Herring tagging in New Brunswick and Gulf of Maine coastal waters 1982–1983.

Age-1 herring were targeted for tagging using T-bar anchor tags in SWNB and GoM nearshore fisheries using seines or weirs in late August to October in 1982 and 1983 (Creaser and Libby, 1986). The age-1 herring tagged in 1982 were not reported in the previous section (Creaser and Libby, 1988). The effective recapture time reported was 14 days. Tag recoveries were reported by quarter of the year. Recoveries were reported in all quarters and only recorded up to 1985. A total of 7 161 herring were tagged in SWNB and all 97 recaptures were in SWNB. Of the 7 923 herring tagged in the GoM, 7.7% were recaptured in SWNB (Table 1).

Herring tagging in 4VWX from 1998 to 2003

Tagging studies using T-bar anchor tags were conducted on both nearshore and spawning herring as part of a large tagging effort that occurred between 1998 and 2003 (Mouland *et al.,* 2003). The studies are divided into the nearshore fishery (largely captured in the SWNB weir fishery), an overwintering herring study, herring captured on spawning grounds, and herring tagged along coastal Maine. Updates to this tagging study were documented in Waters and Clark (2005) and returns presented here include all of those tag return updates, and it is not clear whether an effective recovery date was not applied.

Tagged juveniles were released near Jeffrey's Ledge (GoM) in 1999 (study initially described in Waters *et al*., 2000). A total of 1 389 juvenile and pre-spawning herring were tagged and 3 tags were recovered in coastal Maine and one in SWNB (Table 1). A number of distinct tagging

efforts were made from the SWNB weir fishery. The first consisted of tagging 27 818 juvenile (1- to 3-year-old) herring captured in weirs in 1999 and 2002. This study was a preliminary study for the NB weir project launched later (Waters and Clark, 2005). Herring returns (0.95% recovery) up to 2003 were recorded and 89.1% were recaptured in SWNB. The greatest movement was to Southern NS (7.9%) with small numbers of fish recaptured in Georges Bank, GoM, Upper BoF, and Eastern NS (Table 1).

A total of 46 152 overwintering herring were tagged in the Eastern NS zone, either at Chebucto Head or Chedabucto Bay (Fig. 1) from 1999–2002. While Chebucto Head was the dividing line between the Eastern and Southern NS zones used herein, it was considered as Eastern NS for the purposes of this review. The effective recovery rate was 0.84% and half of the recaptures were in Eastern NS, 37.5% in Southern NS, 4.1% in upper BoF and 8.2% in SWNB, and a few recaptures in New England (Table 3). A total of 31 024 spawning herring were tagged on German Bank and Trinity Ledge (Southern NS), Scots Bay, and Eastern Shore (Eastern NS). The effective recovery ranged from 0.15 to 0.63% among zones. Scots Bay herring were mostly recaptured in that zone but did move to the three other Canadian zones as well (Table 3). Very few herring were tagged at Eastern Shore (1 941) and only one tag was recovered outside of the tagging zone in Southern NS. The majority of fish (24 175) were tagged on German Bank and Trinity Ledge (Southern NS; Fig. 2) and 72.7% of recaptures were in this zone and recaptures were observed in all other zones with the exceptions of Eastern NS (Table 3).

Weir herring tagging project 2002–2004

A larger NB weir tagging study (Waters and Clark, 2005) followed the preliminary NB weir study that was conducted from 1998 to 2001. A total of 75 440 primarily juvenile herring were tagged using T-bar anchor tags in SWNB weirs from August to November 2002, May to October 2003, and May to October 2004. An additional 2 517 herring were tagged near Grand Manan (SWNB) in the autumn and spring purse seine fishery and these data are included in the overall summary for SWNB. Recaptures were reported to the end of 2004 and the effective recovery rate was 2.6%. More than 90% of recaptures were in SWNB, 4.3% in Southern NS, 1.3% in GoM, 1.2% in upper BoF, and a few recaptures in Georges Bank and New England. A small number of herring (1 230) were also tagged in the NS weir fishery as part of this study. Of the four recovered tags, three were recaptured in the Southern NS area and one in SWNB.

US Herring tagging project 2003–2006

Adult herring in pre-spawning condition were tagged using T-bar anchor tags in the GoM (2003–2006) and Georges Bank (2005) zones from July to October and in the New England zone (2003–2006) zone from January to April. Herring were assumed to be representative of the spawning stocks in the GoM and Georges Bank zones and of overwintering herring in the New England zone (Kanwit, 2006; Kanwit and Libby, 2009). The targeted size for tagging was age 3+ and herring were tagged from the purse seine and midwater trawl fisheries. No effective recovery time was applied and recoveries were reported until May 2007.

Of 45 411 overwintering herring tagged in New England, the return rate was 0.32% with the highest returns in GoM (37.5%), Southern NS (28.5%), and New England (23.6%). Returns were also observed in SWNB and as far as Scots Bay in the upper BoF (Table 2). For pre-spawning herring, in GoM, 40 150 tags were applied with a recovery of 0.35%. Returns were 72.7% in GoM and returns were observed in all zones (with the exception on Eastern NS) in low proportions (Table 3). For pre-spawning herring, on Georges Bank, 10 325 tags were applied with a low recovery of 0.09% or 9 individual tags. Returns were biased due to little directed fishing effort on Georges Bank but the returns showed recoveries in GoM, New England, and overwintering in Eastern NS (Table 3).

Migration of herring captured at the Scots Bay and German Bank spawning areas in 2005

In a study conducted in 2005, Clark (2006) examined the movement of herring from the Scots Bay (upper BoF; 5 047 tags) and German Bank (Southern NS; 8 580 tags) spawning areas. T-bar anchor tags were used and herring were tagged from the purse seine fishery. As tagging was performed at different intervals, the reproductive stage ranged from spawning to spent. Effective recovery time was set at two days and as there were four and five tagging efforts at Scots Bay and German Bank, respectively, spanning more than one month, this effort biased recaptures at the spawning locations. Effective recovery was 3.0% for Scots Bay and 0.61% for German Bank. Outside of the tagging zone, the recaptures were relatively high in SWNB (31% and 17% for Scots Bay and German Bank, respectively), Scots Bay recoveries were also in GoM (3.1%) and southern NS (5.4%) and 2.1% of German Bank recoveries were in Eastern NS (Table 3).

Tagging of herring on the German Bank spawning ground 2009–2011

A tagging program using T-bar anchor tags was conducted on the German Bank spawning ground in cooperation with the commercial purse seine fishery in 2009, 2010, and 2011 (Maxner *et al.,* 2010; Melvin *et al.,* 2014, updates from DFO unpublished data). A total of 23 047 tags were applied in 2009 to 2011 and recapture was documented for the period up until the end of 2019. Effective recovery time was set at 2 days and effective recoveries were 0.60 to 0.86% among years. The majority (93.9%) of returned tags were recovered in Southern NS (Table 3). Two tags (3.8%) were recovered in the GoM, eight tags (4.5%) in Eastern NS, and one tag (0.6%) near Grand Manan in SWNB. The focus of these tagging events was for evaluating turnover on the German Bank spawning ground so recoveries from the tagging area are strongly biased.

Data summary

More than 750 000 tagged herring were released in NAFO areas 4WX5YZ since the 1950s and more than 15 000 tag returns were reported (Tables 1–3). Results were tabulated as juveniles (Table 1), mixed (adult/juvenile), overwintering or adult summer feeding/ autumn migrating (Table 2), or spawning adults (Table 3). While results are not always consistent, even between replicated studies (*e.g.*, Stobo, 1982), there is a general trend for juvenile herring to have limited movements, and adult herring to move more widely, and in greater numbers. In particular, juvenile herring tagged in coastal GoM and the SWNB weir fishery showed little movement, or tended only to move between the GoM and SWNB zones (*e.g.*, MacKenzie and Tibbo, 1961; Waring, 1981, Creaser and Libby, 1986, 1988; Table 1). In contrast, spawning herring (Table 3) and mixed (adult/juvenile) and overwintering, and adult feeding/migrating herring (Table 2) generally moved among several tagging zones. In particular, the two studies of Stobo (1982) where more than half of tagged fish were captured outside of the tagged zone and the study by Kanwit (2006) that showed herring from US spawning grounds overwintering in Canadian waters and herring from Canadian spawning grounds overwintering in US waters.

Discussion

Extensive tagging studies over the past seven decades in NAFO areas 4WX5YZ have provided considerable insight of herring movement between fishery management areas. The basis of herring management is that different sub-populations are formed by spawning aggregations, and that there is a reasonable amount of homing to maintain those population structures (Stephenson *et al.,* 2009). This is supported by tagging studies with herring in ripe and running condition tagged on spawning grounds only being recovered from the same spawning ground in subsequent years (Stobo, 1987; Wheeler and Winters, 1984; Stephenson *et al.*, 2009; Melvin *et al.,* 2014). Further support for the hypothesis of homing is that there was no colonization of Georges Bank by the adjacent GoM spawning areas after it collapsed in 1977 (Grosslein, 1987) and little recovery of Trinity Ledge following a collapse in the late 1980s (Stephenson *et al.,* 2009), despite adjacent spawning areas (GoM and German Bank, respectively) remaining occupied.

While sub-populations are separated at spawning, they also appear to remain separated for the first few months of larval life (Grosslein, 1987; Sinclair *et al.*, 1981). The evidence in the literature is that herring larvae from SWNS/BoF spawning areas are generally retained in the SWNS/BoF area (Sinclair and Iles, 1985; Bradford and Iles, 1993; Stephenson *et al.,* 2009; Stephenson *et al.,* 2015) and vertical migration has been proposed as the mechanism for larval retention in the BoF (Stephenson and Power, 1989). In the GoM, larval herring move inshore and metamorphose into juvenile herring in the spring (Overholtz *et al.,* 2004). It is believed that they only travel small distances until autumn when they move offshore to overwinter near the bottom before returning inshore in the spring as age two and recruit to the weir fishery (Overholtz *et al.,* 2004).

Juvenile herring have been captured in weirs for more than a century in the SWNB area (DFO, 2020b). The assumption that juvenile herring from SWNB are associated with GoM and Georges Bank adults dates back to at least 1973 and it was hypothesized that juvenile abundance in SWNB may indicate future recruitment to the Georges Bank fishery (ICNAF, 1973). Meristic studies by Anthony and Waring (1980; cited in Overholtz *et al.,* 2004) suggested juvenile herring populations in coastal Maine and SWNB were augmented by juveniles from Georges Bank. Further support for a link between US spawning components and the SWNB weir fishery were based on studies of age-1 length frequency distributions in SWNS (Messieh, 1970; Koeller, 1979). Observed changes in juvenile growth in SWNB in the 1980s was coincident with the collapse of the Georges Bank fishery which suggested a link between the two areas pre-collapse (Sinclair *et al.,* 1981). Sinclair *et al.* (1981) did, however, suggest that there is mixing of GoM and SWNS juveniles along the coast of Maine and in the BoF and this is the earliest report that a portion of the juveniles in SWNB may be from SWNS spawning grounds. The Georges Bank fishery was large in the 1960s and early 1970s and

juveniles from the Georges Bank spawning area may have historically dominated the SWNB weir landings; however, the relative abundance of different spawning components of herring in NAFO areas 4WX5YZ today is much different, with greater abundance in SWNS/BoF than in GoM and Georges Bank. Messieh (1970) examined monthly length frequency distribution of age-1 herring in Passamaquoddy Bay from 1965 to 1968 and identified three different size groups that corresponded to spring, summer, and autumn spawners. He suggested that at least one group was from the GoM based on water circulation patterns. Koeller (1979) also examined length-frequency distributions of juvenile herring along the NB side of the BoF. He also found three unique length-frequency distributions of age-1 herring and suggested mixed aggregations of juvenile herring in the BoF from at least 3 different spawning areas. It has been recognized for decades that the coastal Maine and SWNB areas are a juvenile nursery for multiple spawning areas including SWNS (Sinclair *et al.,* 1981); however, the current management of herring in the US and Canada assumes that herring from the SWNB weir fishery originate from the GoM and Georges Bank spawning stocks.

Since the 1950s a substantial number of the tagging studies on juvenile herring have been conducted in the GoM and SWNB areas (McKenzie and Tibbo, 1961; Creaser and Libby 1986; Mouland *et al.,* 2003; Waters and Clark, 2005) because this is the juvenile nursery area in NAFO areas 4WX5YZ. The results of those studies consistently show relatively short distance movements of juvenile herring, and the US studies showed that juvenile recaptures outside of the GoM were predominately in SWNB. Many of the tagging locations of juveniles in the GoM studies were close to the GoM/SWNB zone boundary, so movements between zones are relatively short distances in many cases. Tupper *et al.* (1998) and Overholtz *et al.* (2004) speculated that the coastal GoM and SWNB areas serve as the juvenile nursery area for many spawning components in the region (*i.e.*, Georges Bank, GoM, and Southern NS). The coastal GoM and SWNB areas are the primary juvenile nursery areas in the SWNS/BoF area so juvenile herring that were hatched on the primary spawning grounds in SWNS/BoF (*i.e.*, German Bank and Scots Bay) are most likely in the SWNB/coastal Maine areas (Tupper *et al.,* 1998). Adult herring tagged on Canadian spawning grounds and overwintering areas from 1998–2002 were recaptured in the SWNB weir fishery (Waters and Clark, 2005) providing evidence that herring from Canadian spawning grounds are landed in the SWNB weir fishery. Adult herring tagged during the spawning season on German Bank were recovered in the SWNB weir fishery (Clark, 2006), and herring tagged from the purse seine fishery in SWNB that count towards the TAC for the SWNS/BoF fishery were also recovered in the SWNB weir fishery (DFO, unpublished data).

The 2006 Transboundary Assessment Review Committee (TRAC, 2006) considered the tagging information from Waters and Clark (2005) and did conclude that there is a mix of Scotian Shelf and GoM spawners in the SWNB weir fishery but noted that there is no way to estimate the proportion of herring from each stock area. Similarly, the 2006 assessment team for 4VWX herring concluded that the Waters and Clark (2005) tagging data easily refute the hypothesis that herring landed in the SWNB weir fishery are all of US origin. Despite these results, the most recent US (NFSC, 2018) and Canadian (DFO, 2020a) assessment reports assume all SWNB weir fishery landings (adult and juvenile) are from the US stock (GoM and Georges Bank spawning components).

Tagging studies of adult spawning herring have been conducted on all the primary spawning populations within NAFO areas 4WX5YZ and show a much different result than juvenile tagging studies. Adult herring undergo substantial migrations from their spawning areas to summer feeding and overwintering areas in all the zones examined herein within one season after spawning. There was no overall directional trend in the movement of adult herring and patterns have even been observed to change from year to year. This lack of overall directional trend in the movement and variation among years may be related to several factors including: differences in fishing patterns, changes in environmental conditions, and changes in the relative abundance of different spawning components over time and these make efforts to account for herring stock structure in assessment and management difficult. Attempts to develop a two-area (GoM and Georges Bank) stock assessment model in the US failed because of lack of information to estimate movement rates between the areas (NFSC, 2018). The two-area model, however, did not incorporate any tagging data and such data are necessary to reliably estimate movement parameters (Goethel *et al.*, 2019). Correctly estimating movement rates in stock assessments has been shown to be more important than correctly identifying the underlying population structure (*e.g.*, meta-population versus natal homing; Goethel *et al.*, 2019; Bosley *et al.*, 2022). Given the interannual variation in movement rates for herring, continued consideration of multi-area stock assessments will likely require periodically (*e.g.*, 2–3 years) conducting tagging studies to ensure accurate and precise estimation of movement rates, which would require a substantial amount of resources to implement (Goethel *et al.*, 2019).

The Kanwit (2006) tagging study provided some insight into migrations. Recoveries showed a clear pattern of short term residency within 100 days of tagging, longer distance migrations to other zones after 100 days, and recoveries were close to the tagging location around one year after tagging. Scots Bay is known to be a spawning ground and not a feeding or overwintering area. Recaptures at Scots Bay from herring tagged in GoM and New England suggest that these fish were feeding or overwintering in US waters and spawning in the upper BoF. Similarly, a tag recovered in the Chedabucto Bay area of NS in the winter from tagging on Georges Bank suggests overwintering of US fish in Canadian waters.

Overall, the pattern of herring movement from tagging studies is consistent with the conceptual figure of herring stock structure (Fig. 3) that was proposed by Stephenson *et al.* (2009). Herring spawn in discrete areas and that is well established (Overholtz *et al.,* 2004; Melvin *et al.,* 2009). The question of larval drift from those spawning areas has been addressed by a number of studies reviewed by Stephenson *et al.* (2009) and the consensus was that there is limited larval movement away from the spawning grounds; however, there is some overlap of larval retention areas from different spawning grounds (*e.g.*, German Bank and Scots Bay; Stephenson *et al.,* 2015) consistent with the Stephenson *et al.* (2009) conceptual figure (Fig. 3). The tagging data reviewed in the present study support a

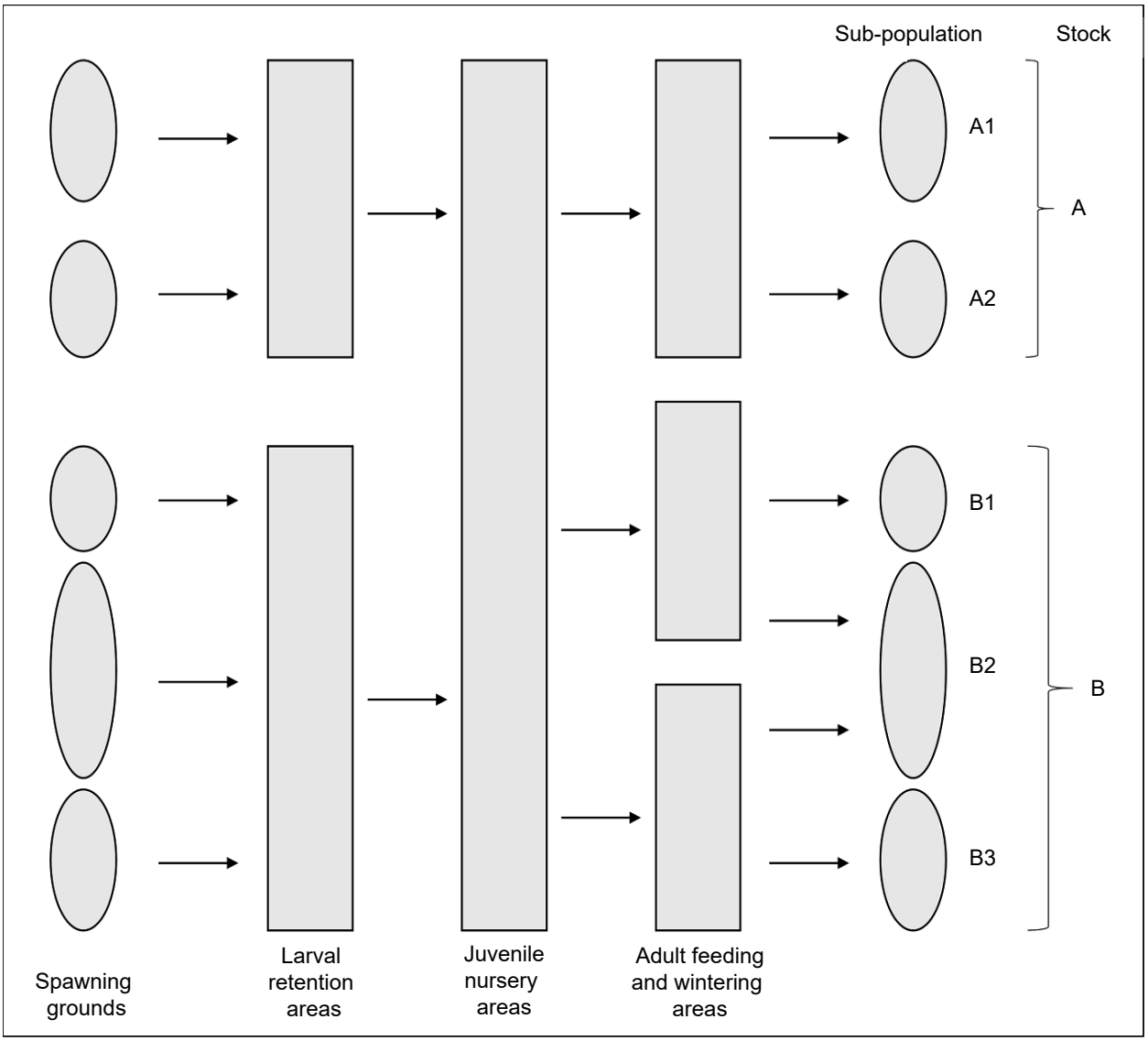

Fig. 3. Conceptual diagram of herring sub-population overlap, modified from Stephenson *et al*. (2009).

common juvenile nursery area in NAFO areas 4WX5YZ with limited movements and as herring become sexually mature, longer distance movements occur and support the overlap of adult feeding and overwintering areas from adjacent sub-populations. The spawning of individuals at the same location in multiple years has been documented, a necessary, but not sufficient condition to prove homing to natal spawning grounds.

There are limitations of tagging studies to evaluate population structure in NAFO areas 4WX5YZ. No tagging study can follow herring from larvae to adult to evaluate the level of homing to the natal spawning grounds. The inability to tag small herring also precludes any studies on fidelity to natal spawning grounds (Tupper *et al.,* 1998). Different tagging methods (*e.g.*, opercular tags, T-bar anchor tags) were used in the studies summarized in this review. The choice of tagging method can result in different mortality rates of tagged individuals (Nakashima and Winters, 1984). The shedding of tags over time and the differential rates among tagging methods can also bias the recapture data (Nakashima and Winters, 1984). Collection method (*e.g.*, purse seine vs. weir) and experience of the tagger are also expected to influence tagging survival. The interpretation of tagging data in any quantitative sense is limited due to the biases in tag returns. Methods to adjust tag return data (*e.g.*, catch-weight, Creaser and Libby, 1988) to account for probability of recapture can remove some of the bias, but the targeting nature of fishing fleets, costs associated with travel to offshore fishing grounds (*e.g.*, Georges Bank and offshore Scotian Shelf), and closure of fishing areas (*e.g.*, spawning areas in the GoM) will always bias the tag return data. In the context of stock assessments, parameters can be estimated in some cases to account for some biases in tag-recapture data (*e.g.*, non-random mixing of tagged fish), and this should be considered if such stock assessments are developed (Goethel *et al.*, 2019). The tagging studies are also strongly biased towards short-term recaptures. For example, only 20% of tag returns had a recovery time of more than 30 days and only 5.2% of tag returns had a recovery time of more than 300 days from DFO studies conducted since 2009 (DFO, unpublished data). Additional challenges with tagging data are uncertainty with recapture location (*e.g.*, when a tag is discovered months after recapture in frozen bait), different return rates depending on market (processed fish vs. bait fish), and hesitancy in reporting transboundary tags (DFO, 2007).

Alternative methods for evaluating stock structure in NAFO areas 4WX5YZ have been explored but research has been limited. Herring in Georges Bank to Cape Cod were shown to have fewer pectoral rays than herring from the coastal GoM and NS (Anthony and Waring, 1980), differences in parasites have been observed between sub-populations (reviewed in Tupper *et al.,* 1998), and some genetic studies have been conducted but variation was insufficient to distinguish between sub-populations (*e.g.*, Kornfield *et al.,* 1982; McPherson *et al.,* 2003), with the exception of differences between spring and autumn spawners. More recent research in Europe on herring stock structure, has utilized several alternative techniques to tagging, including genetics (*e.g.*, Bekkevold *et al.,* 2011; Lamichhaney *et al.,* 2012, 2017), otolith microchemistry (*e.g.*, Geffen *et al.,* 2011; Moll *et al.,* 2019), growth patterns in otoliths, (*e.g.*, Brophy and Danilowicz, 2002), and otolith shape (Libungan *et al.,* 2015) to further elucidate population structure. Acoustic tags have been successful used to track movement of herring (*e.g.*, Eggers *et al.,* 2015; Langård *et al.,* 2015) and may serve as an alternative to traditional tagging methods. Lamichhaney *et al.* (2012) compared over 400 000 single nucleotide polymorphisms in herring from the northern Atlantic and the Baltic Sea. High variability was found in several thousand of those polymorphisms and clearly distinguished Baltic from north Atlantic Herring, supporting that Baltic herring are a subspecies. Another recent study of Baltic Sea herring used otolith microchemistry to characterize herring natal areas (Moll *et al.,* 2019). Otoliths deposit minerals over time and those minerals provide a unique fingerprint of specific regions. These techniques are not restricted to determining natal origin as the habitat history of the entire life of a fish is documented within the otolith. The use of such techniques has advanced knowledge of Eastern Atlantic herring populations well beyond what is known of Western Atlantic populations.

Conclusions

Over 60 years of herring tagging studies have been conducted in the BoF/GoM/Scotian Shelf region (NAFO areas 4XW5YZ) and show generally consistent results indicating short distance movement of juvenile herring in coastal Maine and SWNB and movements of mature herring from their natal spawning grounds to shared feeding and overwintering areas in adjacent geographic zones, including transboundary movement. Although there has been evidence for decades to suggest that juvenile herring from coastal Maine and SWNB are from the SWNS/BoF, GoM, and Georges Bank spawning areas, management assumptions of the SWNB weir fishery have not changed and current management is based on the hypothesis that all herring (juvenile and adult) landed in the SWNB weir fishery are of US (spawning grounds) origin. Although in the 1960s and early 1970s, the Georges Bank fishery was large and juveniles from the Georges Bank spawning area may have dominated the SWNB weir landings, the spatial distribution of herring today is

much different, with greater abundance in SWNS/BoF than in GoM and Georges Banks. Recent tagging studies continue to support the hypothesis that juvenile herring in SWNB are from a mix of spawning areas in NAFO areas 4XW5YZ and the proportion of mixing is unknown. There are limitations to the evaluation of tagging data (*e.g.*, from biases due to fishery timing and location) and limitations to the comparisons among tagging studies due to different methodology, experimental design, and changes in the spatial distribution and relative abundance of herring over time. Further traditional tagging studies are unlikely to add substantially to the present knowledge. Further research using alternative methods such as well-developed genetic and microchemistry techniques may be the most promising means to significantly advance our understanding of stock structure in NAFO areas 4XW5YZ.

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