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An Interdisciplinary Assessment of Winter Flounder (*Pseudopleuronectes americanus*) Stock Structure

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Abstract

An interdisciplinary review was undertaken to evaluate the stock structure and management of winter flounder (*Pseudopleuronectes americanus*) throughout its geographic range in the northwest Atlantic. Information on morphology, tagging studies, genetics, larval dispersal, life history traits, environmental signals and meristics was considered. In the coastal waters of the United States, winter flounder are managed as three stock units; Georges Bank, Gulf of Maine and Southern New England/Mid-Atlantic. In Canadian waters, winter flounder are managed as three stock units: western Scotian Shelf (NAFO Div. 4X), eastern Scotian Shelf (NAFO Div. 4VW), and the southern Gulf of St. Lawrence (NAFO Div. 4T). Estuarine spawning, which likely plays an important role in reproductive isolation and population structure, is non-existent on Georges Bank and Browns Bank, variable in more northern habitats and may be obligate in southern New England. Contingent groups are likely present in several regions, and merit further research. Despite evidence for local population structure, information from tagging, meristic analysis, and life history studies suggest extensive mixing within stock units, thereby supporting the current U.S. management units. Genetic analysis and parasite markers indicate that Canadian management units are distinct. However, examination of inshore and offshore winter flounder within Division 4X suggests little interchange occurs between these groups. Based on their distribution and life history traits, several flounder stocks likely exist within the Div. 4T management area. A stock composition analysis of mixed-stock fisheries would be useful to facilitate the management and assessment of winter flounder in both U.S. and Canadian waters.

Keywords: winter flounder, *Pseudopleuronectes americanus*, stock identification, stock structure.

Introduction

Accurate stock assessment and effective fishery management requires identification of self-sustaining groups within species. Stock identification involves interdisciplinary analysis of life history information, genetics, geographic variation of phenotypic traits, movement and environmental signals (Cadrin *et al.*, 2005). Advances in several of these disciplines warrant reanalysis and re-evaluation of stock structure as new information arises (Begg and Waldman, 1999).

Although stock identification techniques have been used in fisheries science for over a century, no consensus has been reached on how to best define a unit stock (Waldman, 2005a). Early definitions of the term stock were based on the utilization of a species by fisheries. More recent definitions of fish stocks have focused on demographics, and imply that a degree of spatial and temporal discreteness is needed for a stock to evolve (Waldman, 2005a). Hilborn and Walters (1992) defined a stock as an arbitrary group of fish large enough to be essentially self-reproducing, with members of each group having similar life history characteristics. Ihssen *et al.*, (1981) succinctly described a unit stock as "…an intraspecific group of randomly mating individuals with spatial or temporal integrity."

Stock assessment models assume that individuals within a stock exhibit homogenous vital rates and life cycle closure (Cadrin *et al.*, 2005). When the assumed stock structure differs from the biological stock structure, the vital rates used to assess the stock may be inaccurate, leading to erroneous assessment results (Rothschild and Jiao, 2011). Therefore, well informed stock boundaries are necessary to manage and assess fish stocks accurately. For example, if two distinct biological stocks with different vital rates are managed as a single unit, a common catch limit (or Total Allowable Catch) may lead to the overexploitation of the less productive component, and the under utilization of the more productive component (Ricker, 1958). Problems with assessment models can also arise (*e.g.*, retrospective patterns), when fishery landings are classified to the wrong stock area.

Stock identification studies that utilize multidisciplinary methods often produce the most accurate results (Coyle, 1998). Certain approaches (*e.g.*, meristics and microsatellite markers) can be used to detect for differences in fish stocks that may have arisen in the recent past, while other techniques (*e.g.*, allozymes, coding DNA) are more conservative, and require longer periods of isolation for differences to become recognizable between stocks. An interdisciplinary approach also creates a more robust baseline, making more techniques available for use in subsequent stock composition analyses.

Winter flounder are found in coastal waters (0–125m) of the Northwest Atlantic, from North Carolina to Newfoundland (Fig. 1; Bigelow and Schroeder, 1953; McCracken, 1963; Pereira *et al.*, MS 1999; Collette and Klein-MacPhee, 2002), and the distribution of this species is centered between New Jersey and Nova Scotia (Perlmutter, 1947). Winter flounder are managed as three stock units in U.S. coastal waters; Gulf of Maine, Georges Bank, and Southern New England/Mid-Atlantic (SNE/MA; Fig. 2; Brown and Gabriel, MS 1998). The winter flounder resource is managed as three stock units in Canadian waters (Fig. 3): (1) Browns Bank, St. Marys Bay and Bay of Fundy winter flounder are managed concurrently in NAFO Div. 4X; (2) winter flounder from the Scotian Shelf and points eastward are managed together in NAFO Div. 4VW; and (3) winter flounder are managed as one unit in the Southern Gulf of St. Lawrence in NAFO Div. 4T. Winter flounder are present in coastal waters around Newfoundland (NAFO Subarea 3), but due to sparse data and a limited directed fishery, this species is not managed under a catch limit in this area (DFO, MS 1996).

The stock structure of winter flounder has been investigated since the early 1900s (*e.g.*, Kendall, 1912; Lobell, MS 1939). Early research on winter flounder was focused primarily on migration, life history rates and analysis of meristic characters. Over time, more disciplines such as genetics, parasitic characters and hydrodynamic modeling were used to evaluate winter flounder stock structure. Currently, newer methods such as otolith chemical analysis (Jackman *et al.*, MS 2010; Pruell *et al.*, 2010) and telemetry tagging (Sagarese, MS 2009; DeCelles and Cadrin, 2010; Fairchild, MS 2010) are being used to examine the stock structure of winter flounder.

The objective of this review is to synthesize information on the stock structure of winter flounder (*Pseudopleuronectes americanus)* throughout its geographic range by reviewing benchmark case studies from a variety of disciplines. The synthesis is used to assess the appropriateness of current management units in both the United States and Canada, based on the available scientific information. In regions where stock boundaries are uncertain, opportunities for future research are discussed.

Review of Stock Identification Information

Life History Traits

Dispersal of early life stages- Winter flounder exhibit relatively isolated metapopulation structure in the bays and estuaries along the east coast of North America (Perlmutter, 1947; Saila, 1961). This species spawns adhesive and demersal eggs (Klein-MacPhee, 1978), which limits dispersion. Larvae are pelagic, and undergo metamorphosis after an average of two months in the water column (Chambers and Leggett, 1987). Winter flounder larvae are bottom-oriented and negatively buoyant, and have been observed to be more abundant near the benthos (Pearcy, 1962; Klein-MacPhee, 1978).

In the Mystic River estuary in Connecticut, Pearcy (1962) found that while net transport in the estuary was seaward, net transport in the bottom layers of the estuary was landward. Pearcy (1962) noted that winter flounder larvae will regulate their vertical position in the water column in relation to the tide, which will promote the retention of larvae within the estuary and allow juveniles to settle in close proximity to their hatching site. Hydrodynamic modeling studies have estimated that rates of larval retention in estuaries is likely high (Crawford and Carey, 1985; Chant *et al.*, 2000). Thus, estuarine spawning and nursery grounds appear to be closely linked (Pearcy, 1962; Pereira *et al.*, MS 1999). However, the fate of larvae spawned in coastal and offshore areas is poorly studied, and warrants further attention (*i.e.*, DeCelles *et al.*, MS 2010).

Life History Traits- Life history parameters such as growth and age at maturity can be used to distinguish among discrete stocks of fish because these parameters are phenotypic expressions of the interaction between genotypic and environmental influences (Begg, 2005). For winter flounder these parameters have been derived using both fishery dependent and fishery independent

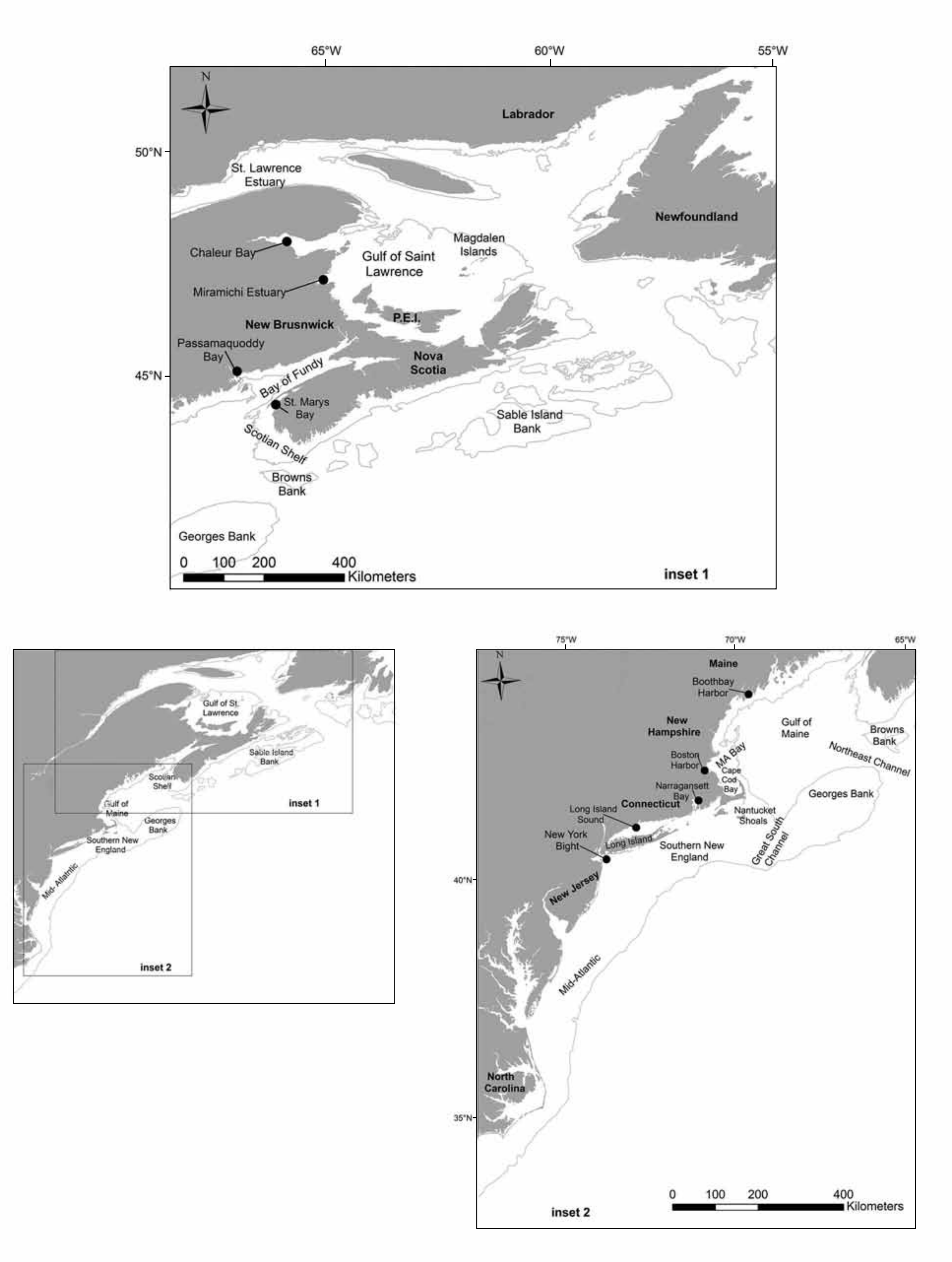


Fig. 1. Geographic range of winter flounder.

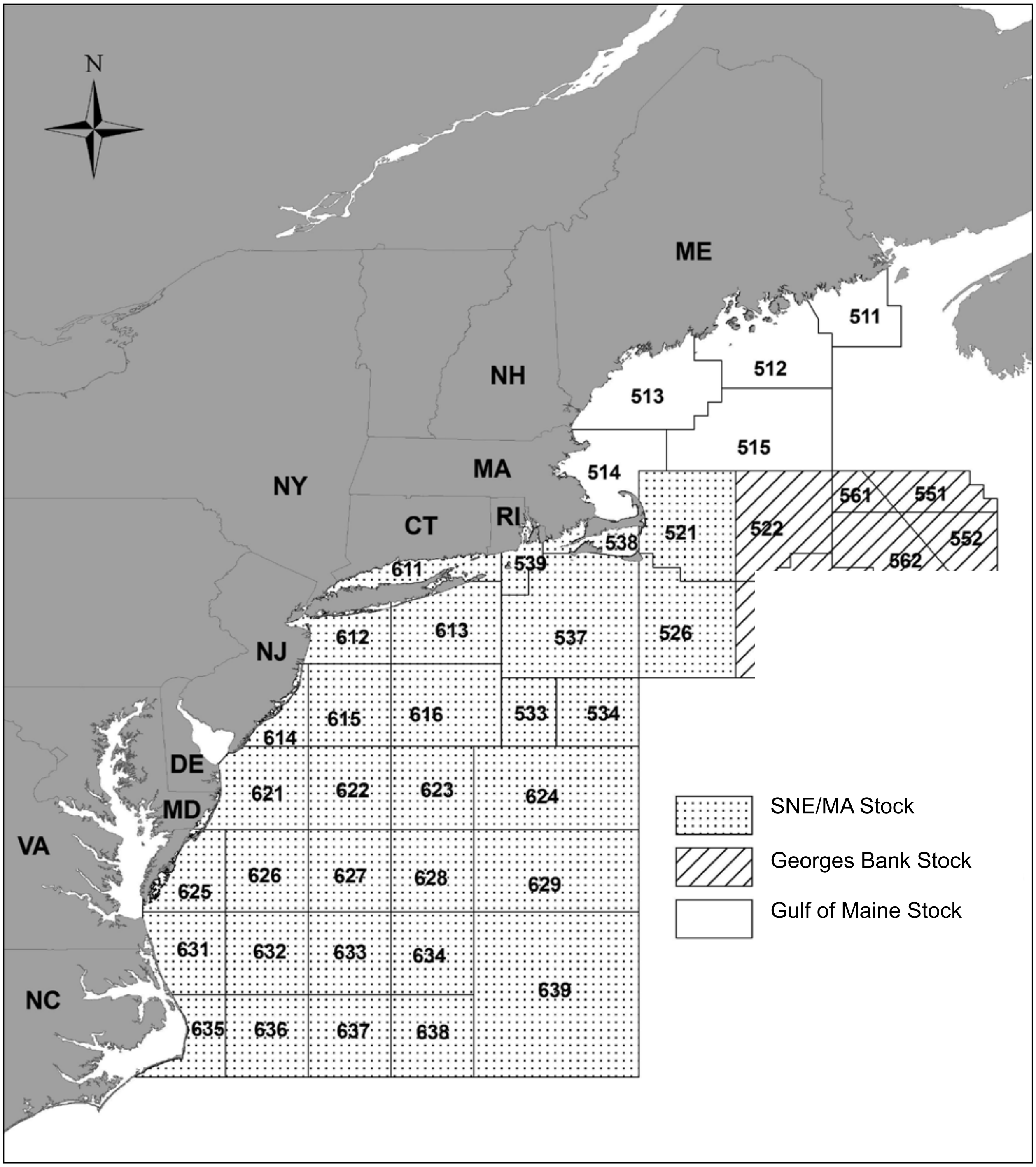


Fig. 2. Areas used to define winter flounder stocks in U.S. waters.

sources of data. Winter flounder exhibit faster growth rates in southerly latitudes, and females typically grow faster and attain larger sizes than males (Table 1).

Analysis of scale annuli patterns (Lux, 1973) and tagging data (Howe and Coates, 1975) found that winter flounder on Georges Bank exhibit faster growth rates than those in the SNE/MA and Gulf of Maine stocks. Butts and Litvak (2007) used a common garden to demonstrate that larvae sired by Georges Bank winter flounder are genetically selected for faster growth and higher survival than larvae sired by males from Passamaquoddy Bay. Based on tag return data (Howe and Coates, 1975) and aged scale samples (Witherell and Burnett, 1993), winter

Table 1. Von Bertalanffy growth parameters for winter flounder throughout its geographic range.

Stock Area	Region	Sex	K	$L_{inf\,(cm)}$	t_0	Source
SNE/MA	Narragansett Bay, RI	Male	0.27	39.0	-0.23	Berry *et al*., (1965)
	Narragansett Bay, RI	Female	0.29	45.1	0.07	Berry *et al*., (1965)
	South of Cape Cod	Male	0.25	47.7	–	Howe and Coates, (1975)
	South of Cape Cod	Female	0.34	48.8	–	Howe and Coates, (1975)
	South of Cape Cod	Male	0.31	45.9	0.16	Witherell and Burnett, (1993)
	South of Cape Cod	Female	0.31	49.0	0.25	Witherell and Burnett, (1993)
Georges Bank	Eastern Georges Bank	Male	0.37	55.0	-0.05	Lux, (1973)
	Eastern Georges Bank	Female	0.31	63.0	0.05	Lux, (1973)
	Georges Bank	Male	0.37	53.4	–	Howe and Coates, (1975)
	Georges Bank	Female	0.45	62.2	–	Howe and Coates, (1975)
Gulf of Maine	North of Cape Cod	Female	0.37	45.5	–	Howe and Coates, (1975)
	North of Cape Cod	Male	0.41	39.8	0.38	Witherell and Burnett, (1993)
	North of Cape Cod	Female	0.27	49.0	0.07	Witherell and Burnett, (1993)
4X	St. Marys Bay	Combined	0.34	43.9	0.35	McCracken, (MS 1954)
	Scotian Shelf	Male	0.45	39.7	0.41	Neilson and Hurley, (MS 1986)
	Scotian Shelf	Female	0.30	46.3	0.92	Neilson and Hurley, (MS 1986)
4T	Northumberland Strait	Combined	0.25	40.2	0.38	McCracken, (MS 1954)
	St. Lawrence Estuary	Combined	0.22	37.6	0.73	Vaillancourt *et al*., (1985)

flounder growth rates are slightly faster in the SNE/MA stock than in the Gulf of Maine (Fig. 4). However, Berry *et al.* (1965) calculated slower growth rates for winter flounder in Narragansett Bay, Rhode Island.

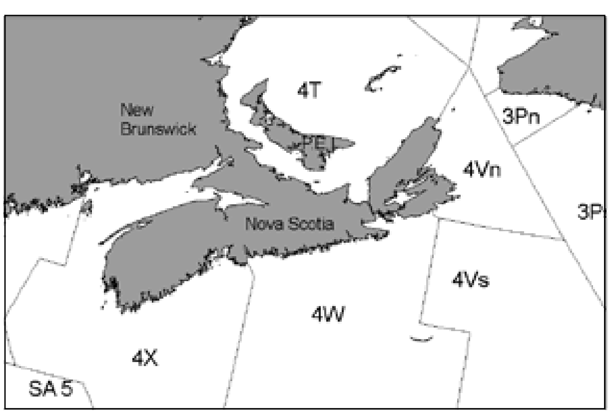
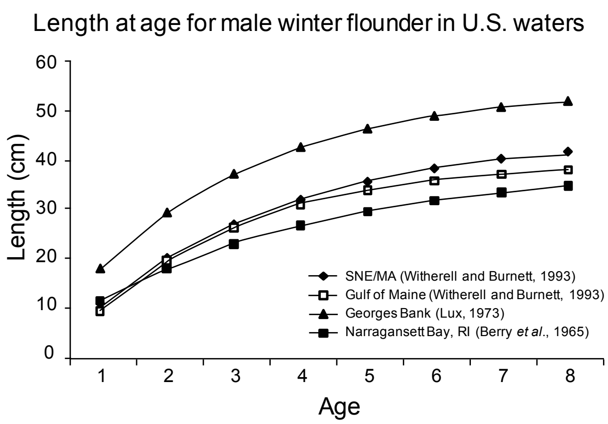


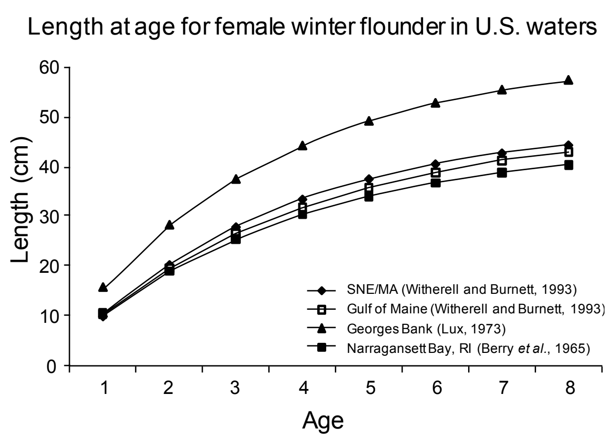
Fig. 3. Geographical areas used to define winter flounder stocks in Canadian waters.

Growth rates of winter flounder in Canadian waters also exhibit a latitudinal gradient. Winter flounder have been observed to grow faster in the Div. 4X stock area than in the Div. 4T stock area (Fig. 5). Growth rates within the Div. 4T area are dynamic, as winter flounder in the northern Gulf of St. Lawrence (St. Lawrence Estuary) exhibit slower growth than flounder in the Southern Gulf of St. Lawrence (Fig. 6; McCracken, MS 1954; Vaillancourt *et al.*, 1985). Fraboulet *et al.* (2009) captured spawning flounder from three regions in Canada: Passamaquoddy Bay, Chaleur Bay, and the St. Lawrence estuary. Common garden experiments suggested that larval growth rates had a strong paternal component, and that larvae sired by males from the St. Lawrence estuary exhibited the slowest growth rates.

Winter flounder exhibit a latitudinal gradient in maturity at age throughout their geographic range, with individuals maturing faster in more southerly latitudes (Collette and Klein-MacPhee, 2002). Estimates of age and size at 50% maturity of winter flounder are given in Table 2. Differences in the timing and location of spawning events are useful stock identification criteria because they can lead to reproductive isolation among stocks by reducing gene flow (Bailey *et al.*, 1999). Winter flounder exhibit a latitudinal gradient in time of spawning. While peak spawning times vary interanually, spawning typically occurs earlier in southern latitudes (Table 3).

For heavily exploited fish species like winter flounder, the selective pressures introduced by harvesting may influence certain life history traits, such as age at maturity (Kuparinen and Merila, 2007). Because the magnitude of fishing intensity varies between stocks, fisheries-induced evolution may act to accentuate, or diminish, the differences in vital rates between winter flounder stocks. In many regions, winter flounder has been heavily exploited by commercial and recreational fisheries for over a century (Perlmutter, 1947). Therefore, it may be difficult to detect the influence of fisheries-induced evolution using contemporary data and monitoring.





Figs. 4 and 5. Growth curves for male and female winter flounder in U.S. waters.

Morphology

Meristics- Fin ray counts have been used successfully to investigate winter flounder stock structure. Geographic variation in meristic characters, such as fin ray counts, between different stocks of fish suggest that there is little interchange between stocks, and reproductive isolation is possible. Meristic characters are the products of interactions between the genetics of an individual and its environment (Waldman, 2005b).

Kendall (1912) reported that winter flounder from Georges Bank possessed significantly more fin rays than those from inshore regions, and initially described these offshore specimens as a new species (*P. dignabilis*). Kendall also noted that Georges Bank winter flounder possessed shorter heads, had different coloration, and attained larger sizes than flounder taken inshore. Perlmutter (1947) observed that winter flounder from the Georges Bank stock had significantly more anal, dorsal and pectoral fin rays than flounder from the SNE/MA and Gulf of Maine stocks areas. Lux *et al.* (1970) obtained similar findings for Georges Bank flounder using anal and dorsal ray counts. Lux *et al.* (1970) also reported that adult winter flounder from the SNE/MA stock had significantly more fin rays than those sampled from the Gulf of Maine. Pierce and Howe (1977) sampled young of the year winter flounder at 23 estuarine locations throughout Massachusetts waters. They also concluded that winter flounder in the SNE/MA stock possessed more fin rays than flounder in the Gulf of Maine. However, Pierce and Howe (1977) did not detect any significant differences in fin ray counts between estuaries, suggesting that individual estuaries do not contain discrete stocks.

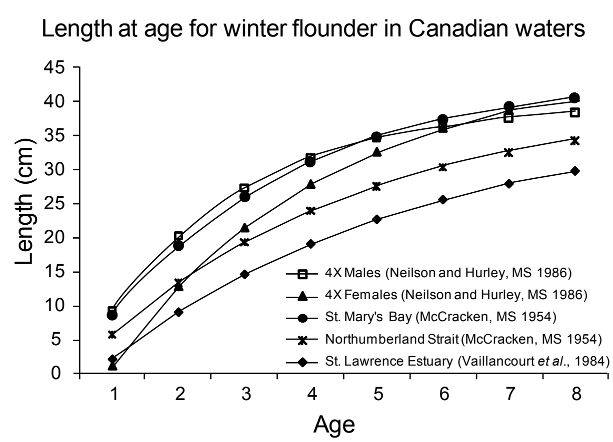


Fig. 6. Growth curves for winter flounder in Canadian waters.

Table 2. Estimates of age at 50% maturity (A_{50}) and length at 50% maturity (L_{50}) of winter flounder.

Stock	A_{50} Males (y)	A_{50} Females (y)	L_{50} Males (cm)	L_{50} Females (cm)	Citation
SNE/MA	2.0	3.0	20–25	20–25	Perlmutter, 1947
	3.3	3.0	29.0	27.6	O'Brien *et al*., MS 1993
	3.1	3.0	28.0	28.3	Witherell and Burnett, 1993
Georges Bank	1.9	1.9	25.6	24.9	O'Brien *et al*., MS 1993
Gulf of Maine	3.3	3.5	27.6	29.7	O'Brien *et al*., MS 1993
	3.3	3.3	27.2	28.7	Witherell and Burnett, 1993
Gulf of St. Lawrence	–	–	21	24	DFO, MS 2010
Newfoundland	6.0	7.0	21.0	25.0	Kennedy and Steele, 1971

Environmental signals

Patterns of parasitic infestation – Parasites can be useful tools in stock identification studies. If a fish becomes infected with a parasite that has a known endemic range, it can be inferred that the fish was within that range within the life span of the parasite (MacKenzie and Abaunza, 2005). When groups of fish have unique parasitic fauna, it can be inferred that there is limited movement of individuals between those groups.

Scott (1982) examined parasitological differences between winter flounder in the southern Gulf of St. Lawrence (NAFO Div. 4T) and the western Scotian Shelf (NAFO Div. 4X). Significant geographic variation was found between the two areas for three parasite species; *Derogenes varicus, Fellodistomum furcigerum* and *Lecithaster gibbosus*. Scott (1982) concluded that winter flounder in the two regions are distinct stocks.

McClelland *et al.* (2005) examined 189 adult winter flounder from four regions: St. Marys Bay, Georges Bank, Browns Bank, and Sable Island Bank. Seven parasite species were examined, including five species of digenetic trematodes and two species of larval nematodes. Individual fish could be classified to their sampling site with an 84% overall classification accuracy using a discriminant function analysis. Parasite characteristics provided evidence that the Georges Bank stock was distinct from groups of winter flounder in adjacent Canadian coastal waters.

Biochemical analysis – Similar to patterns of parasitic infestation, chemical contaminants can serve as acquired marks and be used to infer isolation or mixing among groups of fish (Pawson and Jennings, 1996). Carr *et al.* (1991) sampled winter flounder at a polluted site (Boston Harbor, MA) and a relatively pristine control site (Plymouth Bay, MA). Carr *et al.* (1991) measured several biochemical parameters as well as histopathogical conditions for each group of fish and found that about 50% of the fish collected in Boston Harbor had apparent apoptotic hepatic lesions (AAHPC), while lesions were not detected in any of the fish collected from Plymouth Bay. Other biochemical parameters (*i.e.*, amino acid concentrations, glycogen levels) also differed significantly between the two sites. Given the substantial differences in chemical contamination, it can be inferred that little or no interchange occurs between the two areas, despite their geographic proximity.

Gardner *et al.* (1989) examined the prevalence of liver disease in winter flounder collected at eight locations in the SNE/MA and Gulf of Maine stock areas. Liver disease was rarely detected in flounder sampled offshore in the SNE/MA area (9%), and was common in flounder from inshore locations such as New Bedford Harbor (57%) and Narragansett Bay (3 163%). In the Gulf of Maine stock, liver disease was prevalent in flounder sampled from Boston Harbor (83%), but less common in flounder captured in Cape Cod Bay (22%). Moore and Stegeman (MS 1992) and Moore *et al.*, (2005) found that liver disease was often present in winter flounder sampled

Table 3. Spawning seasons of winter flounder in different regions. The range of spawning times is indicated with a grey block, and peak spawning times are indicated with a black block.

Stock	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Citation
SNE/MA			▒	▒	■	▒			Pearcy, 1962
	▒	▒	▒	▒	▒				Fairbanks *et al*., MS 1971
			▒	▒	■				Buckley *et al*., 1991
					▒	▒			Monteleone, 1992
			▒	■	■	▒	▒		Collette and Klein-MacPhee, 2002
Georges Bank						▒	▒		Kendall, 1912
						▒	▒		Bigelow and Schroeder, 1953
					▒	▒	▒		Reid *et al*., MS 1999
Gulf of Maine					▒	■	▒		Bigelow and Schroeder, 1953
					▒	▒			Lux and Kelly, MS 1982
						▒	▒		Normandeau Associates, MS 2009
					▒	■	▒		Fairchild *et al.*, MS 2010
Passamaquoddy Bay							▒		McCracken, 1963
							▒		Fraboulet *et al.*, 2009
St. Lawrence Estuary								▒	Fraboulet, 2009
Newfoundland					▒	▒	■	■	Kennedy and Steele, 1971
								▒	Van Guelpen and Davis, 1979

from urban areas near Boston Harbor. However, liver disease was extremely rare in flounder taken from eastern Cape Cod Bay, suggesting that there was little movement of winter flounder between Boston Harbor and eastern Cape Cod Bay. While these studies were not conducted for stock identification purposes, chemical biomarkers have potential application to be used in examining stock boundaries for winter flounder.

Genetic analysis

Microsatellite Analysis – Microsatellite characters are currently the most suitable genetic tools available for stock identification research. Microsatellites have high genetic variation that can be detected at individual loci, they can be analyzed relatively easily, and there are a large number of loci that can be screened (Wirgin and Waldman, 2005).

Microsatellite studies of winter flounder in Canadian waters revealed the existence of at least four distinct stocks (McClelland *et al.*, 2005). Mature winter flounder were sampled from four locations; Georges Bank, Browns Bank, Sable Island Bank and St. Marys Bay, and analyzed using four microsatellite loci. The Georges Bank sample was found to be the most genetically distinct, while the Browns Bank and Saint Marys Bay samples had the least genetic dissimilarity. Fish were classified to their capture site with 86–96% accuracy using a discriminant function analysis.

Studies using microsatellite markers suggest that winter flounder may exhibit fine-scale population structure in the SNE/MA stock. Using six microsatellite loci, Crivello *et al.*, (2004) found evidence of genetic differences amongst larvae from three spawning areas

(Niantic, Thames and Westbrook rivers) in Long Island Sound, NY. Buckley *et al.*, (2008) used six microsatellite loci to investigate the genetic population structure of winter flounder larvae sampled throughout Narragansett Bay, RI. Buckley *et al.*, (2008) concluded that several local populations of winter flounder may be present in Narragansett Bay.

Gene expression- Fletcher and Smith (1980) and Fletcher *et al.* (1985) examined the timing of antifreeze protein formation and termination exhibited by winter flounder in four locations: Long Island, NY; Nova Scotia; Passamaquoddy Bay; and Newfoundland. Their research found that the timing of gene expression differed in populations between the four regions, and suggested that these differences may be genetically based, implying that the populations are distinct. Price *et al.*, (1990) detected differences in the timing of antifreeze protein mRNA expression between populations of winter flounder from Long Island, NY and New Brunswick, Canada, but found that the timing of gene expression was similar between winter flounder sampled from Long Island and Newfoundland. Hayes *et al.* (1991) analyzed the copy number and arrangement of antifreeze protein genes in winter flounder from nine locations. A large copy number for the antifreeze protein gene was found in flounder sampled from locations where ice or low temperatures commonly occur (Shinnecock Bay, Bay of Fundy and Newfoundland). In areas where winter temperatures are warmer (Passamaquoddy Bay, Georges Bank, and Browns Bank), the copy number for this gene was reduced. In addition, Browns Bank and Georges Bank flounder had dissimilar copy numbers and tandem components, suggesting that these groups were genetically distinct, despite their close geographic proximity. However, the results of Hayes *et al.* (1991) should be considered with caution, because only one fish was sampled from each location.

Seasonal Movements and Applied Marks

Tagging studies can provide important insight into the stock structure of marine fish. Movement data obtained from tagging can be used to estimate the geographic ranges of different stocks, the physical and environmental barriers that restrict movement between groups, and the rates of interchange between individuals in different stock areas. Groups of fish that are discrete in time or space are managed more appropriately as a single unit. However, if multiple groups of fish exhibit overlapping distributions, they are typically managed more appropriately as a single stock.

Mark-recapture studies have shown that winter flounder often return to the same spawning grounds over multiple years. However, the degree to which winter flounder exhibit spawning site fidelity is unclear, and this behavior has been interpreted differently by several authors. Lobell (MS 1939), Perlmutter (1947) and Saila (1961) claimed that winter flounder exhibit local spawning. Phelan (1992) stated that winter flounder display a homing tendency, while others have claimed that winter flounder exhibit natal homing (Danila and Kennish, MS 1982; Pruell *et al.*, 2010). In many cases, it appears that the conclusions reached by the researchers were dependent upon the scale of the tagging study. Perlmutter (1947) tagged winter flounder from New Jersey to Maine, and divided the tagging area into ten large strata for analysis. Ninety four percent of tagged individuals were recaptured within the stratum in which they were tagged, and limited movement was observed during the spawning season. Perlmutter (1947) deduced that winter flounder display local spawning behavior, but the strata he used for analysis were too large to determine if flounder displayed homing or spawning site fidelity to a specific estuary. Tagging studies conducted at smaller scales (*i.e.*, Danila and Kennish, MS 1982; Scarlett and Schneider, MS 1986) have observed that the majority of tagged flounder exhibited fidelity to a specific spawning site. However, in each study, a proportion of flounder were recaptured on other spawning grounds, indicating that a degree of straying exists within local populations. Phelan (1992) observed that flounder tagged in the Inner New York Bight exhibited fidelity, as many individuals were recaptured in close proximity to their release location (spawning site) after over 100 days at liberty.

The seasonal movements of winter flounder differ between the three U. S. stocks. Seasonal movements in the Gulf of Maine are typically localized and confined to inshore waters (Perlmutter, 1947; McCracken, 1963; Howe and Coates, 1975). Howe and Coates (1975) reported that the weighted mean displacement of tagged individuals in the Gulf of Maine was only 4.3km. In this region, adults are typically found in deeper coastal waters during the winter months, and move inshore to shallow coastal waters in the spring as temperatures increase (Bigelow and Schroeder, 1953; Howe and Coates, 1975; DeCelles and Cadrin, 2010).

Winter flounder in the SNE/MA area undergo more extensive migrations, typically leaving shallow bays and estuaries in the spring and summer months as water temperatures increase above 15°C. Several tagging studies documented a general trend for SNE/MA flounder to disperse to the south and east during the summer months (Perlmutter, 1947; Saila, 1961; Howe and Coates, 1975; Powell, MS 1989; Phelan, 1992). During the spring and summer, some flounder in the SNE/MA stock will move short distances to cooler coastal waters, while others undertake long distance migrations. For example, Powell

(MS 1989) observed that some adult flounder tagged in Narragansett Bay dispersed eastward to Nantucket Shoals and the waters south of Marthas Vineyard. During their summer migration, members of localized inshore groups intermix in coastal waters, a phenomenon described by Phelan as a "dynamic assemblage". Based on tag-recapture data, the weighted mean displacement of winter flounder tagged in the SNE/MA stock area was 26.8km (Howe and Coates, 1975). Flounder on Georges Bank remain offshore year round (Howe and Coates, 1975), and seasonal movement patterns on Georges Bank are difficult to distinguish from patterns in fishing effort (Coates *et al.*, MS 1970). Individuals in the Georges Bank stock are not dependent upon estuaries to complete their life cycle.

Tagging studies indicate that the rate of interchange between the three U. S. stocks is low. Howe and Coates (1975) reported little interchange of tagged flounder between SNE/MA and the Gulf of Maine (1.7%), and between the SNE/MA and Georges Bank stocks (0.49%). These findings suggest that the three management units of winter flounder in U.S. coastal waters are relatively discrete, and that reproductive isolation is likely between these stocks.

Tagging studies have provided evidence of contingent structure in the SNE/MA and Gulf of Maine winter flounder stocks. Contingents are cohesive groups of fish within a population that exhibit a common migration pattern (Cadrin and Secor, 2009). Contingent migrations may make a stock more resilient to overfishing, increase genetic diversity, and cause variable susceptibility to anthropogenic impacts (Secor, 1999; Hilborn *et al.* 2003). Contingent structure within winter flounder stocks warrants further research, and contingents should be considered explicitly in management strategies and designations of Essential Fish Habitat.

In the SNE/MA stock, evidence of contingent structure has been observed using mark-recapture experiments. Historically, two groups of winter flounder were thought to be present off Long Island; a migratory group and a resident ("bay") group (Lobell, MS 1939; Perlmutter, 1947). Lobell (MS 1939) and Olla *et al.*, (1969) documented the presence of a resident group of flounder that remained in Great South Bay, NY throughout the summer, where temperatures were as high as 24°C. A recent acoustic telemetry experiment (Sagarese, MS 2009) found evidence of a resident group of adult flounder, which remained in Shinnecock Bay, NY throughout the summer. Scarlett and Schneider (MS 1986) also found evidence for partial migration in winter flounder that were tagged in the Shark and Manasquan Rivers, NJ. In most years, tagged flounder dispersed to deeper coastal waters during the summer months. However, in 1984, few offshore movements were observed, and nearly all flounder were recaptured in close proximity to their release sites.

Evidence suggests that coastal spawning contingents of winter flounder may be present in SNE/MA stock. Phelan (1992) reported that some flounder tagged in the New York Bight were recaptured in coastal waters, rather than estuaries, during the spawning season. Phelan postulated that these individuals likely did not spawn offshore, and were either late inshore spawners or possibly did not spawn at all to conserve body mass. More recently, Wuenschel *et al.* (2009) collected ripening winter flounder off the coast of New Jersey in January, which suggested that adults remain on the inner continental shelf to spawn, migrate rapidly to estuaries prior to spawning, or exhibit both behaviors.

Contingent structure has also been recognized in some regions of the Gulf of Maine. Based on tag return data, Howe and Coates (1975) concluded that groups of flounder may be spawning in coastal waters, rather than estuaries. Recently, acoustic telemetry has been used to study the movements and distribution of adult winter flounder. Acoustic telemetry allows the behavior of individual fish to be tracked with high spatial and temporal resolution, and allows for the recognition of contingent behavior (Secor, 1999). Using acoustic telemetry, DeCelles and Cadrin (2010) observed two contingents of winter flounder, which exhibited divergent spawning behavior in Plymouth Bay, MA. One contingent spawned in coastal waters, while another contingent was observed migrating to estuaries during the spawning period. In the southern Gulf of Maine, Fairchild (MS 2010) observed that the majority of winter flounder tagged with acoustic transmitters remained in coastal waters during the spawning season, while only a small number migrated to estuaries during the spawning season.

McCracken (1963) discussed the seasonal distribution of winter flounder in several regions of Canada. In St. Marys Bay and Passamaquoddy Bay, New Brunswick (NAFO Div. 4X) winter flounder dispersed to deeper water during the winter months, and gradually moved inshore to shallow water to spawn during the spring. During the summer months, some large fish dispersed to deeper waters in the bays, while other remained in the shallows. In Pubnico Harbor, Nova Scotia, McCracken (1963) found that flounders began to return to the shallow waters of the bay in April. During the summer months, adult flounder left the bay, and moved to coastal waters where water temperatures were cooler. Dickie and McCracken (1955) observed very little interchange of tagged winter flounder between St. Mary's Bay and Cape St. Mary, Nova Scotia, suggesting that the two populations were virtually discrete, despite their geographic proximity.

Winter flounder in the Gulf of St. Lawrence exhibit a patchy distribution. Trawl surveys have found this species to be abundant east and west of the Magdalen Islands, east of Prince Edward Island, in Northumberland Strait, in the Miramichi estuary, and Chaleur Bay (Morin *et al.*, MS 2002). Observations from tagging suggest the seasonal movements of adult flounder in the Gulf of St. Lawrence are limited (DFO, MS 2005). McCracken (1963) observed that in Northumberland Strait, mature flounder will overwinter in cool deep waters, move to shallow inshore areas in the spring, and return to deeper waters (1524 m) during the summer months. Based on trawl surveys, flounder appear to overwinter in deeper waters 10–20 km offshore of the Magdalen Islands (Hanson and Courtenay, 1996). In contrast, winter flounder were observed in the shallow waters of the Miramichi estuary in the southern Gulf of St. Lawrence during the winter (Hanson and Courtenay, 1996). Hanson and Courtenay (1996) reported that flounder began to enter the Miramichi estuary in late autumn, and overwintered in this area, where water temperatures were warmer than the southern Gulf, and where a refuge existed from flowing ice packs. In spring as the salinity of the estuary was reduced by snow melt, adult fish left the estuary and migrated to spawning grounds in coastal waters.

Winter flounder are present in near shore waters (<60 m) along the coast of Newfoundland and Labrador (Kulka and DeBlois, MS 1996), although their distribution in shallow water is not well sampled by commercial catches and trawl surveys. In Conception Bay, Newfoundland winter flounder exhibited seasonal distribution patterns that were similar those undertaken by winter flounder in the SNE/MA stock (Kennedy and Steele, 1971; Van Guelpen and Davis, 1979). Adult flounder remained inshore in shallow waters from September until June. After spawning in May and June, adults migrated offshore to deeper waters to feed. Van Guelpen and Davis (1979) observed that storm-induced turbulence or the formation of ice in shallow waters caused winter flounder to temporarily emigrate to the deeper inshore waters of Conception Bay. Results from a small-scale tagging study indicated that flounder display a high degree of residence in Conception Bay (Van Guelpen and Davis, 1979).

In summary, tagging information suggests that limited mixing occurs between the current management areas. The seasonal movements exhibited by winter flounder vary markedly by region. South of Cape Cod, it appears that local groups of winter flounder mix in coastal waters in summer, and exhibit a degree fidelity to estuarine spawning grounds in winter and spring. In more northern habitats, residence in estuarine habitats is variable, with some groups spawning on offshore banks, others wintering in estuaries, and others occupying estuaries briefly. In offshore regions such as Browns Bank and Georges Bank, winter flounder remain offshore year round. Contingent structure likely exists, as winter flounder have been observed to exhibit both divergent spawning behaviors and partial migration. These divergent life history strategies may have important implications for reproductive mixing or isolation among spawning groups.

Synthesis and Conclusion

Basis for Assignment of Management Stock Units in the United States and Canada

Prior to 1996, winter flounder were managed as four stock units in U.S. waters: Mid-Atlantic, Southern New England, Georges Bank and Gulf of Maine. In 1996 (at the 21st Stock Assessment Workshop, SAW), the Southern New England and Mid- Atlantic groups were combined to form a single unit for assessment purposes (Shepherd *et al.*, MS 1996). The decision to combine these stocks was primarily based on tagging data (Perlmutter, 1947; Howe and Coates, 1975; Phelan, 1992), which indicated that substantial mixing of individuals occurred between the two stock areas. Life history traits (growth rate and length structure) were also observed to be similar between the two units.

The stock structure of Gulf of Maine winter flounder was also reviewed at the 21st SAW. The review concluded that sufficient interchange exists between populations of winter flounder in the Gulf of Maine to manage them as a single stock unit (Cadrin *et al.*, MS 1996). The 28th SAW examined the stock structure of Georges Bank winter flounder and determined that based on (a) tagging data (Howe and Coates, 1975), (b) meristic analysis (Lux, 1973) and (c) differences in life history characteristics (Lux *et al.*, 1970) that winter flounder on Georges Bank should be managed as a separate stock.

The geographic distribution of winter flounder observed during Canadian summer research vessel surveys on the Scotian Shelf (Stobo *et al.*, MS 1997; DFO, MS 1997) and in the Southern Gulf of St Lawrence (Morin *et al.*, MS 2002; DFO, MS 2005) provides the basis for the management units of flounder in Canadian waters. Winter flounder came under TAC management on the eastern (NAFO Div. 4VW) and western (NAFO Div. 4X) Scotian Shelf in 1994. Due to the lack of reliable landings statistics, yellowtail flounder, witch flounder, winter flounder and American plaice are managed concurrently under a single TAC on the Scotian Shelf (DFO, MS 2002).

Winter flounder have been managed under a TAC in the southern Gulf of St. Lawrence (NAFO Div. 4T) since 1996, although the first assessment of this stock was conducted in 1994 (DFO, MS 2005). Several localized stock units (or partially isolated breeding populations) are thought to exist in the region based on geographic differences in resource survey abundance trends, but information to assess local stock units is limited (Morin *et al.*, MS 2002). A sentinel trawl survey was initiated in 2003 to monitor the distribution and abundance of winter flounder in nearshore areas of the Gulf of St. Lawrence (DFO, MS 2005). Winter flounder are distributed in the coastal waters of Newfoundland (NAFO Subarea 3), but are not managed under a TAC system due to continued data limitations (DFO, MS 1996).

Critique of Assigned Stock Units

Questions regarding the stock structure of winter flounder in both U.S. and Canadian waters persist, despite extensive research. Progress in fisheries management and resource conservation requires an understanding of the scales at which winter flounder populations are connected. Connectivity between winter flounder populations is regulated by larval dispersal and the movement of mature fish. We have primarily focused on understanding the movements of adult flounder, and more research is needed to investigate larval dispersal. Contingent structure exists within winter flounder stocks (DeCelles and Cadrin, 2010), but we do not understand how contingents influence the productivity and dynamics of populations. Another important question to consider is the future impact of climate change on winter flounder distribution, dispersal, and ultimately, stock structure.

As stock identification techniques continue to develop and mature, new information will become available to assess winter flounder at finer spatial scales and manage mixed-stock fisheries. Fine-scale management may prove to be beneficial, but there are tradeoffs that must be considered before the existing stock boundaries are changed. Winter flounder is well suited as a candidate for smaller scale management, because of the many local populations in the bays and estuaries along the coast (Perlmutter, 1947). The most important question then becomes, what is the ideal scale for stock boundaries? If we manage at too small of a scale, the requirements of data collection, fisheries enforcement, and stock assessment may become impractical. On the other hand, if we assign management units that are larger than biological populations, stock assessment results will be inaccurate, making the goals of conservation and fisheries management difficult to achieve.

The available literature confirms that the current U.S. stock boundaries are appropriate to manage the three major stock complexes of winter flounder separately. Several lines of evidence support the strategy of managing winter flounder as discrete stock complexes in the SNE/MA and Gulf of Maine regions. Tagging studies *(i.e.*, Perlmutter, 1947, and Howe and Coates, 1975) demonstrated that patterns of seasonal migration vary dramatically between the two stocks. SNE/MA winter flounder exhibit faster growth than the Gulf of Maine stock (Figs. 4 and 5), and spawn earlier in the year (Table 3). Additionally, meristic characters indicate that the flounder resources in these areas are disparate stocks (Perlmutter, 1947; Lux *et al.*, 1970; Pierce and Howe, 1977).

In the SNE/MA stock, most commercial fishing effort occurs when adult fish from each localized stock are mixed in coastal offshore waters. Therefore, stock composition analysis would be necessary to manage winter flounder at a finer spatial scale. In stock composition analysis, individuals caught in a fishery are examined to estimate the relative contribution of each stock to the biomass that is available for harvest in an area (Prager and Schertzer, 2005). Multiple approaches can be used for stock composition analysis (*e.g.*, meristics, genetics and parasite characteristics), based on the differences that exist between disparate stocks. Stock composition analysis in the SNE/MA area would help to address questions regarding the relative contribution of each local population to the fishery harvest, and would allow F to be calculated more precisely for local and regional populations.

Stock composition analysis is particularly needed in the Great South Channel and Nantucket Shoals. This region supported a historical trawl fishery that targeted cod and winter flounder during the summer and autumn. Winter flounder are known to spawn on Nantucket Shoals (Pereira *et al.*, MS 1999), and flounder tagged in this region appeared to remain on Nantucket Shoals and the Great South Channel throughout the year (Coates *et al.*, MS 1970). Winter flounder have also been observed migrating from inshore areas to the Great South Channel and Nantucket Shoals during the summer months (*e.g.*, Powell, MS 1989). Therefore, the fishery in this region likely harvests a mix of flounder stocks that is comprised of migrants which originates from inshore areas, as well as a resident population that resides on Nantucket Shoals and the Great South Channel.

The Georges Bank stock should be managed as a single transboundary resource in the U.S. and Canadian waters of Georges Bank. Winter flounder in this area exhibit the highest growth rates (Fig. 4) and the largest sizes (Table 1) throughout the range of the species. Fin ray counts (*i.e.*, Lux *et al.*, 1970) indicate that winter flounder on Georges Bank are discrete from other units. Additionally, Georges Bank flounder exhibit little interchange with inshore stocks (Howe and Coates, 1975). Genetic studies examining gene expression (Hayes *et al.*, 1991) and microsatellite markers (McClelland *et al.*, 2005) suggest that winter flounder on Georges Bank are distinct from those found on the western Scotian Shelf. Winter flounder on Georges Bank and the western Scotian Shelf also exhibit distinct parasite characteristics (McClelland *et al.*, 2005). The deep waters of the Northeast Channel probably serve as a barrier that restricts movement of winter flounder between Georges Bank and the western Scotian Shelf.

Further research is needed to investigate the stock structure of winter flounder in the Gulf of Maine. Historical tagging data in the Gulf of Maine (Perlmutter, 1947; Howe and Coates, 1975) indicate that seasonal movements are limited, and that several local stocks may exist. Appropriately designed mark-recapture or tag-recovery studies (*e.g.*, Schwarz, 2005) would be useful for examining population structure in the Gulf of Maine. Tagging pre-spawning and spawning flounder throughout the Gulf of Maine would be an effective way to examine mixing rates between individuals in local spawning populations. Analysis of spawning flounder using microsatellite markers would also be useful to reveal the degree of local stock structure that exists in the Gulf of Maine.

At present, there is no research that distinguishes Gulf of Maine winter flounder from those in the Bay of Fundy or the western Scotian Shelf. In addition to tagging studies, life history data collected during trawl surveys should be examined to detect any persistent differences in the vital rates of flounder in these regions (*e.g.*, Begg *et al.*, 1999). These populations may also be connected through larval dispersal. Coupled biophysical individual based models would be useful for examining the possibility of larval transport between the Gulf of Maine and the Scotian Shelf (*e.g.*, DeCelles *et al.*, MS 2010).

Management units of Canadian winter flounder are assigned on the basis of abundance patterns derived from resource surveys. Winter flounder in NAFO Div. 4X are managed under a single TAC that includes four species of flounder (witch, yellowtail, plaice and winter flounder; DFO, MS 2002). Modest investments in fishery sampling would allow separate monitoring, assessment and management of each species. Furthermore, evidence from genetic studies (Hayes *et al*., 1991; McClelland *et al.*, 2005) suggests that winter flounder on Browns Bank may be distinct from those found inshore on the western Scotian Shelf (NAFO Div. 4X). Winter flounder are known to spawn offshore on Browns Bank (Neilson and Hurley, MS 1986). A mark-recapture study could be used to investigate movement between flounder on Browns Bank and inshore areas of the Scotian shelf. If limited interchange exists between these two regions, they may be managed more appropriately as separate stocks, similar to the way winter flounder on Georges Bank are managed as a separate offshore stock.

On the eastern Scotian Shelf (NAFO Div. 4VW), the distribution of winter flounder is restricted to Sable Island Bank. Analysis of parasitic characters and microsatellite markers suggest that flounder on the eastern Scotian Shelf are distinct from other Canadian stocks (Scott, 1982; McClelland *et al.*, 2005). Based on the available literature, winter flounder in the Div. 4VW region appear to be managed appropriately as a single stock.

Winter flounder in the southern Gulf of St. Lawrence stock (NAFO Div. 4T) are geographically isolated from other stock units, and analysis of microsatellite markers and parasite characteristics suggests the flounder in the Gulf of St. Lawrence are distinct from other stocks (McClelland *et al.*, 2005). While multiple stocks of winter flounder are likely present in the southern Gulf of St. Lawrence, the resource is managed as a single stock due to data limitations (Morin *et al.,* MS 2002). Winter flounder exhibit a patchy distribution in the region, indicating that several stocks may be present (Morin *et al.*, MS 2002). Seasonal movements appear to differ between winter flounder in different regions in the Southern Gulf of St. Lawrence (Hanson and Courtenay, 1996). Growth rates (Fig. 5) vary substantially between flounder in the southern (Northumberland Strait) and northern (St. Lawrence estuary) Gulf of St. Lawrence, and common garden experiments suggest the slow growth exhibited by flounder in the St. Lawrence estuary may have a genetic basis (Fraboulet *et al.*, 2009).

Conventional tagging experiments could be used to determine whether interchange occurs between the local winter flounder populations that are present in the Gulf of St. Lawrence. Information gathered during the sentinel trawl survey can be used to identify persistent differences in life history traits between flounder in different regions of the Div. 4T stock. Microsatellite markers could be used to investigate fine-scale stock structure in the Gulf of St. Lawrence.

Contingent structure within winter flounder stocks warrants further investigation and several methods are available to study and understand the behavior of contingents and associated implications for fishery management. Tagging studies (both conventional and acoustic) have been used to identify and evaluate contingent behavior in winter flounder populations. However, each method has inherent strengths and weaknesses that should be considered prior to the start of a study. Acoustic telemetry has shown promise in identifying contingent spawning and migratory behavior for this species (Sagarese, MS 2009; DeCelles and Cadrin, 2010; Fairchild, MS 2010). Coast-wide receiver arrays, which were proposed by Grotheus and Able (2007), would be a useful tool for examining the prevalence of coastal spawning winter flounder groups. Acoustic telemetry studies have the potential to provide high resolution, fishery independent data on the movement and behavior of individual winter flounder. However, this technology is expensive, and problems associated with the burial of tagged fish can confound data analysis (Sagarese, MS 2009; Grotheus and Able, MS 2010). Conventional tags are easier to deploy and are much less costly than acoustic transmitters. However, the quality and quantity of data obtained from conventional tagging studies is often limited (Bridger and Booth, 2003). In addition, tag return data may often reflect the distribution of fishing effort, rather that the distribution of fish (Jacobsen and Hansen, 2005). Further, tag return rates may be low during periods when fishery catches are restricted.

Spawning locations can be inferred from areas where eggs are sampled (Schultz *et al.*, MS 2007), because winter flounder spawn adhesive and demersal eggs (Klein-MacPhee, 1978). Benthic ichthyoplankton sampling was used to identify coastal spawning grounds in Plymouth Bay, MA (Scherer, 1984) and in Connecticut estuaries (Schultz *et al.*, MS 2007), and similar techniques could be applied to identify coastal spawning in other locations. Directed trawl surveys for adults during the spawning season would also help to identify the magnitude of coastal spawning by winter flounder.

Interdisciplinary stock identification analyses provide biologists, assessment scientists and fishery managers with a more holistic perspective on the spatial structure of marine fish populations. Incorporating results from multiple disciplines improves stock delineation (Hohn, MS 1997, Begg and Waldman, 1999), and in many instances, disparate approaches *(i.e.*, genetic and phenotypic) offer complimentary information (Coyle, 1998). Interdisciplinary stock identification would ideally be based on coordinated sampling designs in which the same specimens are analyzed using different approaches (Begg and Waldman, 1999; Abaunza *et al.*, 2008). Therefore, employing a multidisciplinary approach will be critical for addressing the questions that remain regarding winter flounder stock structure.

Recent studies using advanced technology, such as acoustic telemetry, have revealed the presence of complex spatial structure in populations of winter flounder. Accounting for this spatial structure in fisheries management and stock assessment is challenging, and will require new analytical approaches and higher resolution data (*i.e.*, Cadrin and Secor, 2009). To manage winter flounder stocks with greater spatial resolution, concurrent advances in stock identification and stock assessment methodologies will be needed.

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