

# Temporal changes in maturation, mean length-at-age, and condition of spring-spawning Atlantic herring (*Clupea harengus*) in Newfoundland waters

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We investigated temporal trends in some life-history traits of Atlantic herring. Population size of Newfoundland herring stock complexes declined precipitously through the 1970s. Maturation age and size also decreased substantially, but not until the late 1980s. Although significant effects were found for region and gear type, these were only minor compared with the general trend. No effects were found for sex. Changes in maturation age and size can represent an evolutionary response to fishery-induced selection, or phenotypic plasticity as a result of a compensatory response to stock declines, or a response to other changes in the environment. Length-at-age and body condition decreased concurrently with changes in maturation, suggesting that declines in maturation age and size were not a compensatory response to reduced stock sizes. This supports the hypothesis of evolutionary changes in maturation. However, increases observed in the most recent year classes, and concurrent changes in other species, suggest that changes in the environment may have also affected age- and size-at-maturation.

**Keywords:** Atlantic herring, body condition, fishery-induced evolution, fishery management, maturation, mean length-at-age, Newfoundland, phenotypic plasticity, temporal change.

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## Introduction

Iteroparity is an important reproductive strategy for many fish species because it helps to ensure individual reproductive success in environments characterized by long periods with unfavourable conditions for the survival of eggs and larvae (Leaman and Beamish, 1984). A broad age range within a spawning population also helps to reduce recruitment variability (Lambert, 1990; Marteinsdottir and Thorarinsson, 1998; Secor, 2000; Hsieh *et al.*, 2006). For some species, older fish have been shown to play a key role in sustaining the population because the size and viability of eggs and larvae increases with the size and age of the female (Chambers *et al.*, 1989; Zastrow *et al.*, 1989; Buckley *et al.*, 1991; Bobko and Berkeley, 2004). Regardless of how it evolves, structural diversity within a fish population appears to be critical for ensuring its long-term sustainability.

Historically, the importance of maintaining structural diversity within exploited populations has not always been recognized. A fishery may harvest selectively, often removing a larger proportion of older fish. Conover and Munch (2002) have shown that this erosion may have serious consequences for sustained production because it can lead to a reduction in the number of larvae produced, a shortening of the spawning season, and a reduced chance that some larvae will encounter favourable conditions for survival. Berkeley *et al.* (2004) demonstrated that age truncation

may reduce sustained production, even at the levels of fishing mortality that are considered sustainable in terms of yield.

It is a common response for fish to mature at a smaller size and younger age when population sizes are reduced by exploitation (Trippel, 1995; Morgan and Colbourne, 1999; Engelhard and Heino, 2004; Melvin and Stephenson, 2007). Two hypotheses have been put forward to account for such changes in maturation: the compensatory response (also known as phenotypic plasticity), and the evolutionary response (Engelhard and Heino, 2004). The compensatory-response hypothesis predicts that reduced stock size leads to relaxed competition for resources and therefore increased growth rate. With faster growth rates, fish attain the size required for maturation more quickly. The evolutionary-response hypothesis predicts that exploitation leads to selection for early maturing genotypes because the relative contribution of late-maturing individuals to egg production decreases with increasing mortality.

Most fishery-management strategies do not account for either selective harvesting or changes in maturation, but are founded on the assumptions that all larvae have an equal probability of survival, regardless of parental age, and that the effects of fishing are reversible (Marshall *et al.*, 1998; Berkeley *et al.*, 2004). These simplistic assumptions are in contrast to the ample evidence for rapid life-history evolution (Reznick *et al.*, 1990; Haugen and Vollestad,

2001; Hendry, 2001; Quinn *et al.*, 2001) and for the slow rates of recovery of populations from overexploitation (Hutchings, 2000, 2001). The implications of compensatory vs. evolutionary responses are important to fishery management. If earlier maturation is a compensatory response, the change is predicted to be reversible in the short term. However, if an evolutionary response is involved, the observed change is harder to reverse and may persist over a long time-span (Law, 2000). Conover and Munch (2002) suggest that ignoring these consequences is incompatible with the precautionary approach to resource conservation.

The Atlantic herring (*Clupea harengus*) is an iteroparous species, spawning annually for as long as 15 or 20 years. In Newfoundland waters, herring reach the northern limit of their range in the Northwest Atlantic, and strong year classes tend to occur sporadically (Winters and Wheeler, 1987). Under these unfavourable conditions, maintaining a broad age range within the spawning stock may be crucial for the sustainable exploitation of the population.

Wheeler and Winters (1984) identified five herring stock complexes in the coastal waters off east and southeast Newfoundland (Figure 1). Before the 1970s, fixed-gear (bar-seine, trap, and gillnet) fisheries in these areas were small, with average annual landings not exceeding 1000 t (Wheeler *et al.*, 2006) and being largely associated with the demand for herring as bait for the cod fishery (Pinhorn, 1976). With the introduction of a mobile purse-seine fleet in the mid-1970s and the recruitment of two large year classes in the late 1960s, annual landings increased substantially to a peak of 31 200 t in 1979. Annual instantaneous fishing mortality rates (ages 5–8) increased concurrently from <0.03 in 1966 to 0.22 in 1979 (Wheeler and Winters, 1996). Annual quotas were first introduced in 1977, but these were exceeded by ~50% up to 1979. This overshoot, combined with poor recruitment through the 1970s, led to a precipitous decline

in the entire population in the late 1970s (Figure 2; Wheeler *et al.*, 2001). Purse- and bar-seine fisheries during autumn and/or winter still dominate in respect of landings, accounting for 75% of the 6400 t landed in 2007 (Wheeler *et al.*, 2008).

One of the management measures employed in the Newfoundland herring fishery is a minimum landing size of 29 cm (total length). When set in the early 1970s, this limit was designed to protect all 2-year-old fish, and some 3-year-olds, from commercial exploitation. At the time, 29 cm approximated the length-at-50%-maturity, thereby ensuring that ~50% of the herring spawned at least once before being exploited by the commercial fishery. Current regulations allow a maximum of 10% undersized herring (by number) in purse-seine landings. Over the past decade, purse-seiners have encountered increased percentages of undersized herring in their catches in some areas. Fishers contend that growth rates are lower and that maturity is reached at smaller sizes than in the past and have requested that fishery managers consider reducing the minimum landing size.

We examine changes in size- and age-at-maturation in herring in Newfoundland waters since the 1970s and investigate whether these can be related to changes in stock size and/or environmental changes. We also examine temporal changes in body condition to determine whether earlier maturation is likely to reflect a compensatory response related to reduced stock size. Finally, we discuss the merits of reducing the minimum landing size in the herring fishery.

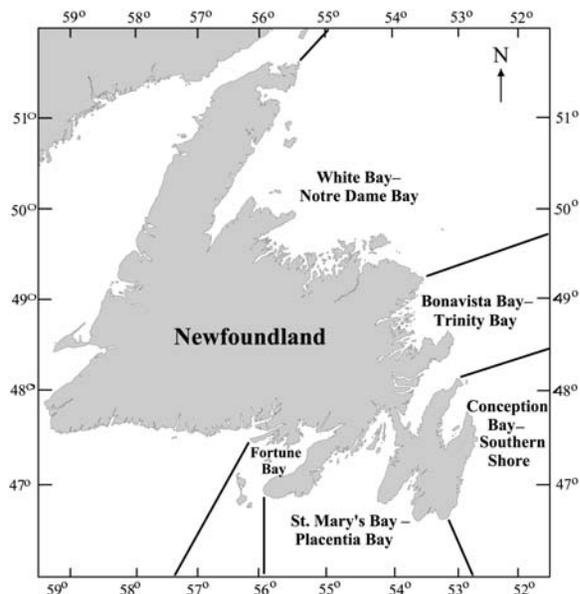
## Material and methods

### Data collection

Biological samples have been collected annually from the coastal stocks off east and southeast Newfoundland (Figure 1) since 1964 as part of the Department of Fisheries and Oceans (DFO) research programme to study the biology of Atlantic herring and to assess stock status. Following Morgan and Colbourne's (1999) approach for American plaice, maturation, growth, and condition have been analysed by year class rather than yearly, as it is the year class that grows and matures.

Both spring- and autumn-spawning herring occur in all five herring stock complexes. For all fish sampled, spawning type has been determined by both maturation stage and otolith characteristics (Parsons and Hodder, 1975). Age readings from otoliths use 1 January as the defined birth date. We have restricted our analyses to the spring-spawning component because this type dominated in the commercial catch-at-age data during the period investigated (Wheeler *et al.*, 2001). To minimize intra-annual growth effects, only those samples collected between January and June were used. Because spring-spawning herring actively feed during the second half of the year, time of sampling during this period could have a major effect on interannual growth comparisons. Although condition may vary between January and June, because this is a critical period for the transfer of body mass to gonads, sample sizes would be too small to obtain a reliable annual estimate if a shorter period had been selected.

Samples have been collected annually from commercial fisheries and research surveys since the early 1960s and from commercial gillnet fishers under contract to DFO since 1982 (Wheeler *et al.*, 2006). Most samples (~75%) were collected by purse-seine and gillnets; other gear types include bar-seines, traps, midwater trawls, otter trawls, jiggers, and handlines. As a consequence of the contract with gillnet fishers to provide samples during the



**Figure 1.** Map of Newfoundland indicating east and southeast coastal herring stock complexes. Northern stocks include White Bay–Notre Dame Bay, Bonavista Bay–Trinity Bay, and Conception Bay–Southern Shore; southern stocks include St. Mary's Bay–Placentia Bay, and Fortune Bay.

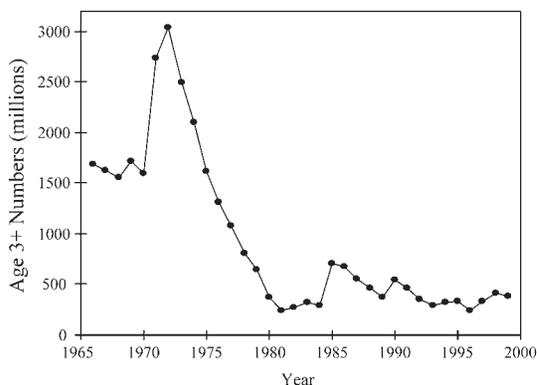
spawning period (April through June), the proportion of samples from gillnets (mesh sizes 50.8–76.2 mm) has increased from <50% before 1982 to >80% thereafter. Sample sizes by gear type were insufficient to examine changes in maturation for each gear and year class separately. However, herring gillnets are known to be length-selective. Winters and Wheeler (1990) demonstrated that selection curves are multimodal and that fishing power varies with mesh size. Therefore, samples taken with this gear were treated separately from those taken by other gears, which were considered to be non-selective.

Similarly, sample sizes by stock complex were insufficient to examine maturation changes for each area and year class separately. However, all areas are affected, to varying degrees, by the cold Labrador Current, which is known to influence herring growth rates (Winters and Wheeler, 1987). The inshore branch of this current sweeps south along the northeast coast of Newfoundland and the Avalon Channel before dissipating as it turns west along the south coast (Lazier and Wright, 1993). Based on the relative influence of this current, samples were separated into a northern region (White Bay–Notre Dame Bay, Bonavista Bay–Trinity Bay, and Conception Bay–Southern Shore) and a southern region (St Mary's Bay–Placentia Bay, and Fortune Bay).

## Analyses

Estimates of population numbers of spring-spawning herring (age 3+) were available for three of the five stock areas (White Bay–Notre Dame Bay, Bonavista Bay–Trinity Bay, and Placentia Bay–St Mary's Bay) from an extended survivor analysis for the period 1966–1995 (Wheeler and Winters, 1996) and from an integrated catch-at-age analysis for the period 1970–1999 (Wheeler *et al.*, 2001). No population estimates were available for Conception Bay–Southern Shore or for Fortune Bay. However, because the populations in the three stock areas exhibited similar trajectories over the period, the combined estimates were assumed to have been representative for all five stocks (Winters and Wheeler, 1987). Average population numbers from the two sources provide a time-series from 1966 to 1999 (Figure 2).

We used maturity ogives to examine changes in maturation. Unfortunately, maturity ogives depend not only on the genetically determined maturation tendency of individual fish but also on the



**Figure 2.** Mean population numbers of age 3+ spring-spawning herring (White Bay–Notre Dame Bay, Bonavista Bay–Trinity Bay, and St Mary's Bay–Placentia Bay combined), 1966–1999 (from Wheeler and Winters, 1996; Wheeler *et al.*, 2001).

prevailing conditions for growth and survival (Olsen *et al.*, 2005). Heino *et al.* (2002) introduced the use of probabilistic maturation reaction norms (PMRNs) to disentangle compensatory and evolutionary responses (reviewed by Dieckmann and Heino, 2007). PMRNs describe the probability of an individual *becoming* mature, usually as a function of its age and size, whereas maturity ogives describe the probability of an individual *being* mature as a function of its age and size. A shift in cohort-specific PMRNs over time is interpreted as being consistent with, although not direct evidence of, a genetic change at the population level (Marshall and Browman, 2007). However, the calculation of PMRNs requires sample sizes much larger than those available for the herring in this study.

Information on a maximum of 42 year classes (1962–2003) is available for the analysis of maturity and growth (Table 1). Length-at-50%-maturity (L50) and age-at-50%-maturity (A50; Table 2) were estimated for all year classes from a generalized linear model (GLM) with probit link (Dobson, 2002), using the function `glm()` in R (R Development Core Team, 2008). Maturity status (immature vs. mature) was entered as the *y*-variable, and either length (mm) or age (years) as the covariate. Fish were classed as immature or mature, based on the maturity stage of the gonad (Parrish and Saville, 1965): stages 1 and 2 represent gonads in the developmental stage before first spawning (immature), whereas stages 3–8 represent mature to spent gonads (mature). Year class (1962–2003) was included as an explanatory factor with 41 degrees of freedom. Gear type (selective vs. non-selective), region (north vs. south), and sex (male vs. female) were included as factors, each with two levels. The effects of gear type, region, and sex were assumed to be the same for each year class. The L50 (or A50) was estimated as the negative of the regression intercept divided by the slope, and 95% confidence intervals for the ratio were computed by Fieller's theorem (Finney, 1971). Year classes were excluded from the analysis if the total number of fish sampled at ages 2, 3, or 4 was <30. These were considered to be critical ages because herring mature between 2 and 4 years of age (in the analysis, the probability of being mature is zero below age 2 and one above age 4).

Only fish of ages 3–10 were included in the length analysis because younger age groups were underrepresented in the commercial samples; fish older than 10 years have been combined in the database as a plus group. Sample sizes for lengths-at-age ranged from 17 (age 3; 1983 year class) to 5108 (age 6; 1968 year class).

Mean somatic condition (excluding gills, stomach, and gonads) was estimated by size class for ages 3–5 using Fulton's condition factor:  $K = (W/L^3) \times 10^6$  (*W*, weight in grammes; *L*, total length in millimetres). Fish were grouped in 4 cm length intervals, and condition factors were only included in the analysis if sample sizes were  $\geq 10$  per size class, age group, and year class.

## Results

Herring numbers decreased precipitously through the 1970s (Figure 2), the estimate for 1981 being <10% of the estimated value for 1972. Numbers increased moderately during the 1980s and remained relatively stable at a low level (compared with the 1960s and early 1970s) throughout the remaining period.

The GLM analyses for L50 and A50 indicated that sex was not, or only marginally, significant, whereas gear type, region, and year class were highly significant (Table 2). It was therefore necessary to include gear type and region in subsequent analyses.

**Table 1.** Number of spring-spawning herring sampled from January through June, by age and year class, for sexes, areas, and gears combined.

Year class/Age	1	2	3	4	5	6	7	8	9	10	Total
1962*	0	0	0	15	13	35	20	17	48	98	246
1963	–	1	131	2 186	2 469	649	776	1 289	964	145	8 610
1964*	–	–	8	19	22	59	293	724	88	209	1 422
1965	–	2	18	21	48	65	151	36	217	207	765
1966	198	309	562	808	564	1 009	1 428	1 361	677	1 134	8 050
1967	1	17	42	203	333	197	223	118	203	109	1 446
1968	54	308	685	2 778	3 555	5 108	4 750	4 924	4 630	4 000	30 792
1969	1	2	36	23	<b>200</b>	789	1 918	1 574	953	2 197	7 693
1970	–	61	179	<b>126</b>	<b>88</b>	137	86	139	303	401	1 520
1971	25	407	<b>247</b>	<b>228</b>	<b>122</b>	118	64	89	27	41	1 368
1972	3	276	<b>400</b>	<b>488</b>	<b>525</b>	379	500	355	97	149	3 172
1973	2	12	<b>81</b>	<b>80</b>	<b>70</b>	79	41	19	39	55	478
1974	–	478	<b>1 316</b>	<b>1 602</b>	<b>2 091</b>	1 150	209	395	363	159	7 763
1975	–	26	<b>129</b>	<b>203</b>	<b>154</b>	38	84	29	32	53	748
1976	100	11	<b>422</b>	<b>61</b>	<b>155</b>	411	143	182	87	61	1 633
1977	–	46	<b>282</b>	<b>73</b>	<b>94</b>	73	68	84	40	20	780
1978	–	77	<b>454</b>	<b>219</b>	<b>106</b>	147	97	97	41	27	1 265
1979	–	372	<b>82</b>	<b>170</b>	<b>584</b>	675	342	127	208	236	2 796
1980	–	25	<b>260</b>	<b>430</b>	<b>556</b>	492	344	445	313	537	3 402
1981	–	37	<b>218</b>	<b>185</b>	<b>202</b>	193	177	142	168	209	1 531
1982	1 157	976	<b>1 036</b>	<b>3 198</b>	<b>3 766</b>	4 392	4 794	3 623	2 652	1 827	27 421
1983	1	–	<b>17</b>	<b>64</b>	<b>399</b>	878	854	631	470	551	3 865
1984	–	8	<b>109</b>	<b>101</b>	<b>120</b>	156	113	133	148	315	1 203
1985	100	145	<b>313</b>	<b>845</b>	<b>767</b>	671	613	429	409	81	4 373
1986	50	22	<b>465</b>	<b>640</b>	<b>469</b>	532	370	283	77	51	2 959
1987	1	42	<b>1 261</b>	<b>1 882</b>	<b>2 858</b>	3 034	2 384	704	519	241	12 926
1988	1	23	<b>57</b>	<b>123</b>	<b>517</b>	655	194	121	105	63	1 859
1989	3	5	<b>140</b>	<b>219</b>	<b>313</b>	70	90	92	34	41	1 007
1990	–	580	<b>305</b>	<b>1 355</b>	<b>648</b>	980	619	399	166	116	5 168
1991	433	565	<b>402</b>	<b>1 014</b>	<b>1 918</b>	1 971	1 241	935	644	220	9 343
1992	5	31	<b>188</b>	<b>254</b>	<b>429</b>	461	350	174	179	68	2 139
1993*	–	–	1	5	7	29	32	87	29	33	223
1994	2	2	<b>47</b>	<b>550</b>	<b>522</b>	274	281	61	68	49	1 856
1995	–	4	<b>207</b>	<b>649</b>	<b>468</b>	680	168	143	69	92	2 480
1996	–	7	<b>1 014</b>	<b>376</b>	<b>610</b>	557	832	549	419	–	4 364
1997	–	6	<b>66</b>	<b>271</b>	<b>99</b>	169	83	54	–	–	748
1998	–	10	<b>74</b>	<b>157</b>	<b>181</b>	206	153	–	–	–	781
1999	–	17	<b>401</b>	<b>1 803</b>	<b>1 738</b>	1 335	–	–	–	–	5 294
2000	–	3	<b>105</b>	<b>267</b>	<b>196</b>	–	–	–	–	–	571
2001	–	7	85	143	–	–	–	–	–	–	235
2002	–	28	331	–	–	–	–	–	–	–	359
2003*	1	16	–	–	–	–	–	–	–	–	17
Total	2 138	4 964	12 176	23 834	27 976	28 853	24 885	20 564	15 486	13 795	174 671

All year classes were included in the calculation of L50 and A50 except those marked with an asterisk (because of small sample sizes at ages 2–4). Year classes 1964–2000 were used for mean length analysis. Data for deriving condition factors are emboldened.

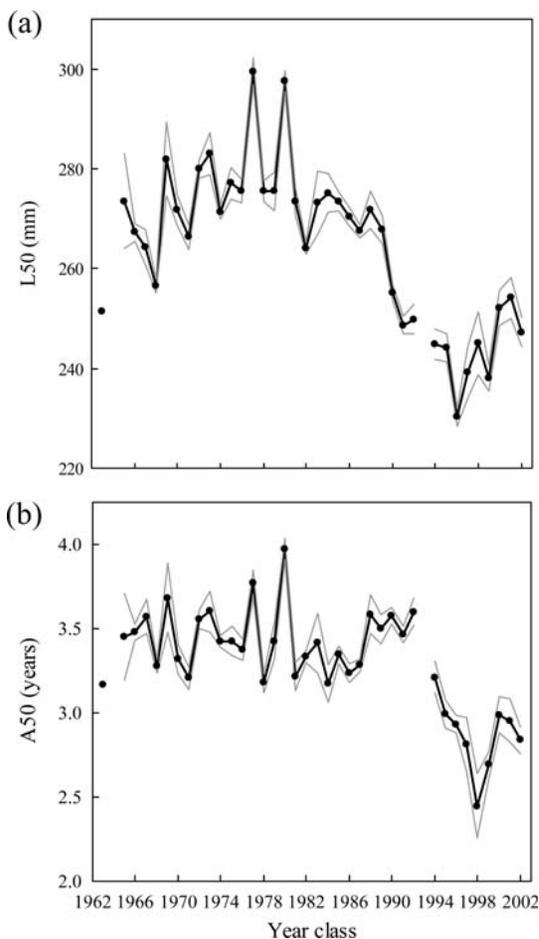
Although the L50 (Figure 3a) has been variable, it has remained relatively stable for the 1965–1989 year classes, with a mean of 27 cm, followed by a downward trend for the year classes from 1990 on, resulting in a reduction of 15% for the 1996 year class (23 cm). Subsequently, the L50 has shown an upward trend, but the value for the 2002 year class (25 cm) was still below the level observed initially.

The A50 (Figure 3b) has shown a similar pattern, but the downward trend started ~4 years later, with the 1994 year class, and the minimum was reached in the 1998 year class (2.5 years), more than 1 year below the value for the 1992 year class (3.6 years). As with L50, maturation age increased in the most recent years, but the value for the 2002 year class (2.8 years) was still below the level observed initially.

Figure 3 is based on all data but has been standardized to show the results for the non-selective gears in the northern region. Because we assumed that the effects of gear and region were the same for each year class, the corresponding graphs for other gear and region combinations run roughly parallel and follow the same pattern. The fitted L50 was ~1.1% lower for selective gears in the northern region, ~1.2% higher for non-selective gears in the southern region, and ~0.1% for selective gears in the southern region. The corresponding A50s were ~4% lower, 9% lower, and 13% lower. Exploration of the model without the assumption of fixed effects of gear type and region for all year classes confirmed that the overall trends were stronger than the potential bias imposed by the assumption.

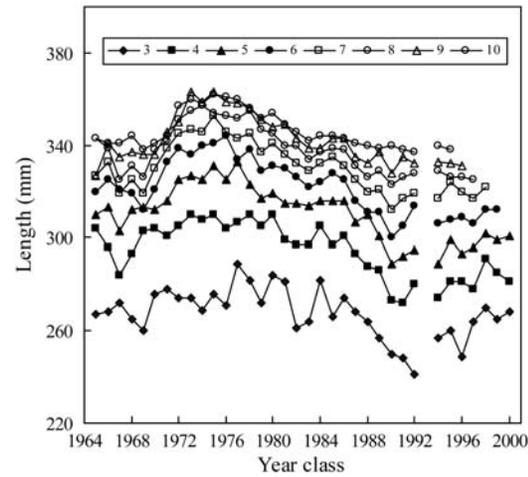
**Table 2.** Regression coefficients from the GLM analysis of L50 and A50, with probit link, including sex, gear type, and region as covariates.

Variable	Estimate	s.e.	p-value
<b>L50</b>			
Intercept	-17.05	0.439	<0.001
Length	0.059	0.0007	<0.001
Sex	-0.027	0.019	0.153
Gear type	0.176	0.028	<0.001
Region	-0.188	0.025	<0.001
<b>A50</b>			
Intercept	-8.25	0.359	<0.001
Age	2.01	0.020	<0.001
Sex	-0.040	0.019	0.034
Gear type	0.257	0.026	<0.001
Region	0.583	0.026	<0.001



**Figure 3.** Length-at-50% maturity (L50; a) and age-at-50% maturity (A50; b) by year class with 95% confidence intervals (all areas combined, but standardized to reflect non-selective gear in the northern region; see text).

Mean length-at-age exhibited an increasing trend from the year classes hatched in the mid-1960s to those hatched in the mid-1970s (Figure 4), reaching a peak in the 1975–1977 year classes. Subsequent year classes exhibited a decreasing trend in mean length at all ages up to the early 1990s. Mean lengths-at-age for year classes from the early 1990s to 2000 has either stabilized or



**Figure 4.** Mean length-at-age (age groups 3–10) by year class for all areas combined.

increased, but at levels lower than those observed in the mid-1970 year classes.

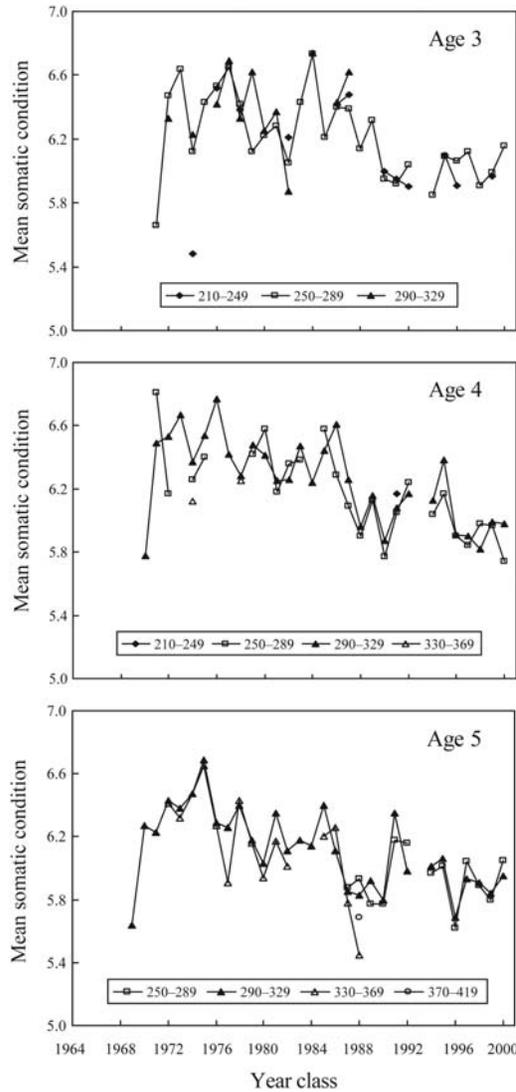
Although highly variable among year classes (Figure 5), the estimated somatic condition by length and age exhibited a decreasing trend for year classes hatched during the mid- to late 1980s. This decrease was generally independent of length and age and occurred concurrently with the observed decrease in L50.

**Discussion**

As in other fish stocks (Dieckmann and Heino, 2007), length- and age-at-maturation of Newfoundland herring have decreased after a precipitous decrease in population numbers. However, unlike other stocks, where changes in maturation occurred concurrently or shortly after the stock decline (Hutchings, 1999; Barot *et al.*, 2005; Olsen *et al.*, 2005), in this case the lag was substantial. Whereas population estimates reached their lowest levels in 1981, year classes did not exhibit a decrease in L50 until 1989, i.e. 8 years later. There has been a further lag of some 4 years before A50 decreased. These lags would not be unexpected because offspring produced after population declines need time to become mature.

Mean length-at-age decreased concurrently with decreases in L50 and A50 in year classes hatched during the late 1980s and early 1990s, which suggests that the changes observed represent an evolutionary selection towards maturation at a smaller size and younger age rather than a compensatory response, although samples were not available for fish younger than age 3. This is in contrast to the available information on Atlantic herring in other areas. In the North Sea, growth-related phenotypic plasticity has largely been responsible for the documented changes in maturity, with at most a weak evolutionary response (Engelhard and Heino, 2004). On Georges Bank, growth has been shown to be density-dependent and inversely related to age-at-maturation (Melvin and Stephenson, 2007).

In Newfoundland waters, other fish stocks have shown similar changes in biological characteristics. Age-at-maturation in northern cod decreased in concert with growth rates during the late 1980s and early 1990s, when the stock collapsed (Olsen *et al.*, 2005). During this period, length- and age-at-maturation also decreased in three stocks of American plaice (*Hippoglossoides platessoides*) when population sizes were low, although the temporal variations in growth did not show a long-term trend



**Figure 5.** Mean somatic condition (Fulton's condition factor, excluding gills, stomach, and gonads) for age groups 3–5, by year class and length interval (mm) for all areas combined.

(Morgan and Colbourne, 1999). These striking similarities among three species in Newfoundland waters suggest that there may be a common environmental cue in addition to a species-specific evolutionary response to exploitation.

The observed changes were concurrent with some of the coldest years in the recorded history of Newfoundland waters: water temperatures from 1986 to 1994 were 0.5–1.0°C below normal (Colbourne *et al.*, 1997). Rose (2007) suggested that this was a period of fundamental change in the Northwest Atlantic ecosystem. In particular, capelin, the dominant pelagic forage species, exhibited changes in spatial distribution (Narayanan *et al.*, 1995), vertical distribution (Mowbray, 2002), condition (Carscadden and Frank, 2002), and growth and spawning (Carscadden *et al.*, 1997), none of which could be attributed to overfishing (Frank *et al.*, 1996).

Jobling (1981) suggested that low temperatures may prevent fish in a depauperate population from realizing their growth potential. Temperature also affects the physiological processes underlying growth and may have direct effects on maturation,

for instance in providing seasonal cues (Thorpe *et al.*, 1998; Huber and Bengtson, 1999). This suggests that maturation changes might well have been influenced by the environment, independent of growth or mortality.

The potential impacts of fishing mortality must also be considered, because the change in maturation in herring may reflect the cumulative effect of selectively exploiting older and larger fish in combination with increased natural mortality and poor growth conditions. Although population numbers were low during the period when the changes occurred, the estimated fishing mortality was also low (Wheeler and Winters, 1996). Nevertheless, fishing could still result in evolutionary changes. Barot *et al.* (2005), citing American plaice in Newfoundland waters as an example, suggested that the selective effects of fishing mortality and natural mortality may work in tandem to bring about changes in maturation. Law (2007) suggested that selection pressures are only modest on a year-to-year basis and are more likely to be detected on decadal time-scales. These mechanisms, plus the long lifespan of herring, could help to explain the lag between the precipitous drop in population numbers and the changes in maturation.

Factors such as energy stores, and hence body condition, may also affect the maturation process (Rowe and Thorpe, 1990; Silverstein *et al.*, 1997; Shearer and Swanson, 2000; Grift *et al.*, 2003). At the same length and age, immature fish with higher body weights are likely to have greater probabilities of maturation (Stearns, 1992; Engelhard and Heino, 2004). We observed that somatic condition from January through June decreased concurrently with changes in maturation, which would not support a compensatory response.

Law (2000) suggested that evolutionary responses may be hard to reverse and that the effects are likely to persist over a long time-span. This seems incompatible with the increasing trend in L50 and A50 for herring year classes hatched since the late 1990s, especially because there is no reason to assume that selective pressure by the fishery has suddenly stopped. Olsen *et al.* (2005) demonstrated a reversal in maturation norms for female northern cod within ~3 years of a moratorium, although the affected year classes originated from the period before the moratorium was imposed. Also, Morgan and Colbourne (1999) observed, in American plaice, that size-at-maturity had stabilized or increased slightly. These observations are difficult to reconcile with the evolutionary response theory, and Law (2007) suggested that changes such as those observed in Newfoundland fish stocks provide evidence for responses to environmental cues, rather than for an inherited genetic response. Although the distinction between environmental and genetic responses is not clear-cut, the environment obviously provides a likely explanation of the changes in biological characteristics observed in Newfoundland herring. It would be beneficial to know whether the life-history traits of unexploited species in the area have changed.

Regardless of the actual cause of the observed changes, fishery managers should exercise caution before considering a reduction in the minimum landing size for herring. Ernande *et al.* (2004) showed that evolutionary changes in maturation are minimized when the minimum landing size is such that immature individuals are mostly below the limit. It has also been suggested that earlier maturation may negatively influence reproductive potential, because smaller females not only produce fewer offspring than larger ones, but also produce offspring of poorer quality (Murawski *et al.*, 2001; Berkeley *et al.*, 2004; Hutchings, 2005).

In general, management measures should focus on practices that minimize selective pressures on harvested populations (Kuparinen and Merila, 2007). To reduce the effects of evolutionary responses, both small and large fish should probably be protected (Law, 2007). Conover and Munch (2002) suggest that a maximum landing size may offer advantages for broadening the age structure of the spawning stock, because fast-growing genotypes pass more quickly through the exploited life stage, so would be favoured. Protection of small and large fish requires patterns of fishing mortality that are greatest in fish of intermediate body size. This has been achieved for some “slot-limit” fisheries, using gears such as traps, gillnets, and longlines, where minimum and maximum landing sizes are imposed (Myhre, 1969; Hamley, 1975). Baskett *et al.* (2005) used a modelling exercise to show that marine protected areas could be as effective as other management tools in protecting stocks against fishery-induced selection for early maturation. There are no simple answers and a combination of approaches may be best. However, reducing the minimum landing size in Newfoundland herring would increase rather than reduce the negative effects of selection.

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