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Several Biological Aspects of the Witch Flounder (*Glyptocephalus cynoglossus* (L.)) in the Gulf of Maine–Georges Bank Region

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Abstract

Witch flounder (*Glyptocephalus cynoglossus*) collected in the Gulf of Maine–Georges Bank region during Northeast Fisheries Center bottom trawl surveys in 1980–83 were used to describe growth, length-weight relationships, fecundity, maturation, spawning and distribution. Size-at-age data provided the following von Bertalanffy growth parameters: $L_{inf} = 58.05$ cm (total length), $K = 0.15$ and $t_o = -0.01$ for males, and 61.99 cm, 0.15, and 0.05, for females. Median length at maturity, estimated from probit analysis, was 27.6 cm for males and 33.5 cm for females. Estimates of fecundity, ranging from 48 800 eggs for a 31 cm fish to 508 300 eggs for a 60 cm fish, were comparable to those for fish from Canadian waters. Two areas of concentrated spawning activity in the western and northern portions of the Gulf of Maine were identified. Juvenile and adult witch flounder appeared to be segregated by depth, but the relative position of the life stages with respect to depth varied seasonally.

Introduction

The witch flounder, or grey sole (*Glyptocephalus cynoglossus*), is a small-mouthed, right-sided boreal flounder distributed in deeper, cold waters of the North Atlantic. In the Northwest Atlantic, witch flounder range from Labrador, Canada, to Cape Hatteras, North Carolina, USA, but are not commercially abundant south of Cape Cod, Massachusetts. In USA waters, they are common throughout the Gulf of Maine, as far south as Massachusetts Bay and the Great South Channel, and are also taken frequently on the deeper areas of Georges Bank (Fig. 1).

Relative to other flounders in this region, the witch flounder is a slow-growing, long-lived species of moderate abundance and yield. Most commercial landings are taken as by-catch in fishing operations directed at more abundant species, although its high ex-vessel value compared to other flounders often results in its inclusion as an intended component in mixed fishery situations. At present, the resource in the Gulf of Maine–Georges Bank region is considered to be over-exploited (U.S. Dept. of Commerce, 1989).

No regulations have been imposed upon harvest of witch flounder in this region since the withdrawal of the USA from the International Commission for the Northwest Atlantic Fisheries in 1976. It is, however, one of the demersal species included in the Northeast Multispecies Fishery Management Plan implemented by the New England Fishery Management Council in 1986 (NEFMC, 1985), and, as such, is affected by minimum size limits, mesh size restrictions, and closed areas associated with that plan.

The biology of witch flounder has been well-studied in the East Atlantic (Molander, 1925; Bowers, 1960; Rae, 1969; Steinarsson *et al.*, MS 1989; Nilsen *et al.*, MS 1989), where the species supports moderate-yield fisheries in the North Sea, Irish Sea and off Iceland. The population biology of Canadian stocks has also been studied (Powles and Kohler, 1970; Bowering, 1976, 1978, 1987; Bowering and Misra, 1982; Bowering and Brodie, 1984; Bowering and Stansbury, 1984), but little work has been reported from the Gulf of Maine–Georges Bank region. It was the objective of our study, therefore, to present such an analysis, including information pertaining to growth, length-weight relation-

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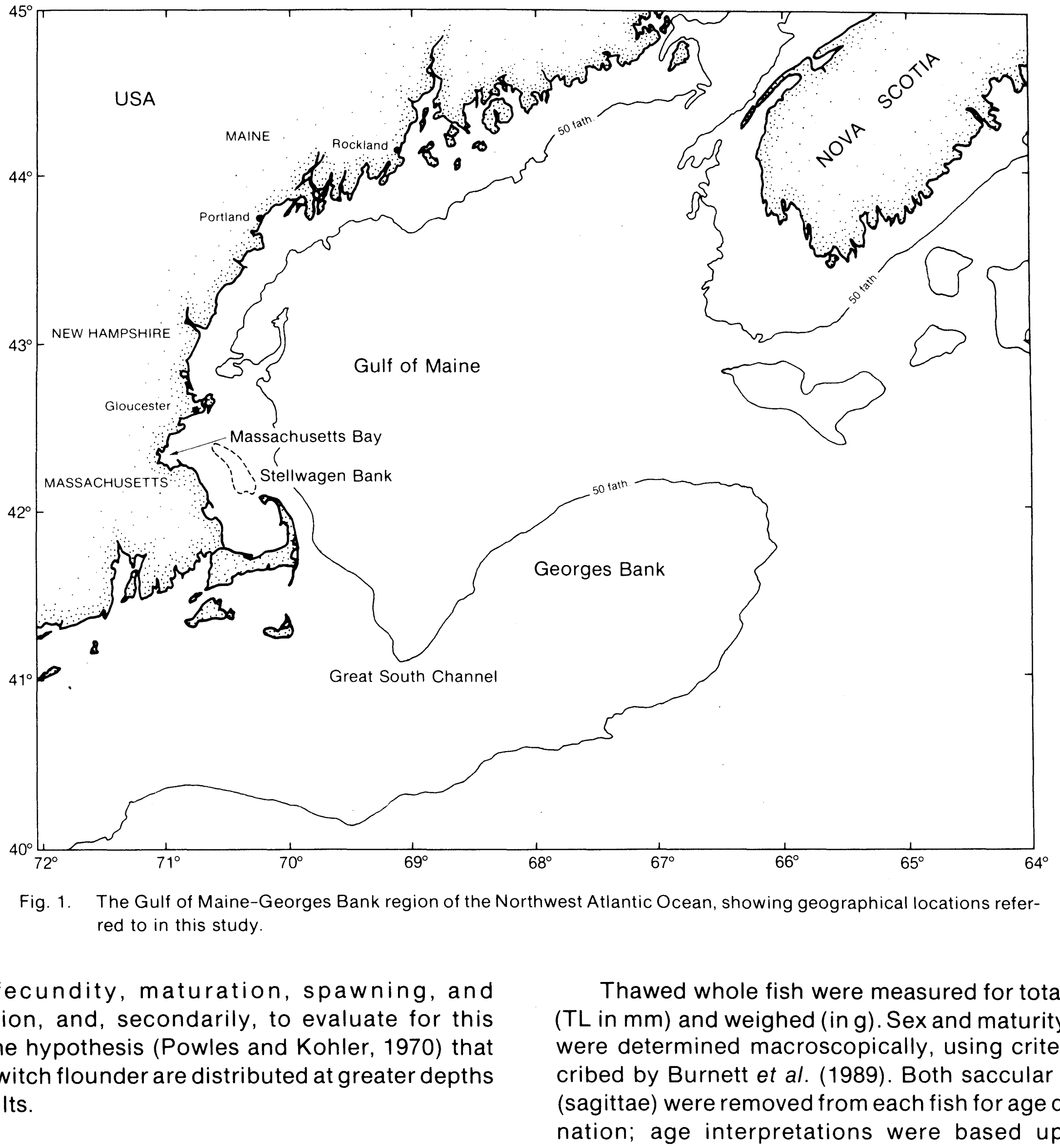

Fig. 1. The Gulf of Maine-Georges Bank region of the Northwest Atlantic Ocean, showing geographical locations referred to in this study.

ships, fecundity, maturation, spawning, and distribution, and, secondarily, to evaluate for this region the hypothesis (Powles and Kohler, 1970) that juvenile witch flounder are distributed at greater depths than adults.

Materials and Methods

A total of 1 652 witch flounder was collected from March 1980 to June 1983. The majority was captured during bottom-trawl survey cruises conducted by the Northeast Fisheries Center (NEFC) in the Gulf of Maine-Georges Bank region in NAFO Subarea 5 (Table 1); details of this stratified-random survey program and sampling gear are given in Azarovtiz (1981). Additional samples were obtained during sea-sampling activities aboard a commercial shrimping vessel near Stellwagen Bank in May 1983, and by commercial trawlers in the Great South Channel in June 1983 (Fig. 1). All specimens except those collected for fecundity analysis were frozen at sea in airtight plastic bags for subsequent measurements.

Thawed whole fish were measured for total length (TL in mm) and weighed (in g). Sex and maturity stages were determined macroscopically, using criteria described by Burnett *et al.* (1989). Both saccular otoliths (sagittae) were removed from each fish for age determination; age interpretations were based upon the number of hyaline zones present in otolith thin-sections (details regarding otolith sectioning, ageing, and validation of ageing methodology are given in Burnett, 1988). Additional data were obtained from NEFC bottom trawl surveys including catch, temperature, and depth information during 1963–84, and maturity-at-length data during 1977–84 (Table 1).

Growth. A total of 1 120 fish was aged using thin-sectioned otoliths. Because stock structure of witch flounder is uncertain within the region, fish from the Gulf of Maine and Georges Bank were combined in growth analyses. Most 1- and 2-year-old fish were not distinguishable by sex and were used in both male and female computations. Although in this region they spawn during May–August (Bigelow and Schroeder, 1953; Colton *et al.*, 1979), a birth date of 1 January was

TABLE 1. List of NEFC cruises and sampling periods from which age, maturity, and distribution data were obtained for witch flounder in the Gulf of Maine-Georges Bank region, 1963-84.

Year	Vessel[a]	NEFC cruise	Sampling period[b]	Data[c]
1963	AL IV	007	13 Nov - 16 Dec	D
1964	AL IV	001	16 Jan - 15 Feb	D
	AL IV	013	22 Oct - 25 Nov	D
1965	AL IV	002	1 Feb - 8 Apr	D
	AL IV	510	7 Jul - 10 Aug	D
	AL IV	014	6 Oct - 9 Nov	D
1966	AL IV	601	18 Jan - 23 Feb	D
	AL IV	614	12 Oct - 13 Nov	D
1967	AL IV	721	17 Oct - 10 Dec	D
1968	AL IV	803	6 Mar - 22 Apr	D
	AL IV	817	10 Oct - 26 Nov	D
1969	AL IV	902	5 Mar - 10 Apr	D
	AL IV	908	14 Jul - 16 Aug	D
	AL IV	911	8 Oct - 23 Nov	D
1970	AL IV	703	13 Mar - 30 Apr	D
	AL IV, DE II	706	3 Sep - 21 Nov	D
1971	AL IV	711	9 Mar - 5 May	D
	AL IV	716	29 Sep - 19 Nov	D
1972	AL IV	722	8 Mar - 28 Apr	D
	AL IV	728	28 Sep - 20 Nov	D
1973	AL IV, DE II	733	19 Mar - 16 May	D
	AL IV	738	26 Sep - 20 Nov	D
1974	AL IV	744	12 Mar - 5 May	D
	AL IV	748	23 Sep - 10 Nov	D
1975	AL IV	753	14 Mar - 12 May	D
	AL IV, DE II	758	7 Oct - 18 Nov	D
1976	AL IV, DE II	762	4 Mar - 8 May	D
	AL IV	767	28 Sep - 23 Nov	D
1977	AL IV, DE II	771	19 Mar - 20 May	M D
	AL IV, DE II	774	27 Jul - 1 Sep	M D
	DE II	778	26 Sep - 5 Dec	M D
1978	AL IV	783	20 Mar - 26 May	M D
	AL IV, DE II	787	25 Jul - 20 Aug	M D
1979	AL IV, DE II	793	21 Mar - 12 May	M D
	AL IV, DE II	794	27 Jul - 1 Sep	M D
	AL IV, DE II	799	12 Sep - 19 Nov	M D
1980	AL IV, DE II	802	16 Mar - 8 May	A M D
	AL IV, DE II	805	11 Jul - 18 Aug	A M D
	DE II	809	17 Sep - 14 Nov	A M D
1981	DE II	037	6 Jan - 28 Jan	A M D
	DE II	811	19 Mar - 24 May	A M D
	DE II	813	23 Jun - 24 Jul	A M D
	DE II, AL IV	816	16 Sep - 7 Nov	A M D
1982	DE II	8201	18 Jan - 12 Feb	A M
	DE II	8202	8 Mar - 8 May	A M
	AL IV	8206	13 Sep - 12 Nov	A M
1983	DE II	8302	28 Feb - 9 Mar	A M
	AL IV	8303	7 Mar - 6 May	A M
	AL IV	8306	12 Sep - 10 Nov	M
1984	AL IV	8402	29 Feb - 27 Apr	M

[a] AL IV = R/V *Albatross IV*; DE II = R/V *Delaware II*.
[b] Standard survey cruise tracks result in the Gulf of Maine- Georges Bank region being surveyed during the latter 3 weeks of each sampling period.
[c] A = Age, length, weight, sex, and maturity observations; M = length, sex, and maturity observations; D = length and distribution information.

used, a standard convention which ensures proper assignation of individual fish to appropriate year-classes (Penttila *et al.*, 1988). Ages were adjusted fractionally from 1 January according to the day of capture to increase the precision of growth calculations. The von Bertalanffy growth model was fitted to length-at-age data with the equation:

$$L_t = L_{inf}\,(1-e^{-K(t-t_o)})$$

where L_t is TL at age t, L_{inf} is asymptotic TL, K is the Brody growth coefficient, and t_o is the hypothetical age at zero length, using a nonlinear curve-fitting package (SAS, 1982).

Length-weight relationships. Length-weight equations for each sex were described using the equation:

$$W = aL^b$$

where W is weight, L is TL, and a and b are parameters to be estimated. Parameters were estimated using non-linear regression (SAS, 1982) as recommended by Zar (1968).

To evaluate possible discrepancies in fish weights associated with freezing and/or thawing, 358 fish were weighed at sea with a digital readout scale with 0.1 g precision. Individual weights following freezing at sea and subsequent thawing were compared to weights prior to freezing using a paired t-test (Snedecor and Cochran, 1980).

Fecundity. Twenty-five females with mature ova were obtained in fresh condition in June 1983 from the Great South Channel. No clear (hydrated) eggs were present in the ovaries, ensuring that spawning had not been initiated prior to collection. Ovaries were prepared for analysis following the procedure of Simpson (1951). Samples were rinsed through 0.303 and 0.505 mm fine mesh screens to remove second generation ova and extraneous tissue. A modified Folsom plankton splitter (Van Guelpen *et al.*, 1982), was used in subsampling total ovary contents; four subsamples, each 1/512 of the original sample, were obtained from each fish for egg enumeration.

A dissecting microscope was used at 5-10X magnification to count eggs. Arithmetic means of the four subsample counts were expanded by a factor of 512 to generate estimates of fecundity. Univariate regressions were performed of fecundity against length, weight, and age to develop predictive relationships. Twenty eggs from each subsample were selected randomly for size determinations; diameters were measured with an ocular micrometer and converted to mm.

Maturation and spawning. The stage of maturity was recorded for 4 721 witch flounder during the 1977-84 NEFC spring bottom trawl surveys. Maturity-at-length data from spring surveys (prior to spawning) were analyzed using probit analysis (Finney, 1971) and maturity ogives were generated by sex for each year. Goodness of fit was evaluated with the Chi-square statistic. The geographic distribution of spawning fish (maturity stages ripe or ripe and running) was examined in order to delineate spawning grounds. The relationship between spawning activity (defined as the number fish in the maturity stages ripe or ripe and running/total number of adult fish) and depth or bottom temperature was examined using regression analysis.

Seasonal distribution. Capture location was analyzed of 20 692 witch flounder taken in NEFC bottom trawl surveys during 1963–81 to evaluate distribution in relation to depth and bottom temperature. The data were partitioned into three groups based upon fish size: juveniles (0–20 cm TL), subadults (21–30 cm TL) and adults (>30 cm TL), to test the hypothesis that juveniles are distributed at greater depths than adults (Powles and Kohler, 1970). These size categories were used because a change in diet occurs at about 20 cm (Bowman and Michaels, 1984) and median length at maturity (L_{50}) for both sexes combined is 30 cm. Estimates of mean depth and temperature, weighted by numbers of fish at each location, were calculated for each group by season, and tested for differences using a non-parametric analysis of variance (Kruskal and Wallis, 1952).

Results

Growth. Growth equations were derived from the 1 120 length-at-age observations which ranged in age from 0 for a fish of TL 5.3 cm to 24 for fish of TL 56.8–62.1 cm. The von Bertalanffy equation parameters for males and for females are given in Table 2. Females attained a greater maximum size than males but appeared to grow at approximately the same rate (Fig. 2), although this was not evaluated statistically.

Length-weight relationships. No significant differences between live weight and frozen/thawed weight were observed, therefore, weight loss due to dehydration was not considered as a source of error. Estimates for parameters a and b, and associated standard errors, are summarized in Table 3 for males, females, and both sexes combined in two sets of units: weight in kg with length in cm, and weight in g with length in mm. Von

TABLE 2. Growth parameters estimates and standard errors (S.E.) obtained from fitting the von Bertalanffy growth model to length-at-age data for male and female witch flounder collected from the Gulf of Maine–Georges Bank region, 1980–83.

Numbers	Parameter	Estimate	S.E.
	Male		
626	L_{inf} (cm)	58.0452	0.6425
	K	0.1533	0.0044
	t_o	-0.0120	0.0547
	Female		
571	L_{inf}	61.9859	0.5607
	K	0.1482	0.0038
	t_o	0.0542	0.0556

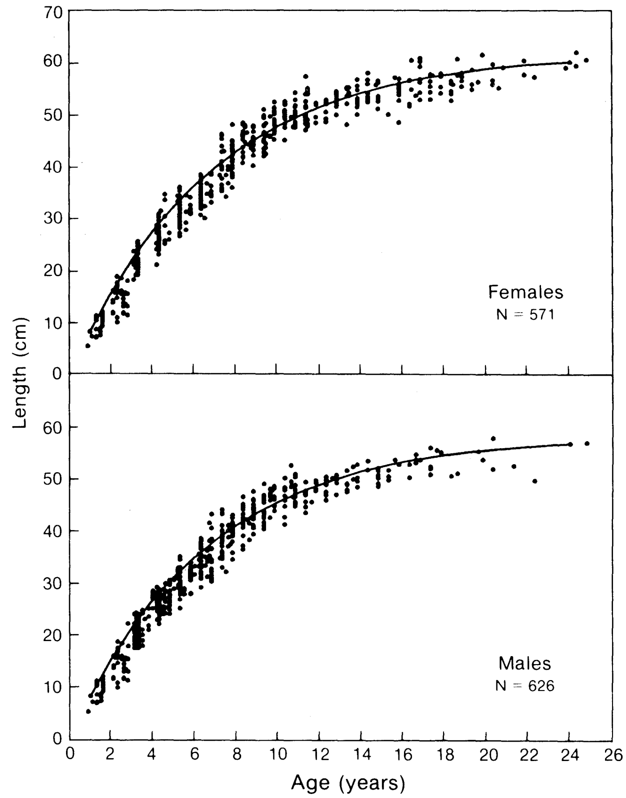

Fig. 2. Von Bertalanffy growth curves for female and male witch flounder from the Gulf of Maine–Georges Bank region, calculated from data collected during NEFC bottom trawl surveys, 1980–83.

Bertalanffy equation expressed in terms of weight (kg) were:

$$W_t = 1.58\ (1-e^{-0.15(t+0.01)})^{3.60} \quad \text{for males, and}$$

$$W_t = 1.93\ (1-e^{-0.15(t+0.05)})^{3.44} \quad \text{for females,}$$

where W_t is weight at age t.

Fecundity. Egg diameters determined from 2 000 measurements had a mean of 1.01 mm (range = 0.67–1.20 mm and standard deviation = 0.128). Because diameters were unimodally distributed and ova had undergone vitellogenesis, it was concluded that only present generation eggs were counted. Egg size was

TABLE 3. Length-weight parameters estimates (a and b) and standard errors (S.E.) for male and female witch flounder collected from the Gulf of Maine–Georges Bank region, 1980–83.

Units	Sex	N	a	S.E.	b	S.E.
cm; kg	Male	889	0.0000007	0.00000001	3.6020	0.0254
	Female	983	0.0000013	0.00000002	3.4434	0.0285
	Combined	1 652	0.0000013	0.00000002	3.4284	0.0291
mm; g	Male	889	0.00000029	0.00000012	3.5234	0.0661
	Female	983	0.00000046	0.00000008	3.4434	0.0285
	Combined	1 652	0.00000047	0.00000009	3.4398	0.0292

not significantly correlated with either fish size or age, but such relationships may have been obscured by the small sample size of 25 fish.

Fecundity estimates ranged from 48 800 eggs for a 31 cm fish to 508 300 eggs for a 60 cm fish. Mean fish length in the sample was 49.6 cm. Coefficients of variation for subsample counts averaged 22.2% (range 4.0–58.2%), a value consistent with the error identified by Van Guelpen *et al.* (1982) when subsampling small fractions. Logarithmically-transformed data (log-log, base 10) provided the best fits when fecundity was regressed separately against length, weight and age. Although all relationships were statistically significant ($P<0.05$), fecundity was most highly correlated with weight, followed by length, and then age (Table 4).

Maturation and spawning. Observed overall sex ratios for witch flounder taken during 1977–84 were essentially 1:1, although the annual percentage of males increased from 46.3% in 1980 to 54.1% in 1984. Goodness of fit tests were highly significant ($P<0.01$) for maturity ogives for each sex in all years. Median length-at-maturity (L_{50}) for males decreased from a mean of 29.6 cm during 1977–81 to a mean of 24.3 cm during 1982–84 (Fig. 3) with a concomitant decrease in the median age-at-maturity (A_{50}) from age 5 to 4. Females, however, did not exhibit this trend, as L_{50} fluctuated around a mean of 33.5 cm (Fig. 4) and A_{50} remained about age 6. Sharp declines in L_{50} for males from 1977 to 1978 and females from 1978 to 1979 are attributed to a large, slow-growing 1973 year-class (unpublished data).

Spawning was protracted, with ripe fish observed from April to November, but too few samples were collected during the summer to identify peak spawning (Table 5). Spawning fish were found at depths ranging from 24 to 360 m, and a bottom temperature range from 2.9° to 8.9° C.

The western and northern portions of the Gulf of Maine were identified as areas of most spawning activity (Fig. 5). Mean depths and bottom temperatures were 126 m and 4.6° C for the western area, and 131 m and 5.1° C for the northern Gulf; however, localities of colder water may delineate the distribution of spawning fish. In both areas, the index of spawning activity in each survey tow was negatively correlated with bottom temperature recorded for that station ($r = 0.81$, $p<0.01$ for the western area, and $r = 0.87$, $P<0.01$ for the northern area). No relationship was detected between spawning activity and depth.

TABLE 4. Results of univariate log-log (base 10) regression analyses of witch flounder fecundity on length[a], weight[b] and age[c] (a = intercept, b = slope, S.E. = standard error, r = correlation coefficient, F = F-test statistic, p = probability).

Variable	a	S.E.	b	S.E.	r	F	p
Length	0.1714	0.1606	3.0919	0.5495	0.761	31.66	0.000
Weight	2.3232	0.1284	1.0540	0.1332	0.855	62.58	0.000
Age	4.3490	0.2077	1.0312	0.3312	0.545	9.69	0.005

[a] $\text{Fecundity} = 1.4839\ \text{Length}^{3.0919}$

[b] $\text{Fecundity} = 210.4747\ \text{Weight}^{1.0540}$

[c] $\text{Fecundity} = 22335.7222\ \text{Age}^{1.0312}$

Seasonal distribution. No significant differences were observed in depth or temperature distributions for subadults and adults; accordingly, these two groups were combined in subsequent analyses. Distributions of juveniles and adults were not significantly different for any season with respect to bottom temperature (Table 6). However, distribution by depth differed significantly ($P<0.01$) for juveniles and adults for all seasons. Adults maintained an annual mean depth of 147 m, while juveniles were found at shallower depths than adults in winter and spring, and greater depths in summer and autumn. Seasonal mean depths for juveniles ranged from 112 m in winter to 198 m in summer and autumn.

Discussion

Although females grew to a smaller asymptotic size, growth rates of witch flounder in the Gulf of Maine–Georges Bank region were generally higher over a comparable life span than those for fish from Canadian waters (Fig. 6; see Bowering and Brodie, 1984, for a discussion of the poor growth of witch flounder in the Gulf of St. Lawrence). This is similar to findings for some other flatfish in the Gulf of Maine, and in Canadian waters, e.g. winter flounder (*Pleuronectes americanus* (Lux, 1973)), and American plaice (*Hippoglossoides platessoides* (Sullivan, MS 1982)). The most likely explanation for faster growth is the warmer temperature regime of the Gulf of Maine-Georges Bank region coupled with the observation that in this region they feed year-around (R. Bowman, Northeast Fisheries Science Center, pers. comm.) as opposed to fasting during winter months in Canadian waters (Roff, 1982). The length-weight relationships calculated in this study compared closely with those derived by Lux (1969) for fish from Nantucket Shoals, and by Powles (1967) and Bowering and Stansbury (1984) for fish from the Scotian Shelf and eastern Newfoundland, respectively.

Up to fish length of 44 cm, fecundity in this study was comparable to that predicted for witch flounder from Newfoundland waters calculated from Bowering's (1978) fecundity-length relationship, however, Bowering's equation predicted higher fecundities for larger fish. Comparisons of fecundity with fish from the East Atlantic were more difficult due to the much shorter life span and smaller maximum sizes of those populations, but the maximum estimated in this study of 508 300

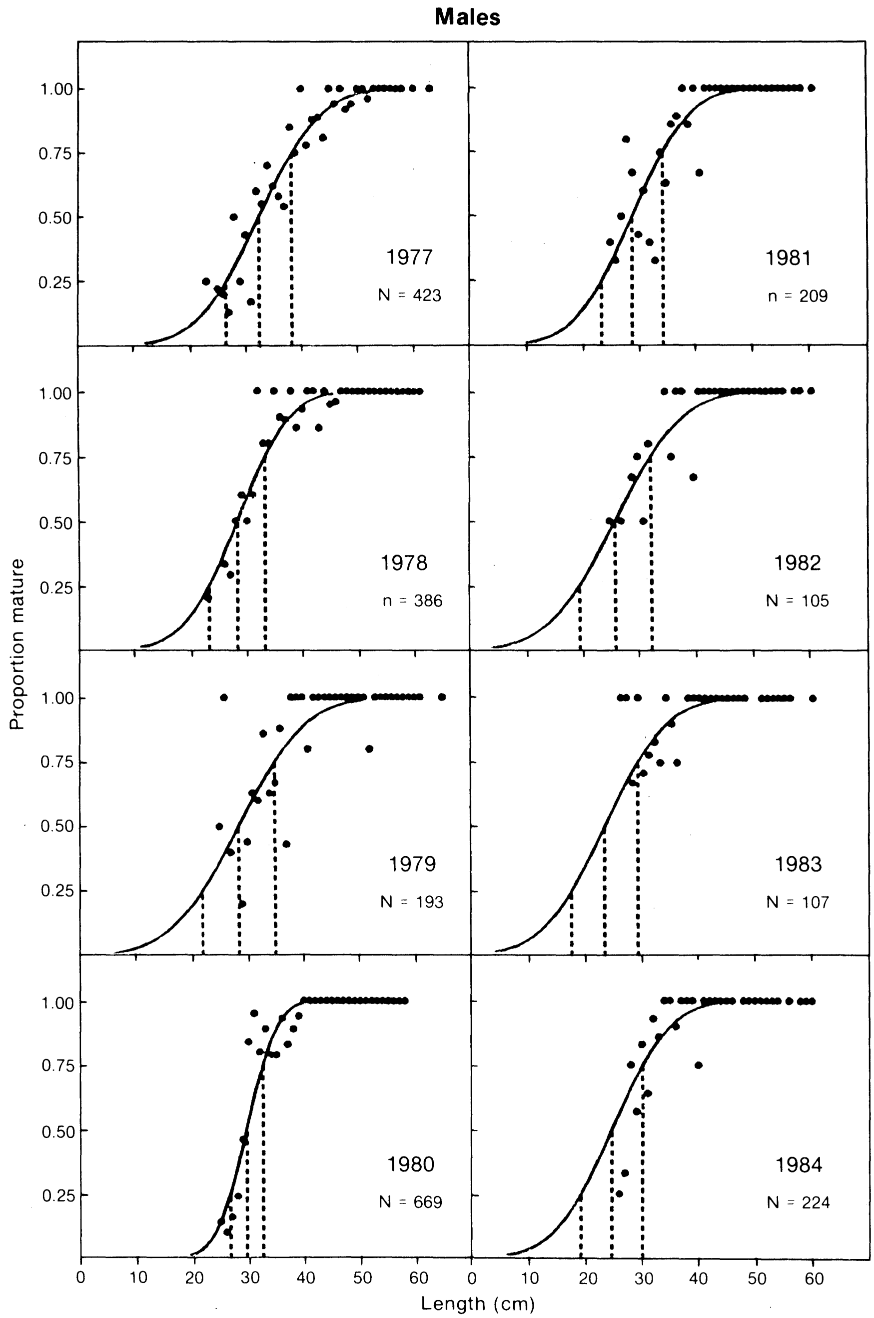

Fig. 3. Maturity ogives for male witch flounder from the Gulf of Maine-Georges Bank region, calculated from data collected during NEFC bottom trawl surveys, 1977–84.

eggs for a 60 cm fish was similar to the maximum observed by Bagenal (1963) of 599 100 for a 42 cm fish from the Firth of Clyde in the Irish Sea region.

Maturation values observed for males in this study were virtually identical to those observed for Newfoundland (Bowering, 1976) and somewhat lower than those for the Gulf of St. Lawrence (L_{50} and A_{50} of about 35 cm and 8.5 years, respectively reported by Bowering and Brodie, 1984). For females, both L_{50} and A_{50} were considerably lower in the Gulf of Maine–Georges Bank region. They were approximately 7 cm and 2 years less than values for Newfoundland (Bowering, 1976), and 10 cm and 5 years lower than those reported for the Gulf of St. Lawrence (Bowering and Brodie, 1984). Maturation of Gulf of Maine–Georges Bank witch flounder occurred at roughly the same size and age as for Icelandic fish (Steinarsson *et al.*, MS 1989), but Molander (1925) and Bagenal (1963) presented evidence suggesting that most fish of both sexes were

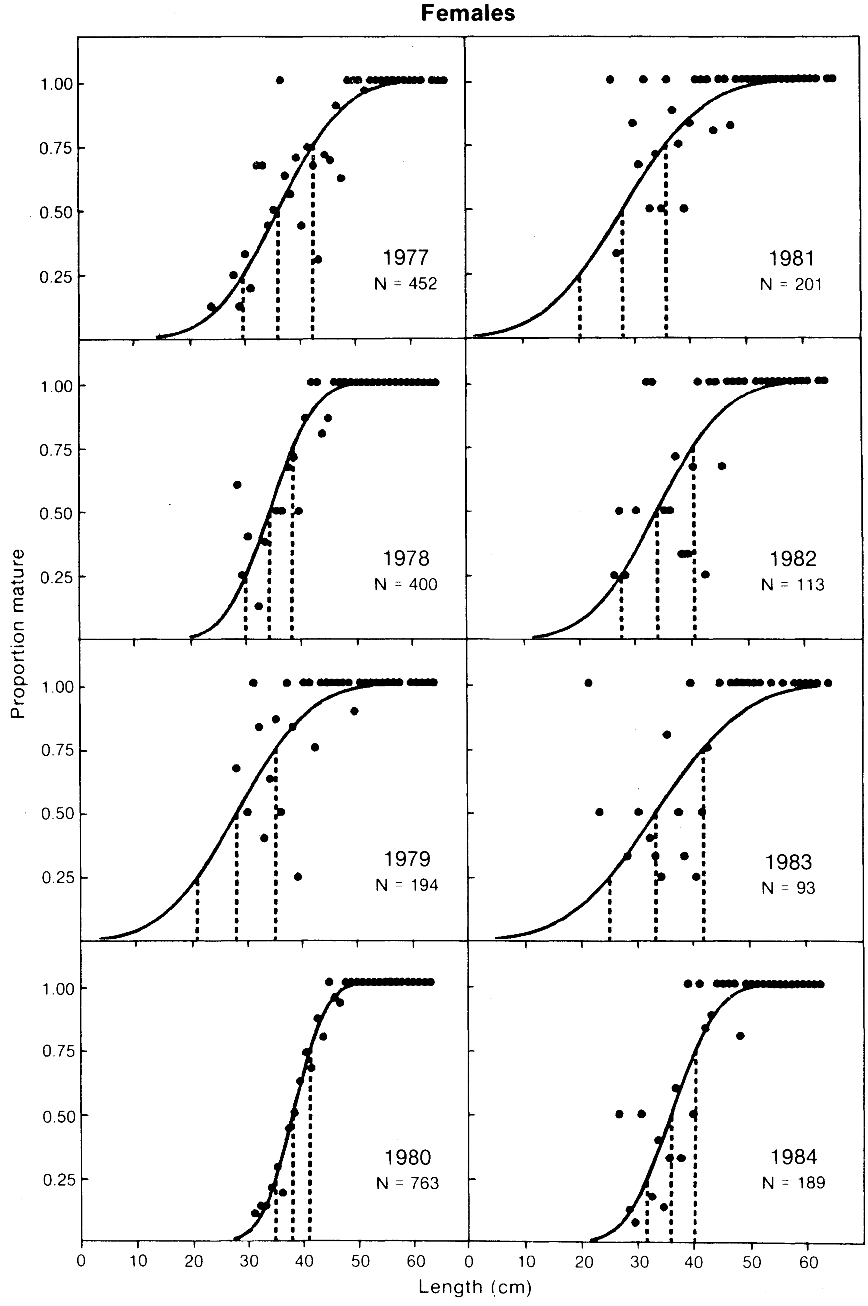

Fig. 4. Maturity ogives for female witch flounder from the Gulf of Maine-Georges Bank region, calculated from data collected during NEFC bottom trawl survey, 1977-84.

TABLE 5. Mean percentages, by season and sex, at each maturity stage of adult witch flounder collected during NEFC bottom trawl survey cruises, 1977-84.

Maturity stage	Males		Females	
	Spring	Autumn	Spring	Autumn
Developing	63.0	36.0	48.0	31.0
Ripe, ripe & running	13.0	5.0	20.0	2.0
Spent	0.0	6.0	0.0	6.0
Resting	24.0	53.0	32.0	61.0

mature by 3 years in the East Atlantic. Faster growth is typically associated with earlier maturation of fish (Alm, 1959; Godø and Moksness, 1987; Jorgensen, 1990), thus the differences in maturation between females from the Gulf of Maine–Georges Bank region and the more northerly Canadian stocks can be attributed to the higher growth rates observed in this study. The apparent lack of such differences for males between regions may relate to the hypothesis proposed by Roff (1982) that male flatfish defer maturation until a size is achieved at which predation is minimized.

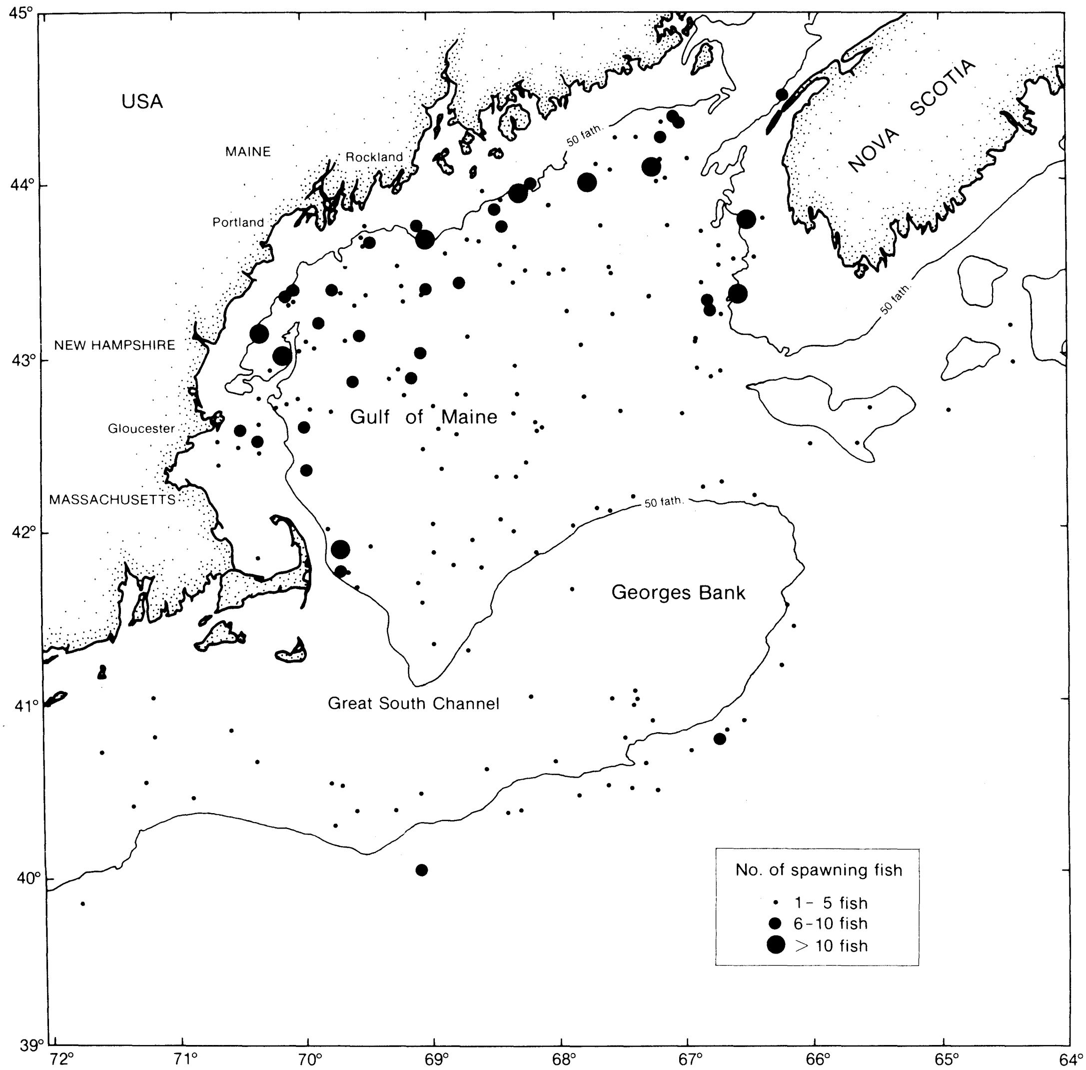

Fig. 5. Distribution of spawning witch flounder collected during NEFC bottom trawl surveys in the Gulf of Maine-Georges Bank region, 1977–84.

TABLE 6. Distribution of juvenile (<21 cm TL) and adult witch flounder collected during NEFC bottom trawl survey cruises, 1963–81, in relation to season, depth and temperature, and tests for significance of differences in distribution by depth and temperature, between juveniles and adults obtained from Kruskal-Wallis analyses (** = significantly different at P<0.01 level; NS = not significantly different, P>0.05).

	Juveniles			Adults			Significance	
Season	Number	Mean depth (m)	Mean depth (°C)	Number	Mean depth (m)	Mean depth (°C)	Depth	Temp
Winter	15	112.1	4.63	1 170	153.2	5.13	**	NS
Spring	121	137.5	5.10	8 826	159.2	5.45	**	NS
Summer	19	198.4	6.22	1 946	131.9	6.17	**	NS
Autumn	148	198.1	7.62	8 099	153.8	7.29	**	NS

The association between localized areas of cold water and spawning activity may embody the mechansim for the formation of dense pre-spawning aggregations observed by Bowering and Misra (1982), Bowering and Brodie (1984) and by Pechenik and Troyanovskii as described in Bowering (1976). Such concentrations could account for the seasonally-variable commercial and survey catch rates reported

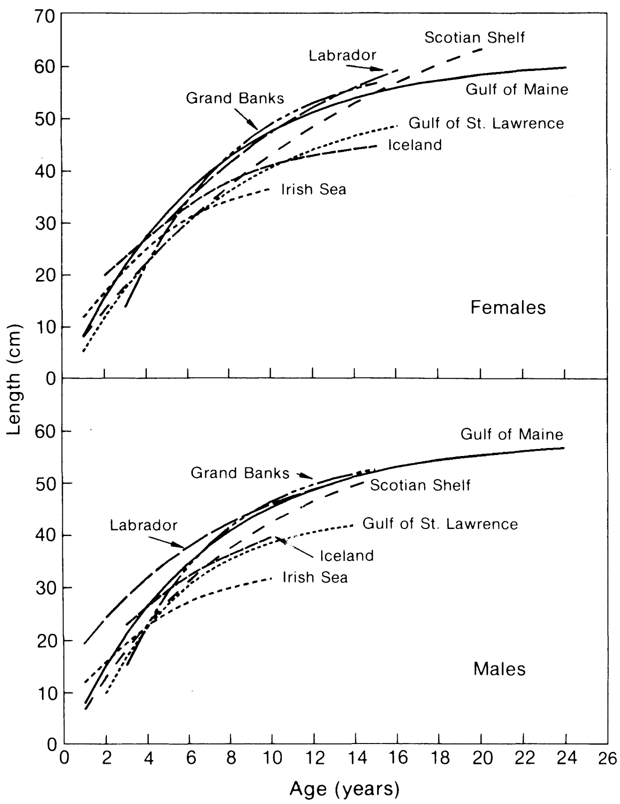

Fig. 6. Comparison of growth curves for female and male witch flounder from the Gulf of Maine-Georges Bank region, and from Canadian waters, Iceland and the Irish Sea (growth rates for Labrador, the Grand Bank, and the Gulf of St. Lawrence from Bowering, 1976; for the Scotian Shelf from Powles and Kennedy, 1967; and for Iceland and the Irish Sea from Bowers, 1960).

for the Gulf of Maine–Georges Bank region by Burnett and Clark (MS 1983).

Powles and Kohler (1970) hypothesized segregated distributions by life stage, with juveniles occupying greater depths than adults, as a mechanism to minimize food competition of juveniles with juvenile Atlantic cod (*Gadus morhua*) and American plaice at shallower depths. Subsequent studies seemed to corroborate the association between juvenile witch flounder and deeper waters. Markle (1975) observed an abundance of juveniles off the slope near Virginia at depths ranging from 166 to 1 408 m, and Markle and Musick (1974) noted that juveniles were dominant at 900 m. Additionally, witch flounder 6–35 cm TL were collected on over half of trawl tows conducted at depths ranging from 273 to 1 371 m during an NEFC 1980 survey for red crab (*Geryon quinquedens*) south of Georges Bank (unpublished NEFC data).

On the other hand, Bowers (1960) reported that, while captures of juveniles were rare, they seemed to occupy the same habitat as the adults. Recent studies (Walsh, 1987; Bowering, MS 1988; Kuzmin, MS 1989) suggest that the conclusions of Powles and Kohler (1970) were biased by gear selectivity and depth range sampled, and that witch flounder life stages are not so discretely separated by depth. In this study, juveniles do not appear to be adequately sampled by the NEFC survey sampling gear; only 303 of the 20 692 witch flounder caught during NEFC surveys from 1963 to 1981 measured less than 20 cm. Bigelow and Schroeder (1939), using a small-mesh trawl (45 mm)in a study of mud bottom fauna in the Gulf of Maine, noted the same absence of small witch flounder.

Kuzmin (MS 1989) reported that, in some years, as much as 50% of witch flounder biomass in NAFO Div. 3LNO was distributed at depths greater than 360 m, the limit of Canadian bottom trawl surveys, and was therefore not sampled. This was not the case in this study, as depths in the Gulf of Maine–Georges Bank region do not exceed 366 m and the entire depth range was sampled during each NEFC bottom trawl survey. However, since the full range of depths which could be occupied by witch flounder was not available in this study area, it is difficult to relate our findings to those of Powles and Kohler (1970) or subsequent studies (Walsh, 1987; Bowering, MS 1988). Rather, the observation in this study is that juveniles do, in fact, occupy seasonally-differing depths compared to adults and this is attributed to differences in prey distribution associated with differences in diet.

Acknowledgements

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References

ALM, G. 1959. Connection between maturity, size and age in fishes. *Rep. Inst. Freshwat. Res., Drottningholm*, **40**: 145 p.

AZAROVITZ, T. R. 1981. A brief historical review of the Woods Hole Laboratory trawl survey time series. *In*: Bottom trawl surveys. W. G. Doubleday and D. Rivard (eds.). *Can. Spec. Publ. Fish. Aquat. Sci.*, **58**: 62–67.

BAGENAL. T. G. 1963. The fecundity of witches in the Firth of Clyde. *J. Mar. Biol. Assoc. U.K.*., **43**: 401–407.

BIGELOW, H. B., and W. C. SCHROEDER. 1939. Notes on the fauna above mud bottoms in deep water in the Gulf of Maine. *Biol. Bull.*, Vol. LXXVI(3): 305–324.

1953. Fishes of the Gulf of Maine. *Fish. Bull. U.S.*, **53**: 577 p.

BOWERING, W. R. 1976. Distribution, age and growth, and sexual maturity of witch flounder (*Glyptocephalus cynoglossus*) in Newfoundland waters. *J. Fish. Res. Board Can.*, **33**: 1574–1584.

1978. Fecundity of witch flounder (*Glyptocephalus cynoglossus*) from the St. Pierre Bank and the Grand Bank of Newfoundland. *J. Fish. Res. Board Can.*, **35**: 1199–1206.

1987. Distribution of witch flounder, *Glyptocephalus cynoglossus*, in the southern Labrador and eastern Newfoundland area and changes in certain biological parameters after 20 years of exploitation. *Fish. Bull. U.S.* **85**(3): 611–629.

MS 1988. Some aspects of the witch flounder fishery on the southern Newfoundland Grand Bank (NAFO Divisions 3NO). *NAFO SCR Doc.*, No. 68, Serial No. N1511, 9 p.

BOWERING, W. R., and W. B. BRODIE. 1984. Distribution of witch flounder in the northern Gulf of St. Lawrence and changes in its growth and maturity patterns. *North. Amer. J. Fish. Manag.*, **4**(4A): 399–413.

BOWERING, W. R., and R. K. MISRA. 1982. Comparisons of witch flounder (*Glyptocephalus cynoglossus*) stocks of the Newfoundland-Labrador area, based upon a new multivariate analysis method for meristic characters. *Can. J. Fish. Aquat. Sci.*, **39**: 564–570.

BOWERING, W. R., and D. E. STANSBURY. 1984. Regressions of weight on length for witch flounder, *Glyptocephalus cynoglossus*, of the eastern Newfoundland area. *J. Northw. Atl. Fish. Sci.*, **5**: 105–106.

BOWERS, A. B. 1960. Growth of the witch (*Glyptocephalus cynoglossus*) in the Irish Sea. *ICES J. Cons.*, **25**: 168–176.

BOWMAN, R. E., and W. L. MICHAELS. 1984. Food of seventeen species of Northwest Atlantic fish. *NOAA Tech. Mem.*, NMFS-F/NEC-28, 183 p.

BURNETT, J. 1988. Witch flounder (p. 109–110). *In*: Age determination methods for Northwest Atlantic species. J. Penttila, and L. M. Dery (eds.). *NOAA Tech. Rep.*, NMFS 72, 135 p.

BURNETT, J., and S. H. CLARK. MS 1983. Status of witch flounder in the Gulf of Maine–1983. *U.S. Nat. Mar. Fish. Serv.*, Woods Hole Lab., Ref. Doc. No. 83-36, 31 p.

BURNETT, J., L. O'BRIEN, R. K. MAYO, J. A. DARDE, and M. L. BOHAN. 1989. The history of maturity sampling and classification schemes used during the NEFC bottom trawl survey program, 1963–1989. *NOAA Tech. Mem.*, NMFS-F/NEC-76, 33 p.

COLTON, J. B., Jr., W. G. SMITH, A. W. KENDALL, Jr., P. L. BERRIEN, and M. P. FAHAY. 1979. Principal spawning areas and times of marine fishes, Cape Sable to Cape Hatteras. *Fish. Bull. U.S.*, **76**(4), 5 p.

FINNEY, D. J. 1971. Probit analysis. 3rd ed., Cambridge University Press, 333 p.

GODO, Ø. R., and E. MOKSNESS. 1987. Growth and maturation of Norwegian coastal cod and Northeast Arctic cod under different conditions. *Fish. Res.*, **5**: 235–242.

JORGENSEN, T. 1990. Long-term changes in age at sexual maturity of Northeast Arctic cod (*Gadus morhua* L.). *ICES J. Cons.*, **46**: 235–248.

KRUSKAL, W. H., and W. A. WALLIS. 1952. Use of ranks in one-criterion variance analysis. *J. Amer. Stat. Assoc.*, **47**: 583–621.

KUZMIN, S. A. MS 1989. Estimation of witch stock in Div. 3LNO according to the data on 1983–88 trawl surveys. *NAFO SCR Doc.*, No. 7, Serial No. N1571, 9 p.

LUX, F. E. 1969. Length-weight relationships of six New England flatfishes. *Trans. Amer. Fish. Soc.*, **98**(4): 617–621.

1973. Age and growth of the winter flounder, *Pseudopleuronectes americanus*, on Georges Bank. *Fish. Bull. U.S.*., **71**: 505–512.

MARKLE, D. F. 1975. Young witch flounder, *Glyptocephalus cynoglossus*, on the slope off Virginia. *J. Fish. Res. Board Can.*, **32**: 1447–1450.

MARKLE, D. F., and J. A. MUSICK. 1974. Benthic slope fishes found at 900 m depth along a transect in the western N. Atlantic Ocean. *Mar. Biol.*, **26**: 225–233.

MOLANDER, A. R. 1925. Observations of the witch (*Glyptocephalus cynoglossus* L.) and its growth. *ICES Publ. Circ.*, **85**: 15 p.

NEW ENGLAND FISHERY MANAGEMENT COUNCIL. 1985. Fishery management plan, environmental impact statement, regulatory impact review, and initial regulatory flexibility analysis for the northeast multispecies fishery. New England Fishery Management Council, Saugus, MA, 459 p.

NILSEN, R., O. K. GUTVIK, E. M. NILSSEN, and C. C. E. HOPKINS. MS 1989. Population parameters of the witch *Glyptocephalus cynoglossus* (L.) (Pisces: Pleuronectidae) from Malangen, northern Norway. *ICES C.M. Doc.*, No. G:3, 33 p.

PENTTILA, J., F. NICHY, J. W. ROPES, L. M. DERY, and A. JEARLD, Jr. 1988. Methods and Equipment (p. 7–16). *In*: Age determination methods for Northwest Atlantic species. J. Penttila, and L. M. Dery (eds.). *NOAA Tech. Rep.*, NMFS 72, 135 p.

POWLES, P. M. 1967. Length-weight relationships for American plaice, witch, and yellowtail, in ICNAF Subarea 4. *ICNAF Res. Bull.*, **4**: 121–123.

POWLES, P. M., and V. S. KENNEDY. 1967. Age determination of Nova Scotian grey sole, *Glyptocephalus cynoglossus* L., from otoliths. *ICNAF Res. Bull.*, **4**: 91–100.

POWLES, P. M., and A. C. KOHLER. 1970. Depth distributions of various stages of witch flounder (*Glyptocephalus cynoglossus*) off Nova Scotia and in the Gulf of St. Lawrence. *J. Fish. Res. Board Can.*, **27**(11): 2053–2062.

RAE, B. B. 1969. The food of the witch. *Mar. Res. Scot.*, **1969**(2): 1–23.

ROFF, D. A. 1982. Reproductive strategies in flatfish: a first synthesis. *Can. J. Fish. Aquat. Sci.*, **39**: 1686–1698.

SAS STATISTICAL SOFTWARE. 1982. SAS Institute, Cary, North Carolina. 921 p.

SNEDECOR, G. W., and W. G. COCHRAN. 1980. Statistical methods. Seventh edition. Iowa State University Press, 507 p.

SIMPSON, A. C. 1951. The fecundity of the plaice. *Fish. Invest. Lond., Ser. II*, **17**(5): 27 p.

STEINARSSON, B. A. E., G. JONSSON, and H. GUDFINNSSON. MS 1989. Preliminary report on recent investigations on the biology and catch and effort data of witch (*Glyptocephalus cynoglossus*) in Icelandic waters. *ICES C.M. Doc.*, No. G:63, 15 p.

SULLIVAN, L. F. MS 1982. American plaice, *Hippoglossoides platessoides*, in the Gulf of Maine, I. The fishery, II. Age and growth, III. Spawning and larval distribution. M.S. Thesis, University of Rhode Island, Kingston, RI, 127 p.

U.S. DEPARTMENT OF COMMERCE. 1989. Status of the fishery resources off the Northeastern United States for 1989. *NOAA Tech. Mem.*, NMFS-F/NEC-72, 110 p.

VAN GUELPEN, L., D. F. MARKLE, and D. J. DUGGAN. 1982.

An evaluation of accuracy, precision, and speed of several zooplankton subsampling techniques. *ICES J. Cons.*, **40**: 226–236.

WALSH, S. J. 1987. Habitat partitioning by size in witch flounder, *Glyptocephalus cynoglossus*: a reevaluation with additional data and adjustments for gear selectivity. *Fish. Bull. U.S.*, **85**(1): 147–153.

ZAR, J. H. 1968. Calculation and miscalculation of the allometric equation as a model in biological data. *Bioscience*, **18**(12): 1118–1120.