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Spatial Differences in Maturity Schedules of Female Dover Sole off Oregon

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ABSTRACT

An assessment of sexual maturity of Dover sole landed in Oregon from 1989 to 1991 indicated that females of the species had a 50% probability of being mature at ages 7.3 to 9.5, depending on when and where the sampling was conducted. Logistic regression models were used to document statistical differences ($P \leq 0.05$) between maturity schedules of fish harvested in the northern and southern regions of the state. There was evidence that fish from southern Oregon waters reached sexual maturity at an earlier age and exhibited higher overall rates of maturity than fish inhabiting northern waters of the state. It does not appear that the statistical findings are of magnitudes that reflect dramatic implications for management, primarily because the vast majority of the fish (at least 90%) did not enter the fishery until mature. It is recommended that additional information be collected regarding other vital parameters of the species, such as estimates of growth rates and mortality coefficients, to ensure exploitation strategies appropriately address the stock structure of Dover sole inhabiting U.S. Pacific coast waters.

INTRODUCTION

Dover sole inhabiting waters off the U.S. Pacific coast have been utilized as a valuable commercial resource for the past 50 years (Yoklavich and Pikitch 1989; Westrheim et al. 1992). Annual landings of Dover sole from 1984 to 1997 have contributed substantially to the total landings of groundfish of the U.S. Pacific coast region (California, Oregon, and Washington), where approximately 10,000 to 21,000 mt have been landed on a yearly basis (Brodziak et al.1997).

The management of fishery resources, such as the Dover sole fishery of the U.S. Pacific coast, is necessarily based on the life history characteristics of the exploited species. Harvest strategies that minimize detrimental effects to the fish resources are largely dependent on scientific analyses of the biological characteristics of commercial landings (Gulland 1983). Stock assessments inherently rely on the availability of information regarding the 'stock parameters' of the exploited species, such as growth, reproduction, and mortality (Shepherd 1988). From a management standpoint, an essential property of a stock is that the parameters that define it remain more or less constant throughout its area of distribution (Sparre et al. 1989). That is, fish stock assessments should be made for each stock separately. Scientific evaluations of the stock parameters of a species, along with studies that address their genetic and migratory characteristics, provide information that together are used to define the stock(s) structure of the marine resource. Henceforth, I use the term 'stock' in the broad context of fish stock assessment and define it following Gulland (1983): "a group of organisms can be treated as a stock if possible differences within the group and interchanges with other groups can be ignored without making the conclusions reached depart from reality to an unacceptable extent."

The objective of this paper was to critically examine the spatial similarity of reproductive parameters of female Dover sole inhabiting marine waters off Oregon. Tagging studies have demonstrated that Dover sole exhibit relatively little latitudinal movement in U.S. Pacific coast waters (Westrheim and Morgan 1963; Westrheim et al. 1992; Brodziak et al. 1997), which indicates the fish may exist as independent stocks with distinct parameters. Additionally, I evaluated estimates of age composition for commercial landings of Dover sole along with the maturity assessment to determine the practical implications for management. The sexual maturity information presented here is a critical component of a complete analysis of the Dover sole fishery of the U.S. Pacific coast, and these results can be directly utilized by management to assess the urgency for separate management policies concerning this groundfish species.

METHODS

Study Design

Dover sole commercially landed at Oregon ports from 1989 to 1991 were analyzed in this study (Table 1). Fish were classified by region according to the location of the harvest using the following coordinate criteria: (1) the north region was from 45°04' N latitude to 47°20' N latitude, including the triangle that is drawn at 220° from 48°29'34" N latitude, 124°43'27" W longitude; and (2) the south region was from 42°25' N latitude to 44°18' N latitude (Figure 1). Boat-trip harvests in the north region were landed at the ports of Astoria and Garibaldi and catches in the south region were landed at the ports of Charleston and Brookings. In general, longitudinal boundaries were not used to define regions, primarily because this component of the sampling design was accounted for by examination of a depth variable in the statistical analyses.

The sexual maturity data were separated into 'homogeneous' time blocks to account for the physiological changes that occur in fish in preparation for and during spawning. It has been demonstrated that the time of sampling is an important variable in maturity studies of Dover sole (Hunter et al. 1992) and thus, analyses should consider this variation to ensure results do not include additional sources of bias that would hamper statistical interpretation. The spawning season for Dover sole off the U.S. Pacific coast from central California to Oregon is generally believed to occur within a six-month period, from approximately December to May (Hunter et al. 1992). However, the exact date that spawning begins and ends in any given year cannot be defined exactly, given that the reproductive cycles of fish are closely related to environmental changes, particularly seasonal changes in light and temperature (Moyle and Cech 1982). I treated the months from June through November as the non-spawning period and the months from December through May as the spawning period (Table 1).

All Dover sole specimens used in this study were collected as part of a broad sampling program conducted by the Oregon Department of Fish and Wildlife to determine various statistics associated with the commercial landings of groundfish species. Many of the regulated fisheries of the U.S. Pacific coast, such as the Dover sole fishery in Oregon, are routinely sampled to determine primarily the age composition of the landings and additionally, to obtain other demographic attributes of the catch, such as length frequency distributions and maturity states. Information was also collected regarding particular attributes of the fishing trip, such as depth at which fish were caught and the gear type used. The sampling designs used to collect these landing data were stratified, two-stage random sampling plans combined with poststratification (Crone 1995).

Sampling duties were the responsibility of two port biologists, an individual assigned to the north region (ports of Astoria and Garibaldi) and another assigned to the south region (ports of Charleston and Brookings). Both port biologists participated in similar training programs and were given identical sampling instructions. Technical support personnel stationed at the regional headquarters in Newport supervised field procedures and routinely conducted meetings to ensure sampling was performed in a standardized fashion.

Sexual Maturity Determination

Only female Dover sole specimens were used in analyses presented here. Maturity assessments of individual fish were made by gross anatomical examination of ovaries and oocytes and a classification scheme similar to the multiple reproductive stage scale proposed by Hagerman (1952). Ultimately, fish were assigned as mature or immature based on the following criteria. Fish were considered mature in cases where: (1) ovaries contained developing or mature ova (yolked or partially yolked oocytes); or (2) ovaries were recently spent or in the later phases of recovering. Fish were considered immature in cases where ovaries were undeveloped and contained no visible signs of developing or mature ova.

The primary advantages of a field-based procedure, such as the gross anatomical examination technique, is that it utilizes relatively simple criteria to assess reproductive states, requires limited manpower and money to administer, and provides generally informative data for management purposes. However, there are more elaborate and definitive techniques to identify states of sexual maturity in species of fish than the gross anatomical examination method. For example, it has been demonstrated that a detailed histological examination of ovaries provides more reliable information than that obtainable from macroinspection techniques employed in the field (Hunter et al. 1992). A major drawback associated with the histological techniques is that they are laboratory-based methods, which are often not logistically or financially feasible within the constraints of many commercial fishery management programs.

Age Determination

Otoliths were collected from each fish (specimen) at the sampling sites and temporarily stored in vials for future processing. The following data were generally recorded for each specimen: species, specimen number, length of fish, weight of fish, and port and date sampled. Otoliths were then immediately sent to a centrally located age-analysis laboratory in Newport.

A break and burn technique was used to prepare otoliths for ageing (Christensen 1964). The break and burn procedure has been demonstrated as a reliable technique for ageing Dover sole otoliths by annual zonation (Chilton and Beamish 1982) and is currently the method used in ageing programs for

Dover sole that are routinely conducted by fishery management agencies in the United States and Canada. No validation studies have been conducted to assess the accuracy of age determination techniques for Dover sole (Yoklavich and Pikitch 1989). However, ageing studies and workshops conducted by the state fishery agencies of Oregon and Washington and the Department of Fisheries and Oceans of Canada have generated several unpublished reports that generally support the break and burn method as a 'valid' technique that can be used to identify annual bands on otoliths of Dover sole (R. L. Demory and R. Mikus, Oregon Department of Fish and Wildlife, Newport, Oregon, personal communication, 1997). A 15% subset of all age samples was analyzed by a second reader to determine the reliability of the age estimates. Analyses presented here incorporated sample data that reflected 100% agreement between readers.

Statistical Analysis Procedures

Data were analyzed with logistic regression. The response variable (i.e., sexual status of a fish) in the analysis was treated as a binary variable (i.e., mature or immature) and a logistic regression model was fitted for a set of explanatory variables that included region as a factor (indicator variable), age as a continuous variable, and the interaction between age and region. Logistic response functions have been found to be appropriate and effective statistical tools to generally describe the proportion of sexually mature fish in a population, for both marine and freshwater species (Hunter et al. 1990; Munger et al. 1994). The aptness of the logistic regression model was investigated following informal goodness of fit examinations (Neter et al. 1989) and residual diagnostics (Hosmer and Lemeshow 1989; Agresti 1990). Model diagnostic procedures based on R^2 measures were not utilized in analyses presented here because of the limitations of these statistics when applied to binary response variables (Agresti 1990).

The estimated logistic response function used in these analyses was,

$$\hat{p}_m = \frac{e^{(b_0 + b_1 \bullet age + b_2 \bullet region + b_3 \bullet age * region)}}{1 + e^{(b_0 + b_1 \bullet age + b_2 \bullet region + b_3 \bullet age * region)}}, \qquad \textbf{(1)}$$

where $\hat{p}_m$ is the estimated probability that a fish is mature and the estimated regression coefficients are b_0 for the intercept, b_1 for age, b_2 for region, and b_3 for age*region. The response variable $\hat{p}_m$ can be practically interpreted as an estimated proportion or percent. The linearized form of the estimated logistic response function above, referred to as the estimated logit response function, illustrates the statistical relationship between logistic and general linear models,

$$\log_e\left(\frac{\hat{p}_m}{1 - \hat{p}_m}\right) = b_0 + b_1 \bullet age + b_2 \bullet region + b_3 \bullet age * region \ , \qquad \textbf{(2)}$$

where $\log_e[\hat{p}_m \,/\, (1 - \hat{p}_m)]$ is the estimated logit.

The estimated logistic response function, equation (1), yields the fitted regression lines (i.e., maturity schedules or curves) for both the north region and south region. Equations (1) and (2) are referred to as the 'full' models in the statistical tests. Fitting this type of logistic response function generates the same results as fitting separate regressions for the north region and south region. Because region is treated as an indicator variable, a simple logistic model is generated for each region, which is analogous to fitting the single explanatory variable age to separate regression models for the north region and south region. This statistical modeling technique was used because it allowed straightforward tests to be conducted for comparing parameters (regression coefficients, β) of the curves between the two regions.

The method of maximum likelihood was used to estimate the parameters of the logistic response functions. Analysis of deviance procedures (McCullagh and Nelder 1989) were used to assess the significance of particular models and document whether the two regions had statistically different logistic response functions. Because 'over-dispersion' (extra-binomial variation) has been demonstrated to occur frequently in logistic regression methods involving binary data, I conducted analysis of deviance procedures (drop-in-deviance F-tests) that assumed the existence of extra-binomial variation (Baker and Nelder 1985; McCullagh and Nelder 1989; Ramsey and Schafer 1997). To account for extra-binomial variation in the analyses, a quasi-likelihood approach was used to adjust the inferences obtained from the drop-in-deviance F-tests (McCullagh and Nelder 1989). The drop-in-deviance adjusted value is referred to as the deviance test statistic.

The above tests are motivated by linear regression theory and least squares estimation, in particular the extra sum of squares approach for tests about regression coefficients. The tests are analogous to analysis of covariance procedures used to compare statistical parameters of two or more linear regression lines.

Specifically, formal tests were conducted for two 'reduced' models within each time block. First, the presence of interaction effects (b_3 for age*region) was tested to determine whether the two logistic curves had equal slopes at the age at which there was a 50% probability that a fish was mature ($Age_{50\%}$):

$$H_0: \beta_3 = 0,$$
$$H_A: \beta_3 \neq 0.$$

Secondly, the significance of the estimated regression coefficients for region (b_2) and age*region was examined to determine whether there was a statistical difference in the elevations (vertical positions) of the two logistic curves at $Age_{50\%}$. This test examines whether the two maturity curves are 'statistically identical' to one another (Neter et al. 1989):

$$H_0: \beta_2 = \beta_3 = 0,$$
$$H_A: \text{not both } \beta_2 \text{ and } \beta_3 = 0.$$

Applying large-sample theory, the distribution of the deviance test statistic is approximated by the F distribution, $F_{(r-f, f)}$, when H_0 holds. Values for the degrees of freedom associated with the distribution are denoted as r and f, for the reduced and full models, respectively.

Note that the sigmoid shape of a logistic curve prevents using straightforward linear regression methods to determine a single value that describes the slope of a curve. Rather, the odds ratio interpretation of the estimated regression coefficient b_1 in a simple logistic model is commonly used to evaluate the rate at which the line increases or decreases. Odds ratios presented here can be practically interpreted as the estimated percent increase in the odds of a fish being mature with each one-year increase in age. Odds ratios were estimated from the simple logistic response function of each region as, $e^{(b_1)}$, where b_1 was the estimated regression coefficient for the explanatory variable age. Confidence intervals (95%) were constructed for odds ratios to provide a measure of the variability associated with these statistics (Neter et al. 1989). The age at which there was a 50% probability that a fish was mature ($Age_{50\%}$) was calculated from the simple logistic response function of each region as, $-b_0 / b_1$, where b_0 was the estimated intercept and b_1 was the estimated regression coefficient for the explanatory variable age.

As discussed previously, the purpose of this study was to evaluate the similarity of maturity schedules of Dover sole between fish harvested and landed in the northern region and southern region of Oregon. Thus, I developed two suites of 'descriptive' models that included explanatory variables of interest and then compared these models using straightforward statistical inference procedures. This study was not concerned with developing a 'predictive' model that included various explanatory variables (such as water temperature, salinity, upwelling indices, etc.), which could be used as the 'best available' prediction tool to determine whether a fish would be mature or immature.

Because it has been demonstrated that the proportion of sexually mature female Dover sole increases with depth (Hunter et al. 1990), I performed preliminary analyses using analysis of variance procedures to determine whether fish were harvested (i.e., sampled) from similar depths between the north and south regions. The depth at which fish were harvested for each boat-trip sample was treated as the measurement variable in an analysis of variance design that consisted of two treatment groups (north region and south region). The statistical power of the analysis of variance tests was estimated following Zar (1984). A formal investigation of the depth variable served two primary purposes in this study: first, to ensure that a sampling bias was not present in the study design, which would have impeded statistical interpretation of the results; and second, to evaluate the a priori importance of an explanatory variable in the models. A depth variable was only indirectly related to the study objective, which required I develop models that were based on a relevant and interpretable set of explanatory variables and exclude covariates that had no meaningful effect on the comparisons of interest.

RESULTS

Results are presented separately for the 'Before' time block (spawning period) and the 'During' time block (non-spawning period). Standard model-checking procedures showed that estimated response functions were monotonic and sigmoidal in shape and that logistic regression was an appropriate tool to analyze and model the maturity datasets of Dover sole.

Depths at which fish were harvested were not significantly different between the north and south regions for both time blocks, $P = 0.12$ for Before and $P = 0.08$ for During. Additionally, the depth variable was generally not a significant ($P > 0.05$) covariate in preliminary model selection analyses. That is, statistical evidence supported the hypothesis that samples were taken at similar depths between the two regions and thus, this term was omitted from the final models. Note that there was low statistical power ($P \cong 0.30$) associated with the analysis of variance tests that addressed the significance of a depth variable between regions. However, given the objectives of the study, I felt that tests associated with relatively low power were not reason alone to include a statistically non-significant term in the subsequent analyses.

The maturity schedules were statistically different (i.e., not identical) between the north and south regions for both time blocks (Figures 2 and 3), $P = 0.05$ for Before and $P < 0.01$ for During (Table 2).

These statistical findings indicated that female Dover sole from the south region matured at an earlier age than fish from the north (e.g., see Age at 50% mature in Table 3). However, a lack of younger fish, which were needed to define the maturity schedules for years one through five, precluded examining the properties of the curves for estimated proportions generally less than 40%. Additionally, comparisons that address age at first maturity depend on the proportion of interest, which varies in accordance with management objectives and the reproductive potential of the exploited species.

Tests that addressed the significance of the interaction term, age*region, were inconclusive (Table 2). For the During time block, the slopes of the maturity curves at $Age_{50\%}$ were significantly different ($P = 0.05$) between the two regions; however this parameter of the logistic curves was not significantly different ($P = 0.72$) between regions for the Before time block.

Odds ratio estimates, i.e., the estimated percent increase in the odds of a fish being mature with each one-year increase in age, were similar between regions for the Before time block (north = 41% and south = 37%), but considerably higher for the south region (43%) than the north region (25%) for the During time block (Table 3). Estimated 95% confidence intervals for the odds ratios indicated that these statistics were variable and not statistically different between regions within each time block ($P > 0.05$).

Estimates of age composition for commercial landings of Dover sole from 1989 to 1995 showed that roughly 10 to 30% of the total landings of Dover sole composed fish less than 10 years old. During this time period, roughly equal amounts of Dover sole were harvested from the north and south regions (e.g., approximately 3,000 mt in each region in 1990) and the total landings in each region consisted of approximately equal numbers of males and females. Results presented here (Figures 2 and 3) indicated that female Dover sole between the ages of 7.3 and 9.5 had a 50% probability of being mature, depending on where and when sampling took place. Thus, a first approximation for the percentage of the total landings of female Dover sole that were immature ranged from 5 to 15%.

DISCUSSION

In general, results from statistical tests indicated that female Dover sole exhibited different maturity schedules between the north and south regions; however, analyses were not conclusive for the Before time block. The maturity curves for the south region were very similar across time blocks; however, the maturity curves for the north region were considerably different for each time block, which may have been due to the small number of samples collected from this region for the Before time block.

Previous research has demonstrated that estimates of length or age at first maturity may be influenced by time of sampling and that these statistics should be derived from samples that are collected prior to the onset of spawning, i.e., during the Before time block (Hunter et al. 1992). This recommendation is based on the premise that gross anatomical examinations of reproductive organs are more likely to be biased during the spawning season than before spawning begins, primarily because during the spawning season ovaries of some post-spawning females regress substantially, which often precludes distinguishing these fish from immature females (Hunter et al. 1992). Additionally, because commercial fishers may target on spawning aggregations, samples collected from landings of Dover sole during the spawning period may contain high numbers of mature fish and thus, not reflect the population(s) at large. Because characteristics of the reproductive parameters of fish are strongly influenced by spawning processes, it is imperative that research studies account for these physiological changes when developing sampling designs for maturity assessments. Sampling schedules that are not rigorously defined in accordance with management objectives will likely produce information that is biased and subject to misleading conclusions.

The statistical differences documented here do not warrant substantial departures from the management approach currently in place for the Dover sole fishery off Oregon. That is, given that the vast majority of female Dover sole commercially landed in Oregon from 1989 to 1995 were sexually mature fish, it is not recommended that different management strategies be adopted at this time for the north and south regions. However, without additional information it would be difficult to assess the relationship between the differences documented here and the intricacies involved in stock assessment modeling used to determine appropriate quota levels for this species.

Previous researchers have suggested that spatial differences existed in maturity schedules of Dover sole stocks inhabiting U.S. Pacific coast waters (Yoklavich and Pikitch 1989; Hunter et al. 1990). However, it is very possible that these differences were due solely to differences in sampling designs and methods used to assess sexual maturity of the fish specimens (Hunter et al. 1992). The work presented here was based on similar sampling techniques, personnel, and maturity assessment criteria, which allowed results to be interpreted with relatively high certainty, recognizing the limitations and potential error of the gross anatomical examination method.

In the absence of genetic information regarding the Dover sole stock(s), management has primarily utilized tagging and biological research to develop harvest strategies. Adult Dover sole off Oregon that do not remain in deep water throughout the year do not appear to make long latitudinal migrations; however, the larvae spend up to one year in pelagic areas far offshore, which suggests that ocean conditions may cause 'individual stocks' to undergo considerable mixing (Pearcy et al. 1977; Westrheim et al. 1992). The amount of mixing between the genetic pools, along with environmental factors, are processes generally considered to strongly influence the vital parameters, such as maturity, associated with a species (Hanski and Gilpin 1991). It is not possible to precisely identify the factors that contributed to the findings presented here. Regardless, the results from this work allow management to proceed with increased certainty under current fishery operations, while other research studies can be developed to ascertain causal factors.

It is recommended that future maturity assessments incorporate young fish, pre-recruit ages, so that maturity schedules can be developed that are based on the entire age composition of a Dover sole stock. Studies that address fecundity, growth, and mortality of the population(s) off Oregon would allow more definitive conclusions to be drawn regarding the differences in vital parameters of the exploited fish stocks and the subsequent management directions taken. Proper assessments can only be carried out when the biology of the species is fully understood; this information is critical to management, which largely develops harvest policies based on the growth potential of fish populations.

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Table 1. Sampling design used to collect Dover sole specimens in Oregon. All samples were obtained from commercial landings using a two-stage random sampling design (Crone 1995).

Date (year / month)	Time block (spawning period)[a]	Sample sizes: Number of boat trips		Sample sizes: Number of fish	
		North	South	North	South
1989 /					
Jan - May, Dec	During	15	8	278	183
Jun - Nov	Before	6	10	121	215
1990 /					
Jan - May, Dec	During	13	12	322	233
Jun - Nov	Before	2	11	77	203
1991 /					
Jan - May, Dec	During	19	17	473	314
Jun - Nov	Before	2	16	49	358
1989-91 /					
Jan - May, Dec	During	47	37	1,073	730
Jun - Nov	Before	10	37	247	776

[a] Before denotes samples were collected before the spawning period while fish were not actively spawning and During denotes samples were collected during the spawning period while fish were actively spawning.

Table 2. Analysis of deviance table for logistic regression models and corresponding tests used in maturity assessment of female Dover sole in Oregon (1989-91). Results are presented separately for two time blocks.

Time block [a]	Model	Deviance	*df* [b]	Test	Drop-in-deviance	*df*	*P* [c]
Before	age+region+age*region	838.71	492				
	age+region	838.93	493	age*region = 0	0.22	1	0.72
	age	848.75	494	region = age*region = 0	10.04	2	0.05
During	age+region+age*region	1,661.32	870				
	age+region	1,668.64	871	age*region = 0	7.32	1	0.05
	age	1,696.50	872	region = age*region = 0	35.18	2	<0.01

[a] Before denotes samples were collected before the spawning period while fish were not actively spawning and During denotes samples were collected during the spawning period while fish were actively spawning.

[b] Degrees of freedom (*df*) statistics were calculated from the total number of observations (ages) aggregated across boat trips. The estimated proportion of mature fish for each age included in a boat-trip sample was treated as an observation.

[c] Probability (*P*) values correspond to drop-in-deviance *F*-tests that included an additional dispersion parameter to account for extra-binomial variation.

Table 3. Results from logistic regression analyses of female Dover sole for the north and south regions of Oregon (1989-91). Parameter estimates of maturity schedules are presented separately for two time blocks.

	Age at 50% mature[a] ($Age_{50\%}$)		Odds ratio[b]	
Time block[c]	North	South	North	South
Before	9.5	7.5	41% (25-57%)	37% (26-58%)
During	7.9	7.3	25% (18-31%)	43% (31-56%)

[a] Age (yr) at which there was a 50% probability that a fish was mature, $Age_{50\%}$, was estimated from the simple logistic response function of each region as, $-b_0 / b_1$, where b_0 was the estimated regression coefficient for the intercept and b_1 was the estimated regression coefficient for the explanatory variable age.

[b] The odds ratio is presented as the estimated percent increase in the odds of a fish being mature with each one-year increase in age. Confidence intervals (95%) for odds ratios are presented in parentheses. Odds ratios were estimated from the simple logistic response function of each region as, $e^{(b_1)}$, where b_1 was the estimated regression coefficient for the explanatory variable age.

[c] Before denotes samples were collected before the spawning period while fish were not actively spawning and During denotes samples were collected during the spawning period while fish were actively spawning.

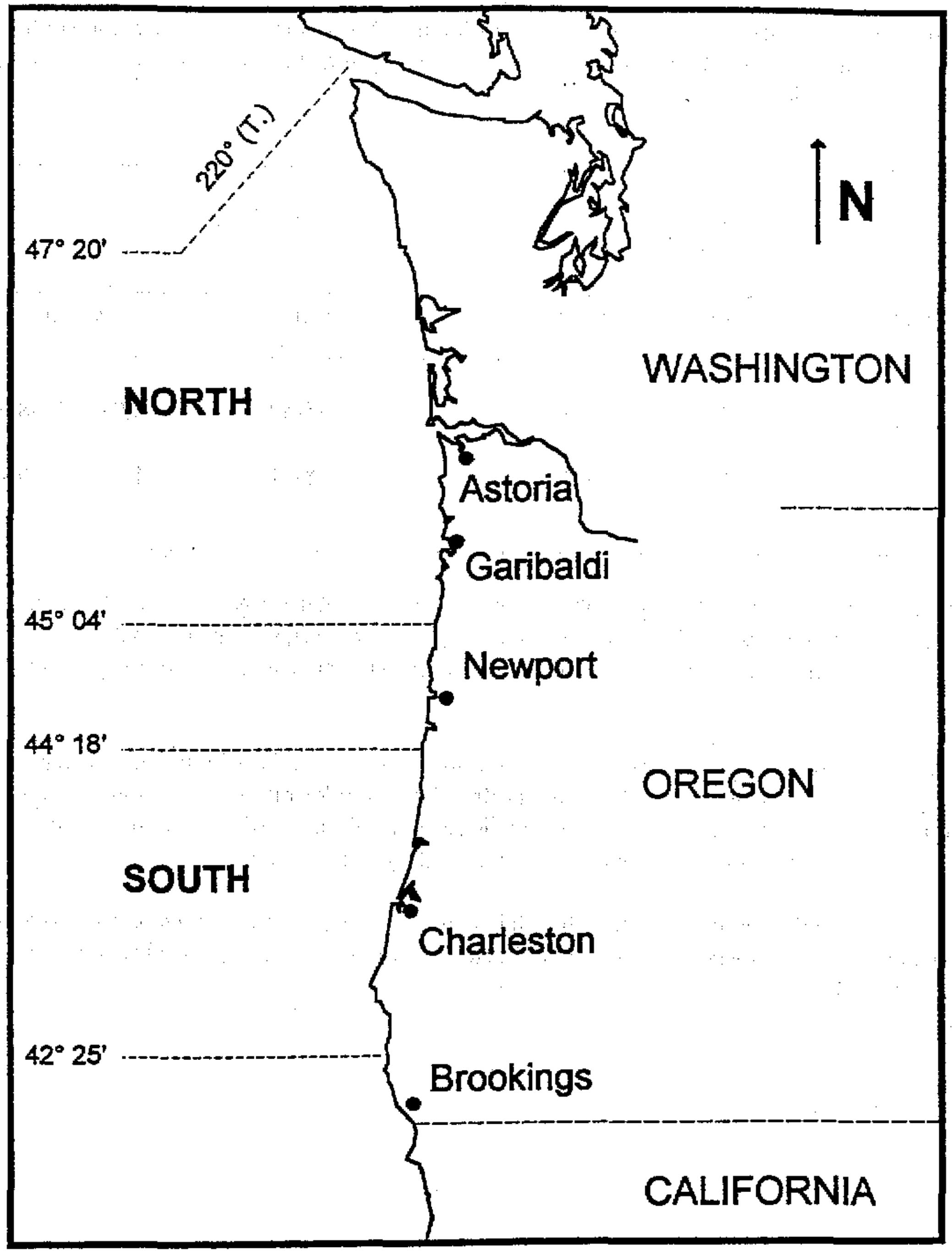

Figure 1. Study area used to conduct maturity assessment of Dover sole commercially landed at Oregon ports (1989-91).

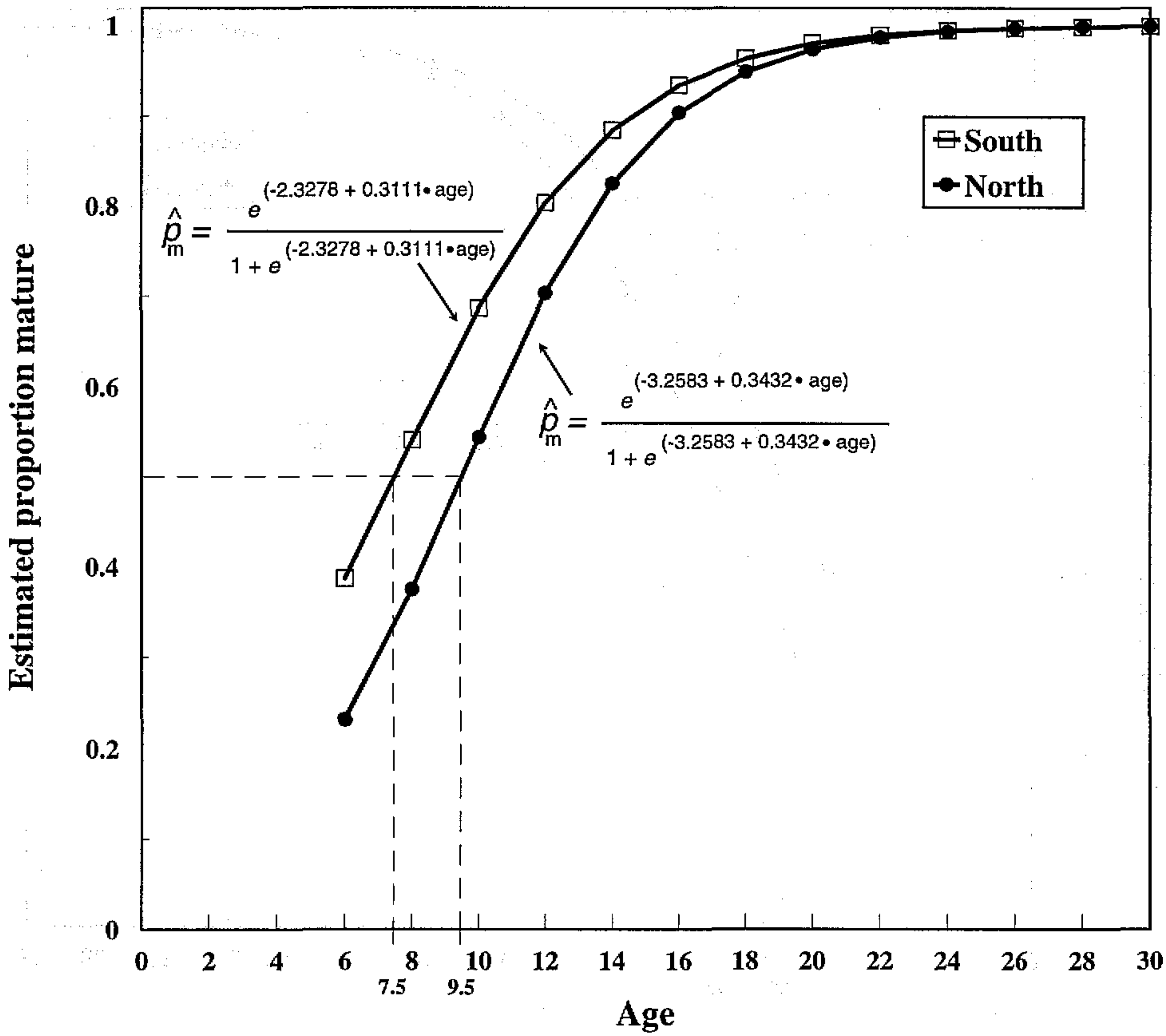

Figure 2. Logistic regression models and associated curves for estimated proportion ($\hat{p}_m$) of female Dover sole that were sexually mature as a function of age (yr). The maturity schedules of fish for the north and south regions of Oregon (1989-91) are compared. Fish were sampled before the spawning period (Before time block).

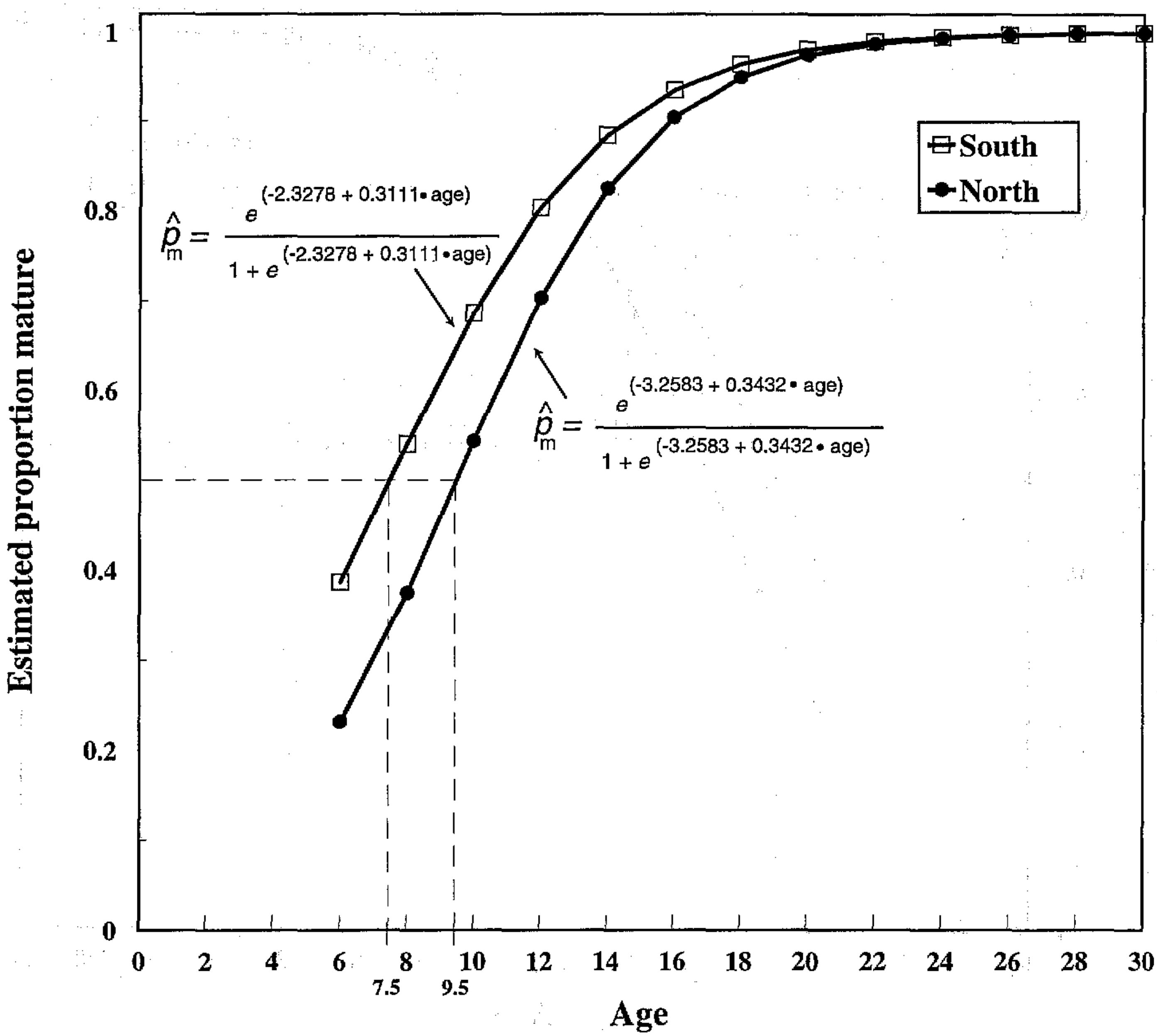

Figure 3. Logistic regression models and associated curves for estimated proportion ($\hat{p}_m$) of female Dover sole that were sexually mature as a function of age (yr). The maturity schedules of fish for the north and south regions of Oregon (1989-91) are compared. Fish were sampled during the spawning period (During time block).