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The influence of seasonal migrations on fishery selectivity

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Based on previous work, dome-shaped fishery selectivity patterns are expected in place of asymptotic patterns when one-way fish movements among areas are considered. It is less clear if this occurs when the "round-trip" seasonal movements are considered. A simulation of a long-distance migrating fish stock (Atlantic menhaden) was used to study the influence of life history and fishery processes on selectivity, under an "areas as fleet" stock assessment context. When age-constant two-way migration was assumed to occur at a low rate, a domed selectivity pattern in the area experiencing the highest fishing mortality was produced, consistent with previous work. However, as the two-way migration rate increased, the domed selectivity pattern diminished and eventually disappeared. When age-varying migration was introduced, with a higher movement probability for older fish, domed selectivity prevailed in the source (i.e. spawning) area. If movement away from the spawning area occurs at younger ages than are selected by the fishing gear, the extent of the dome in this area is reduced. When movement away from the spawning area occurs at ages that are already available to the fishing gear, the dome in the spawning area is exaggerated. The area in which domed selectivity occurred was primarily determined by whether the probability of movement increased or decreased with age. In contrast to previous work that considered one-way or diffusive movement, the temporal or spatial distribution of recruitment and overall fishing mortality did not have a significant influence on selectivity. Building simulations that reflect the life history of the stock can guide assessment efforts by placing priors and constraints on model fits to selectivity patterns and be used to explore trade-offs between model complexity and the ability to produce reasonable management advice. Their development is encouraged as a standard feature in the assessment of migratory fish stocks.

Keywords: age-varying fish movement, areas-as-fleet, fishery selectivity, one- and two-way migration, stock assessment.

Introduction

The age- and size-dependent influences of fishing have long been recognized as one of the most basic processes impacting the productivity of marine populations. Fishery selectivity can be considered to occur at different scales. At the level of the operation of the fishing vessel, selectivity is dependent upon the characteristics of the gear (e.g. mesh size) being used. Selectivity is also dependent upon the availability of fish within the fishing vessel's area of operation. The challenge confronting stock assessments is to determine how these gear and area-related processes combine over time and space to produce stock-level fishery selectivity. A number of studies (e.g. Sampson, 2014) have highlighted the diversity of age-specific selectivity patterns that can be produced under different gear configurations, fleet spatial patterns, and stock characteristics. Thus, stock assessment programmes such as SS3 (Methot and Wetzel, 2013) provide a range of functional relationships (e.g. asymptotic, double-logistic) with which to parameterize selectivity patterns in the model fitting process. Given the importance in correctly characterizing the age or size-specific fishery selectivity, considerable attention is paid in stock assessments to the appropriate relationship to use, the two main ones being asymptotic or "flat-topped" and double-logistic or "domed". Stock assessment scientists have often assumed (e.g. NEFSC, 2008) that a good starting point in any analysis is employing an asymptotic relationship between fishery selectivity and age unless evidence to the contrary is available. Adopting domed selectivity relationships can lead to so-called cryptic biomass of older individuals that is assumed to be present yet unavailable to the fishery. Often, the choice is not between one or the other relationship but rather one on the degree of doming. Unfortunately, these choices are often based upon processes operating on older, larger individuals, which are the least abundant in the population and for which data are generally limited. Thus, statistical support for one selection curve compared with another can often be weak. In these situations, having theoretical support for a preferential model can considerably aid assessment efforts.

In this regard, recent work by Sampson and Scott (2011, 2012) to determine the form of fishery selectivity patterns under different stock and fishery conditions has received considerable attention. They determined that based upon simulated populations, dome-shaped selectivity patterns are to be expected in preference to asymptotic patterns when the influence of fish movements among areas is taken into account. While gear selectivity within an area might be flat-topped, the overall population-level selectivity pattern would likely be dome-shaped due to migration effects. However, building assessment models which explicitly incorporate spatial stock processes is not straightforward. Thus, some recent assessments conducted using a statistical catch-at-age approach (e.g. Stewart, 2005) have aimed to mimic spatially structured fishing by specifying fleets operating in various areas but without explicitly including movement processes. Cope and Punt (2011), in their exploration of the effects of spatial catch histories, were among the first to use the term "areas-as-fleets" to describe this approach to analysing fishery selectivity patterns. This approach was used in the 2015 assessment of Atlantic menhaden (*Brevoortia tyrannus*) (SEDAR, 2015). Waterhouse *et al.* (2014) undertook a comprehensive simulation-based analysis of the "areas-as-fleets" approach, illustrating the range of potential domed selectivity relationships that can be produced and the extent to which these are influenced by fishery spatial structure and stock movement rates.

A key assumption of the work to date on the influence of fish movements on fishery selectivity patterns has been that these movements are one way with fish moving from Area A to Area B and sometimes onto Area C, without returning to Area A, all occurring within one period, generally taken to be a year. Given the well-recognized annual migration patterns of many fish species—movement from spawning to feeding grounds to overwintering areas and back to spawning grounds—this assumption of one-way movement within one year is not biologically realistic for most fishery assessments and is perhaps more pertinent to situations in which fish move from a fished area to one that is lightly or not fished (e.g. Marine protected areas, marine reserves). While there is good evidence to suggest that domed selectivity patterns can be a consequence of one-way movements, it is less clear what would happen when the seasonal movement patterns typically observed in many fish stocks are considered.

This paper explores the influence of biologically realistic, seasonal migrations on the generation of selectivity patterns in fisheries to better inform the stock assessment and management process.

Material and methods

Approach

The general approach taken was to build upon the concepts outlined by Waterhouse *et al.* (2014) of an age-structured fish stock exploited by a fishery operating in an "areas-as-fleet's (AAF) context. A simulation of a typical long-distance migrating fish species, Atlantic menhaden, was constructed and used as a base case operating model which was modified to produce a range of plausible scenarios to study the influence of different fishery and stock processes on fishery selectivity. The first set of explorations emulated, to the degree possible, the previous work of Waterhouse et al. (2014) which assumed one-way movement. These also provide a check to confirm that the current study is applying the AAF theory in a manner consistent with previous work; under the same assumptions, the same results should be obtained. The next set of explorations of the base model involved two-way movement effects, considering both stock and fishery processes. Stock scenarios involved consideration of the overall rate of age-constant movements (two way) between two areas (South and North) as well as the influence of age-specific two-way movement rates. Fishery scenarios involved consideration of the influence of different fully recruited fishing mortalies in each area as well as the duration (season length) and timing (months) of the fishery in each area.

There are a number of benefits to this case study approach. First, constructing a completely generic and idealized migrator would not only be difficult but open to such a wide array of possible influences as to make the problem almost intractable. Second, conclusions drawn from the generic situation would likely be valid for that situation and not be relevant to most situations encountered in nature. This approach is consistent with the concept of undertaking simulations "conditioned" on the available data of the biology and fishery of interest (Rademeyer *et al.*, 2007; Deroba *et al.* 2015). Finally, it allows comparison of the predictions of the base case simulations with empirical observations from the fishery (e.g. seasonal catches), providing a check on the reality of the simulations and thus ensuring that the movement-mortality-selectivity processes, the combinations of which can be many, are represented in a reasonable way.

Operating model

The stock and fishery dynamics of the operating model employ the standard fishery dynamical equations. During each monthly time-step (t), given a starting population number ($N_{t,a,r}$), total mortality ($Z_{t,a,r}$), and "effective" instantaneous migration rate ($E_{t,a,r}$) at age (a) in each of two areas (r), the population numbers ($N_{t+1,a,r}$) at the beginning of the next time-step are calculated:

$$N_{t+1,a,r} = N_{t,a,r} e^{-(Z_{t,a,r}+E_{t,a,r})}. \qquad (1)$$

The total number of age-0 fish entering the population at the first time-step of each year was set at the estimated number of age-0 fish during 1970–1993 from the 2014 Atlantic menhaden benchmark stock assessment (ASMFC, 2015). These age-0 fish were split between the two areas using a scenario-specific proportion (Table 1—"R split").

The total mortality in each area ($Z_{t,a,r}$) is calculated as:

$$Z_{t,a,r} = F_{t,a,r} + M_a, \qquad (2)$$

where $F_{t,a,r}$ is the area-specific instantaneous fishing mortality-at-age, calculated assuming an annual fully recruited fishing mortality (F_{full}), the gear-specific selectivity at age (S_a), and the annual proportion of F_{full} in each area and month ($P_{t,r}$):

$$F_{t,a,r} = F_{\text{full}} \times S_a \times P_{t,r}, \qquad (3)$$

where F_{full} and S_a are set according to the scenario under consideration while $P_{t,r}$ in all scenarios is based upon the observed distribution of catch in the Atlantic menhaden fishery.

The variable M_a is the natural mortality rate at age and is assumed to be invariant with respect to season or area and is the same for all scenarios. Its derivation is described under the base scenario below.

Table 1. Parameter values for scenarios used to explore the influence of migration on areas-as-fleets (AAF) selectivity. Scenario 1 is the base case and is meant to mimic the conditions in the Atlantic menhaden stock and fishery. For all other scenarios, an asterisk indicates the use of base case values.

	Scenario	Stock processes					Fishery processes				
			Seasonal movement probability (pMove)		Migration season				Fishery season		
		R split (S, N)	S → N	N → S	S → N	N →	F_{full}	F split (S, N)	South	North	Input selectivity
Base	1*	0.9, 0.1	$A_{50} = 1.5$; $s = 0.5$; max = 0.8	0.9	April – June	October – December	0.9	0.8, 0.2	Empirical	Empirical	$A_{50} = 1.5$; $s = 0.1$
No and one-way movement	2	0.5, 0.5	0	0	NA	NA	*	*	All year	All year	*
	3	0.5, 0.5	0	0	NA	NA	0.9	0.2, 0.8	All year	All year	*
	4	1, 0	0.05	0	All year	NA	*	*	All year	All year	*
	5	1, 0	0.2	0	All year	NA	*	*	All year	All year	*
Two-way movement stock processes	6	*	0.9	*	*	*	*	*	*	*	*
	7	*	0.5	0.5	*	*	*	*	*	*	*
	8	*	0.2	0.2	*	*	*	*	*	*	*
	9	*	$A_{50} = 0.5$; $s = 0.5$; max = 0.8	*	*	*	*	*	*	*	*
	10	*	$A_{50} = 2.5$; $s = 0.5$; max = 0.8	*	*	*	*	*	*	*	*
	11	*	$A_{50} = 1.5$; $s = 0.5$; max = 0.5	*	*	*	*	*	*	*	*
	12	*	*	*pMove* (S → N)	*	*	*	*	*	*	*
	13	*	*	1-*pMove* (S → N)	*	*	*	*	*	*	*
	14	*	*	*	March – May	*	*	*	*	*	*
	15	*	*	*	May – July	*	*	*	*	*	*
	16	*	*	*	*	September – November	*	*	*	*	*
	17	*	*	*	*	November – January	*	*	*	*	*
Two-way movement fishery processes	18	*	*	*	*	*	0.45	*	*	*	*
	19	*	*	*	*	*	1.80	*	*	*	*
	20	*	*	*	*	*	*	0.5, 0.5	*	*	*
	21	*	*	*	*	*	*	0.2, 0.8	*	*	*
	22	*	*	*	*	*	*	*	June; December	July	*
	23	*	*	*	*	*	*	*	All year	All year	*
	24	*	*	*	*	*	*	*	*	*	$A_{50} = 0.5$; $s = 0.1$
	25	*	*	*	*	*	*	*	*	*	$A_{50} = 2.5$; $s = 0.1$
	26	*	*	*	*	*	*	*	*	*	$A_{50} = 1.5$; $s = 1.0$

A key consideration is how movement among areas is modelled during each time-step in the simulation. Most studies (e.g. Cadrin and Secor, 2009; Waterhouse *et al*., 2014) have modelled movement at the end of a time-step after fishing and natural mortality has occurred. In the current study, movement was assumed to occur continuously throughout each migration "season" (i.e. a series of n consecutive monthly time-steps). At the beginning of each time-step, the starting numbers-at-age for each area ($N_{\mathrm{start,a,r}}$) were multiplied by an age-specific transfer probability matrix ($\mathbf{T_a}$) to achieve the numbers-at-age in each area at the beginning of the next time-step ($N_{\mathrm{end,a,r}}$) that would result from movement alone:

$$N_{\mathrm{end},a,r} = \mathbf{T_a} \cdot N_{\mathrm{start},a,r}. \tag{4}$$

The transfer probabilities in $\mathbf{T_a}$ are based on an assumed age-specific probability of moving from area 1 to area 2 and back from area 2 to area 1 over an entire migration season ($\mathrm{pMove}_{1,2}$ and $\mathrm{pMove}_{2,1}$, respectively). These aggregate seasonal values are divided among the n time-steps that comprise each migration season to provide the cells of the transfer probability matrix for each time-step (seasonal subscript dropped for clarity):

$$\mathbf{T_a} = \begin{bmatrix} \psi_{1,1} & \psi_{1,2} \\ \psi_{2,1} & \psi_{2,2} \end{bmatrix},$$

where $\psi_{1,2} = 1 - (1 - \mathrm{pMove}_{1,2})^{(1/n)}$ = probability of a fish of age a moving from area 1 to area 2 during a time-step. $\psi_{1,1} = 1 - \psi_{1,2}$ = probability of staying in area 1 during a time-step. $\psi_{2,1}$ and $\psi_{2,2}$ are defined in an equivalent manner using $\mathrm{pMove}_{2,1}$.

The "effective" instantaneous migration rate (E) was then calculated as:

$$E_{t,a,r} = \ln \frac{N_{\mathrm{end},a,r}}{N_{\mathrm{start},a,r}}. \tag{5}$$

Thus, $E_{t,a,r}$ takes into account both emigration and immigration to and from each area, and therefore can be either positive or negative depending on the overall movement rate and its direction. These E rates at age are then added to the age-specific estimates of total mortality (Z) in the survival equation (1) to calculate the numbers-at-age in each area at the beginning of the next time-step.

The catch-at-age ($C_{t,a,r}$) in each area in that time-step is then calculated as:

$$C_{t,a,r} = N_{t,a,r} \times \left(\frac{F_{t,a,r}}{Z_{t,a,r} + E_{t,a,r}} \right) \times (1 - \mathrm{e}^{-(Z_{t,a,r} + E_{t,a,r})}). \tag{6}$$

In essence, the average population size in each area from which $C_{t,a,r}$ is calculated can increase or decrease between time-steps dependent on the sign of $E_{t,a,r}$. Note that age is only incremented between years and not between each monthly time-step. Gordon *et al.* (1995) provide a thorough mathematical discussion of a similar modelling framework in which mortality and movement are continuous processes, but the system of equations is evaluated at discrete time intervals. Our model can be seen as an extension of this approach in that we allow movement and fishing mortality rates to vary seasonally to achieve the round-trip migratory loop.

The annual (across all time-steps and areas) population level fishing mortality (F) at age is calculated through a numerical (Newton–Raphson) solution of the Baranov catch equation, given beginning of year population numbers (N) at age, total catch (C) at age (summed across time-steps and areas), and natural morality (M) at age. This provides the average annual fishing mortality on each year class in the population under the assumption that total mortality (Z) occurs at a constant rate during the year. While this assumption is being violated as part of the simulation, it is typical of the assumptions made in most stock assessment models. It also provides a useful metric which allows comparisons with previous work. The population fishery selectivity at age is then calculated by dividing the population level F at age by its maximum value.

The AAF selectivity at age is calculated by first apportioning the population F at age to each area according to the ratio of the area-specific C at age to the total C at age and then dividing the resulting area-specific F at age by its maximum value. As above, these calculations are done in a consistent manner to those of Waterhouse *et al.* (2014), allowing comparisons of the findings in both studies.

The simulation was run for 10 years (which is sufficient duration to achieve equilibrium conditions for a species with a life history such as Atlantic menhaden) and did not involve examination of uncertainty.

Base case scenario

The parameters of the base case (Table 1—Scenario 1) were established to mimic the conditions in the Atlantic menhaden stock and fishery. The 2015 assessment of this stock (SEDAR, 2015) used an AAF statistical catch-at-age framework and provides a relevant example through which to explore the effects of migration on selectivity patterns. Menhaden undergo an annual migration along the US Atlantic coast between a southern spawning ground and more northern feeding areas. The bulk of spawning activity occurs between January and March along the continental shelf off the coast of North Carolina (Warlen *et al*., 2002). Larvae are advected into estuaries along the coast and remain there through their first summer. As the water warms, adults move northward along the coast between April–June. Large-scale tagging experiments in the 1970s revealed that the extent of this northward migration is size dependent, with larger fish found further north during summer (Dryfoos *et al*., 1973; Nicholson 1978). Fish begin moving south in September and accumulate off the coasts of North Carolina and Virginia in autumn to complete the annual migratory cycle. Age-0 juveniles that emerge from the estuaries in late summer are believed to join the autumn migratory population in moving south in winter (Ahrenholz *et al*., 1991).

Two primary fleets comprise the Atlantic menhaden fishery: an industrial fleet whose landings are reduced to fishmeal and dietary supplements and a bait fleet that supplies the lobster and crab fisheries. Both fleets primarily use purse-seines and therefore the gear-related size selection process is similar between them. The reduction fishery has historically accounted for most of the catch and has the longer and more consistent fishery-dependent dataset. For these reasons and to keep model explorations as simple as possible, all analyses focused exclusively on the reduction fishery.

Purse-seines are typically considered to be non-selective with respect to fish size (e.g. Lucena and O'Brien, 2001; Cochrane, 2002; Slotte *et al*., 2007); yet, ages zero and one make up a surprisingly small portion of the catch, despite being the most abundant ages. Our interpretation of this phenomenon is that the younger ages are primarily unavailable to the fishery due to ontogenetic habitat use (i.e. dependence on inner estuaries). Therefore, the gear-related selectivity used as input to the base model was assumed to have a "knife-edge" break between ages 1 and 2. This was accomplished using a logistic function with an A_{50} of 1.5 and small-scale value (0.1), with the input selectivity for age 0 set at a low value (0.1). This produces an input selectivity curve of 0.10 and 0.11 for ages 0 and 1 and 1.0 for ages 2 through 6.

For this study, the US Atlantic coast was split into North (N) and South (S) areas with a dividing line at Chincoteague Island near the Maryland/Virginia border, following the spatial layout of the recent stock assessment (Figure 1). The probability of moving from S to N in spring (April, May, and June) was expressed as a logistic function of age, with a high asymptotic maximum value reflecting the observations from coast-wide tagging experiments (Dryfoos *et al*., 1973; Nicholson 1978). The tagging datasets are less informative for the southward migration, and as such an age-constant probability of moving from the N to S (0.9) was assumed for the months of October, November, and December. No movement was assumed during summer (July, August, and September) and winter (January, February, and March).

An age-dependent natural mortality curve was adopted from the stock assessment, which used Lorenzen's (1996) method of assuming mortality to be a negative power function of body weight. Other conventions adopted from the stock assessment were a March 1 birthdate for all fish; and seven age groups (ages 0–6+). Age 0 fish were assumed to enter the stock primarily in the South (90%) and recruit to the fishery in December.

Over the past 50 years, the Atlantic menhaden population has undergone substantial fluctuations, both in terms of total biomass and range extent. Consequently, the number and distribution of reduction plants has varied over the decades. For this reason, the years 1972–1993 were selected as a reference period for the base model, as

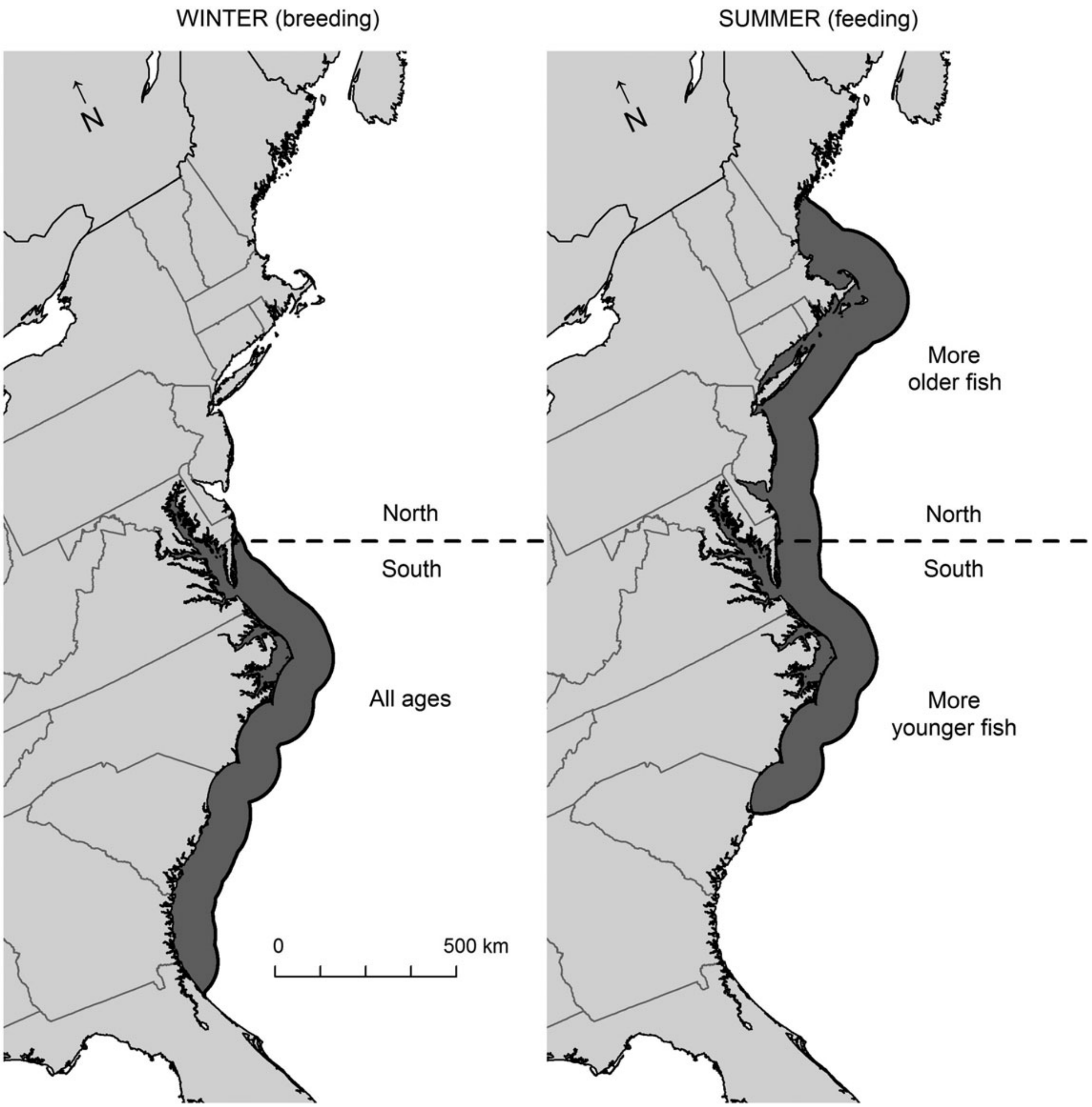

Figure 1. General seasonal distribution of Atlantic menhaden along US Atlantic coast as surmised from tagging studies (Dryfoos *et al*., 1973; Nicholson, 1978), in relation to model areas.

this was a relatively stable time in the fishery, with reduction vessels operating in both areas. Furthermore, this period also represents the longest stretch of consistent fishery selectivity under the 2015 AAF stock assessment. Several values were extracted from either fishery-dependent datasets or assessment output for this period to finish parameterizing the simulation model, including: the mean fishing mortality-at-age 2 (F_{full}); and the mean proportion of total landings by month and area ($P_{t,r}$).

Scenarios

No and one-way movement

Four scenarios were used to emulate the work of Waterhouse *et al.* (2014) using an AAF approach (Table 1—scenarios 2–5). The first two scenarios (2–3) explored the effects of different levels of F split between the N and S areas, given uniformly distributed recruitment and no movement between the two areas.

The next two scenarios (4–5) assumed that recruitment occurred only in one area (S) and explored different rates of one-way directional movement. Contrary to Waterhouse *et al.* (2014), no scenarios explored non-directional, diffusive, movements between the two areas.

While not as expansive as their study, it was considered that the four scenarios considered here were sufficient to confirm that previous results could be reproduced.

Two-way movement

The 21 scenarios which examined the impact of two-way movements on the AAF and population selectivity patterns can be considered in two groups: those involving stock processes (Table 1—scenarios 6–17) and those involving fishery processes (scenarios 18–26). The parameters of the base case (scenario 1) were systematically modified to explore how age-constant (scenarios 6–8) and age-varying (scenarios 9–13) movements influenced the AAF selectivity patterns. For the age-varying scenarios, the logistic relationship between the probability of moving north in spring and age was shifted by -1 age (scenario 9) and $+1$ age (scenario 10), and by assuming a lower asymptotic maximum (scenario 11). Age-specific increasing (scenario 12) and decreasing (scenario 13) probability of N to S movement in autumn were also explored. Seasonal changes in the movements north and south were explored by shifting the migration seasons 1 month earlier or later (S to N: scenarios 14–15; N to S: scenarios 16–17).

Regarding the fishery, a change in the overall F was examined by reducing the mean F_{full} for the reference period by 50% (scenario 18) and by doubling it (scenario 19). Changes to the regional distribution of fishing mortality were explored by assuming equal F in each area (scenario 20) and a higher F in the N area (scenario 21—opposite of the base case). The effect of altering the seasonal distribution of fishing effort was explored by constraining all fishing to discrete pulses (S: June—50%, December—50%; N: July 100%) (scenario 22), and by distributing fishing equally across all months (scenario 23). Finally, the influence of alternative gear selectivity profiles was examined by shifting the age at 50% selection (A_{50}) by -1 age (scenario 24) and $+1$ age (scenario 25), and by assuming a more sloped relationship between age and selectivity (scenario 26).

In each of these scenarios, the behaviour of a number of population and fishery parameters was examined. These are illustrated for the base case (Figure 2). Animations of these scenarios are available in Supplementary Material.

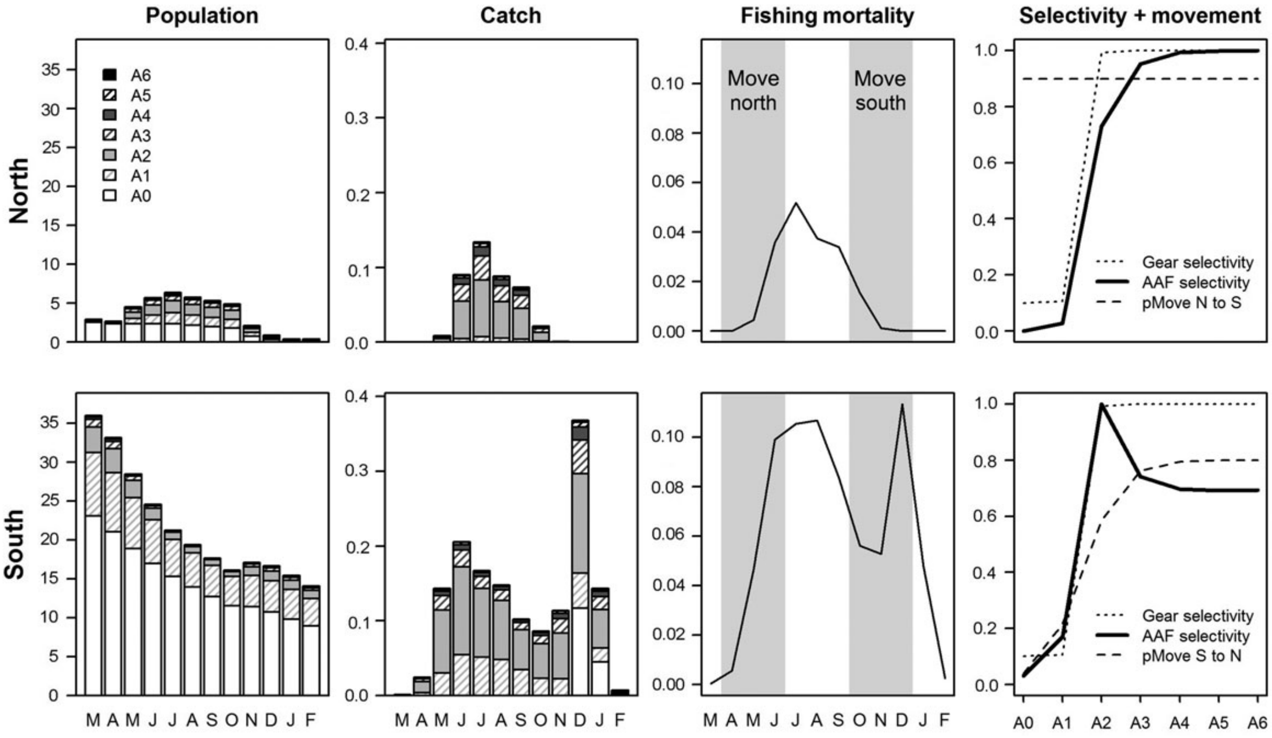

Figure 2. Summary of input parameters and resulting characteristics of the base case scenario. From left to right: Seasonal distribution of: population age structure (column 1), fishery catch-at-age (column 2), and fishing mortality (column 3); age-related profiles of gear selectivity, AAF selectivity and movement probabilities (column 4); values for northern and southern areas shown in top and bottom rows, respectively; note that for seasonal plots (columns 1–3), first month is March, assumed birth month in model; see Supplementary Material to view animated versions of this plot under various scenarios.

Results

No and one-way movement

When equal recruitment and no movement between areas is assumed to occur, the generated AAF selectivity at age curves for the two areas are as indicated by previous work (Waterhouse *et al.*, 2014—scenario 1a). Specifically, the AAF selectivity pattern for the area experiencing the highest proportion of total fishing effort becomes dome shaped, while the other area is flat topped (Figure 3—scenarios 2 and 3; Figure 4). As per Waterhouse *et al.* (2014), the population selectivity curves are domed but not as extreme as the AAF selectivity pattern for the area experiencing the highest proportion of total fishing mortality.

The areal patterns in AAF selectivity do not change markedly when one-directional (S to N) movements of 5 and 20% are assumed (Figure 3—scenarios 4 and 5; Figure 4): there is still strong domed selectivity at age in the S area and increasing selectivity at age in the N area. However, the declining limb of the domed selectivity pattern in the area experiencing the most fishing effort (*S*) becomes exaggerated with increasing movement away from this area. The same patterns apply to the population selectivity patterns

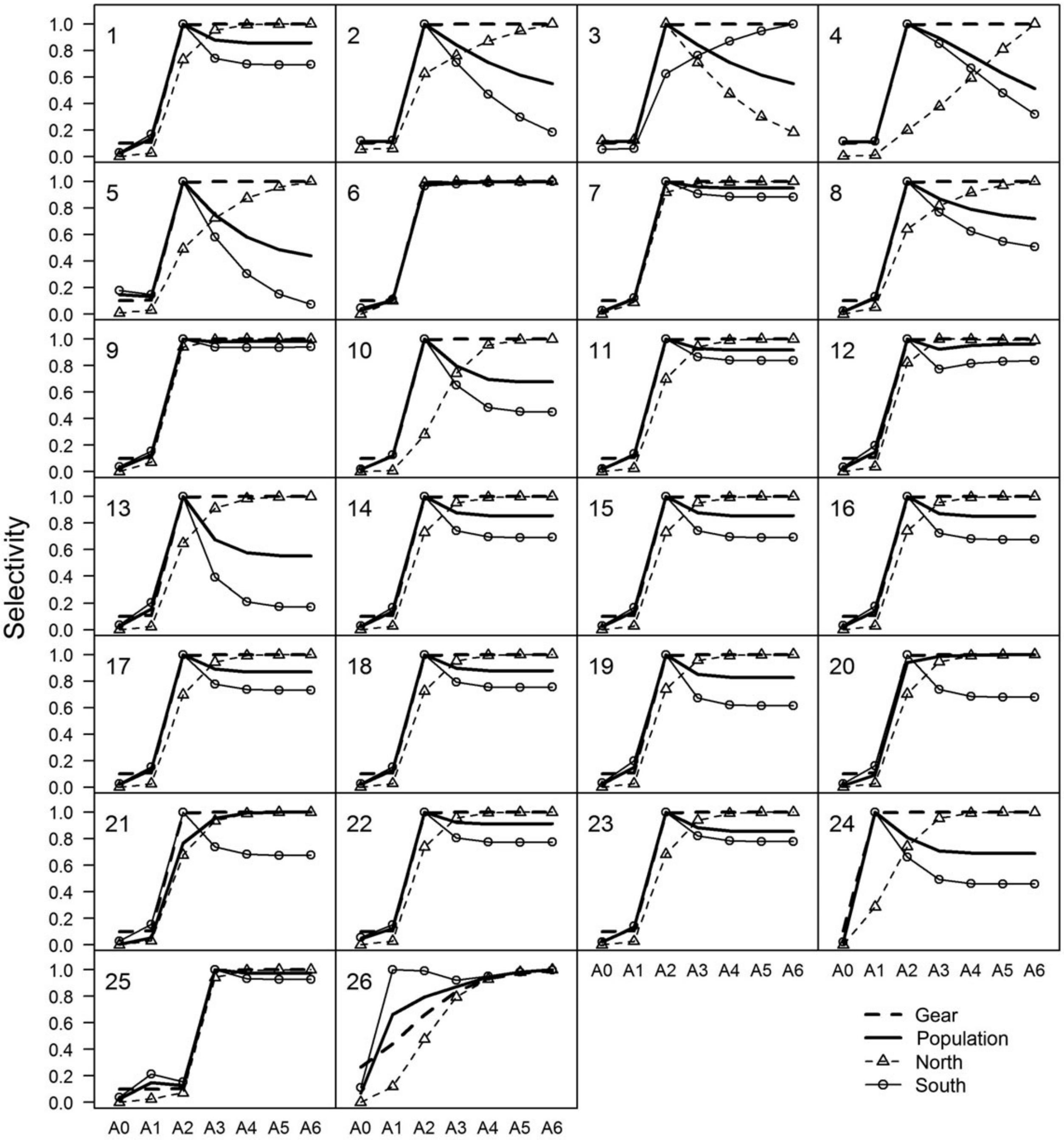

Figure 3. Comparison of gear-specific (input to model), area-specific AAF, and population-level selectivity at age under each scenario; scenario number indicated in upper left corner of each panel.

(Figure 3). Again, these findings are consistent with those of Waterhouse *et al.* (2014), matching their scenarios 4a and 5b in their Figures 4 and 5.

Two-way movement

Both the stock (Figure 5) and fishery processes (Figure 6) resulted in changed AAF selectivity patterns relative to the base case when two-way migration was assumed. In all scenarios in which two-way movement was assumed, domed AAF selectivity curves could not be induced in the N ("feeding") area, with these always occurring in the S ("spawning") area. All but two scenarios yielded domed selectivity in the S area, and all but five scenarios yielded domed selectivity in the population as a whole, although these were not as extreme as the domed AAF selectivity patterns in the S area (Figure 3).

When two-way age-constant migration is assumed to occur at a high rate of 0.9, there are no domed AAF selectivity curves in either area, with the AAF in each area and the population selectivity matching the gear selectivity (Figures 3 and 5—scenario 6). Reducing the rate of age-constant migration in both directions increases the magnitude of the dome in the S area and causes the selectivity pattern in the N area to become more increasing than flat-topped such that the younger ages in the AAF pattern are less selected by the gear (Figures 3 and 5—scenarios 7 and 8). In the extreme, these scenarios reduce to that of the no migration scenario (Figure 4—scenario 2).

Assuming age-varying two-way migrations relative to the gear selectivity changed the above AAF selectivity patterns. When fish begin their northern migration at a younger age than the age at 50% gear selection (A_{50}) but return to the S area at an age-constant movement rate, the dome in the S area is reduced, relative to the base case, and both areas exhibit AAF and population selectivity patterns closer to the gear selectivity (Figures 3 and 5—scenario 9). When fish are selected by the gear before they migrate north (i.e. migration north delayed), the AAF selectivity dome in the S area is exaggerated and the N area has lower selection on younger ages (Figures 3 and 5—scenario 10). Reducing the maximum migration rate from the S to N area caused almost no change in the N selectivity pattern but reduced the dome in the S area because fewer fish were leaving that area (Figure 5—scenario 11). In this scenario, the population selectivity is close to the gear selectivity (Figure 3).

Assuming either a positive (scenario 12) or negative (scenario 13) logistic relationship between age and the N to S migration rate in autumn had little effect on N area selectivity. However, the positive relationship (i.e. older fish more likely to move south) modestly mediated the selectivity dome in the S, compared with the base case; whereas the negative relationship (i.e. younger fish are more likely to move south) exaggerated the southern selectivity dome, again compared with the base case (Figures 3 and 5).

The last stock process examined allowed the timing of the movements north and south to shift by 1 month. These changes did not result in significant changes to the AAF selectivity pattern in

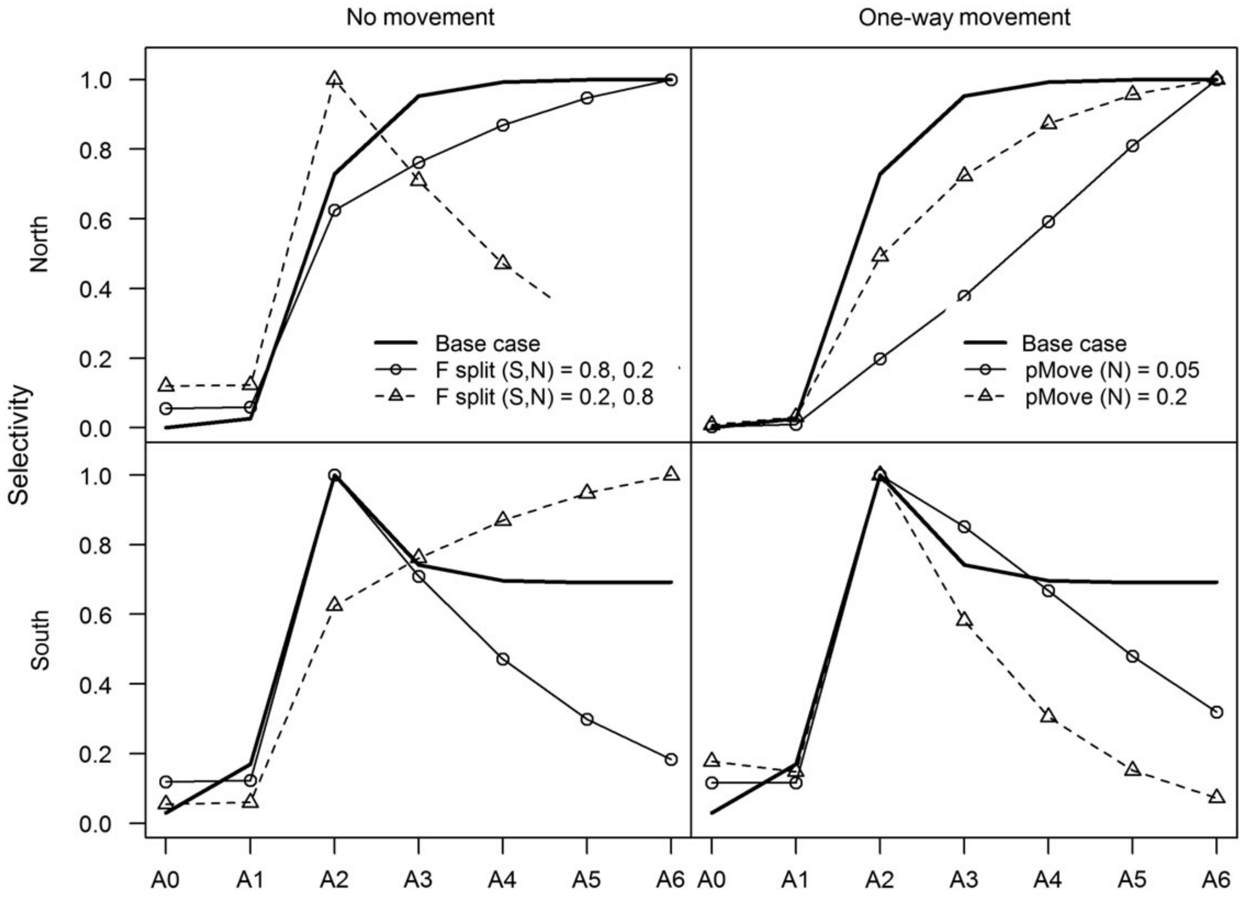

Figure 4. Predicted AAF selectivity profiles for northern (top row) and southern (bottom row) areas under scenarios that considered no movement (left column; scenarios 2–3), and one-way movement of 5 and 20% (right column; scenarios 4–5).

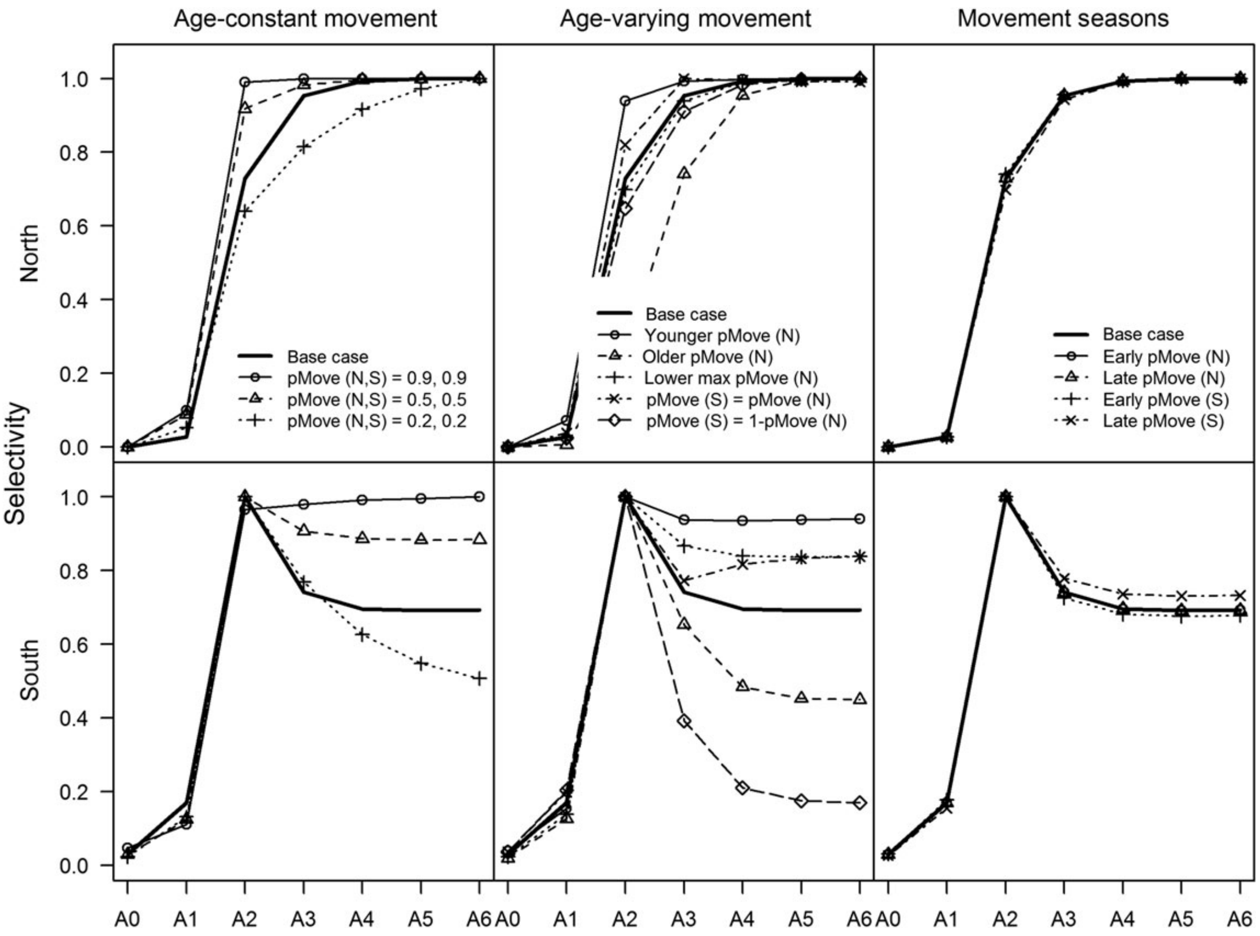

Figure 5. Predicted AAF selectivity profiles for northern (top row) and southern (bottom row) areas under scenarios (age-constant movement: scenarios 6–8; age-varying movement: scenarios 9–13; movement seasons: scenarios 14–17) that considered varying parameters that control stock processes from base case levels.

either area or the population selectivity (Figures 3 and 5—scenarios 14–17) although larger, but less biologically realistic, changes in the timing of the two-way migrations could produce larger changes (see Supplementary Material). For instance, if the migration north occurs earlier in the year, allowing less fishing on larger fish in the spawning area before migration to the feeding areas in the north, a greater domed AAF selectivity could be induced in the south.

Changes in the fishery processes, except for changes in the assumed gear selectivity, did not cause large changes in the AAF and population selectivity patterns. When the fishing mortality rate was decreased by 50% or doubled, the resulting AAF and population selectivity patterns did not change significantly from the base case (Figures 3 and 6—scenarios 18 and 19). Furthermore, altering the relative amount of fishing mortality between areas also had very little influence on AAF selectivity (scenarios 20 and 21). However, the population-level selectivity was more similar to that of the area with the higher F (Figure 3). Changing the timing of the fishing seasons to either a pulse fishery or to a constant fishery throughout the year (changes in $P_{t,r}$) both reduced the dome in the S area, but had little impact on the N area AAF selectivity pattern (Figure 6—scenarios 22 and 23).

As expected, changing the gear selectivity resulted in large changes in the AAF and population selectivity patterns. Shifting the gear selectivity younger or older had the opposite effect of shifting the migration timing younger or older (compare Figure 5—scenarios 9, 10 and Figure 6—scenarios 24, 25). Changing the gear selectivity to be more sloped (less "knife-edged") removed the dome in the S area but created a lower selection on younger fish in the N area (Figures 3 and 6—scenario 26).

Discussion

Sampson and Scott (2011, 2012) concluded that if a stock is not well mixed from a spatial perspective and fishing mortality is not applied uniformly, then under equilibrium conditions, population level selectivity will be dome-shaped across a range of stock- and fishery-related circumstances, although the age-specific gear selectivity follows an asymptotic logistic curve. The strongest domes were observed in the case in which there is no movement between areas. Waterhouse *et al.* (2014), in equilibrium simulations, represented spatial areas by using separate fishing fleets for each area. This allowed consideration of how population and AAF selectivity curves would change compared with the underlying asymptotic gear selectivity. While the overall population selectivity was typically dome shaped, the corresponding AAF selection curves differed by area and from the population and gear selection curves. In general, if fishing mortality was assumed to be uniformly distributed across areas, no matter the distribution of recruitment and

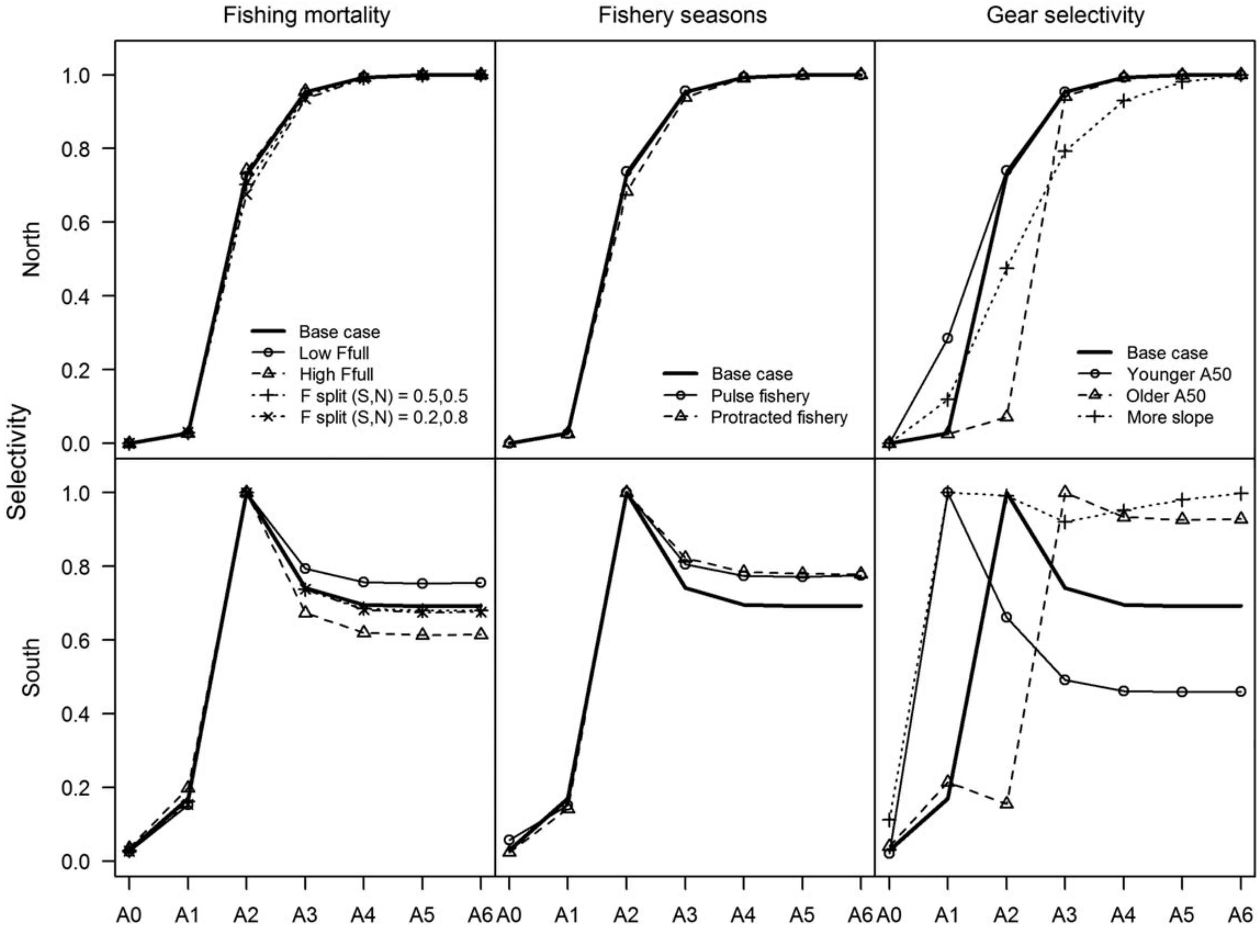

Figure 6. Predicted AAF selectivity profiles for northern (top row) and southern (bottom row) areas under scenarios (fishing mortality: scenarios 18–21; fishery seasons: scenarios 22–23; gear selectivity: scenarios 24–26) that considered varying parameters that control fishery processes from base case levels.

directional movement, the population selectivity curve reverted to that of the gear selectivity. The AAF selectivity curves would only revert to the gear selectivity curves if recruitment and fishing mortality were uniformly distributed across areas. The tendency for AAF selectivity to diverge from the gear selectivity diminishes as non-directional movement rates increase and areal fishing mortality becomes vanishing small.

The above studies generally restricted their explorations to either no, one-way or diffusive movements; furthermore, the movements considered in this earlier work were relatively small (5–20%) compared with the current study and occurred during an annual time-step. When employing these assumptions, the simulations undertaken in the current study corroborated their findings. It is important to consider the biological circumstances under which the results of these studies would be applicable. In the case in which there is limited movement between two areas, it could be argued that the estimated domes are an artefact of model mis-specification as the two areas might better be considered separate populations. However, there are examples of sessile species (e.g. Georges Bank scallops) in which larvae spawned from a common stock settle in different beds. The individuals which inhabit these beds essentially form separate sub-populations with limited movement occurring between them.

One-directional movements during a year could also be argued as a modelling artefact as the dominant paradigm in a stock is that of ontogenic age-specific movements (Cadrin and Secor, 2009). Individuals in the population move in different directions among areas over the course of a year (i.e. breeding → feeding → breeding). There are many examples of such age-specific "loop" migrations including Atlantic (*Brevoortia tyrannus*) and Gulf (*Brevoortia patronus*) menhaden, Atlantic herring (*Clupea harengus*), striped bass (*Morone saxatilis*), many groundfish, and large pelagic species (e.g. Bluefin tuna (*Thunnus thynnus*)) and indeed these movements are not restricted to any one taxanomic group or trophic level. Notwithstanding, a scenario of one-directional movements might apply for a closed area or marine reserve in which there is movement from one area to another area with both experiencing different fishing mortality rates. However, even in this case, it is to be expected that movements are not overall one way as this would result in the accumulation of the stock in one area over time.

The approach taken in this paper is to simulate the movements of a migratory population in time and space to explore the potential consequences of stock and fishery processes for population and AAF selectivity curves. Our results indicate that the extent to which these processes influence selectivity curves is highly dependent upon whether or not age-specific two-way movements are considered and how these correspond to the selectivity profile of the fishing gear.

The simulations in the present study indicated that a high rate of age-constant two-way migration did not induce domed AAF

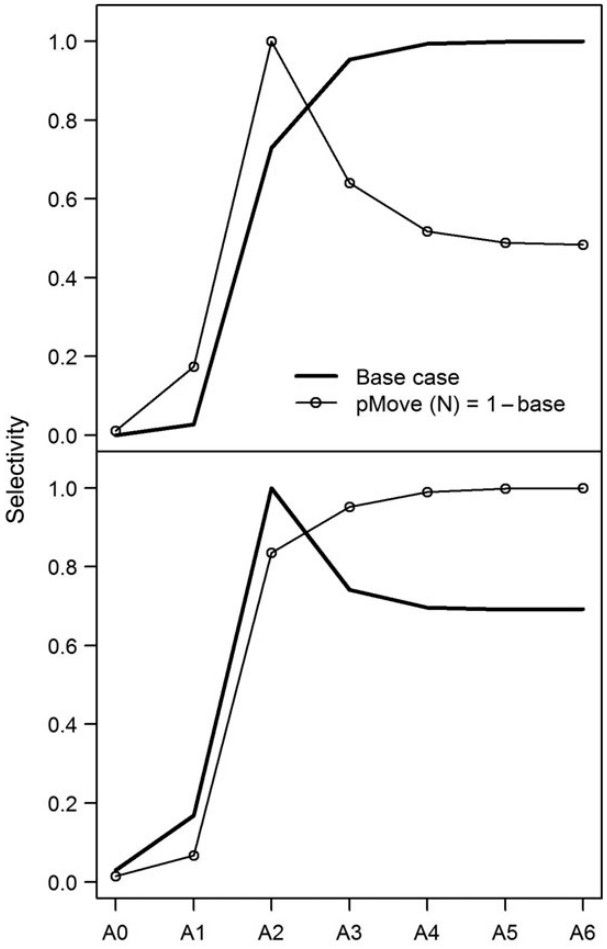

Figure 7. Predicted AAF selectivity profiles for northern (top row) and southern (bottom row) areas assuming a decreasing relationship between age and migration north in spring (i.e. younger fish are more likely to migrate; pMove $(N) = 1 - $ base). All other parameters are identical with the base case.

selectivity curves in either the "spawning" or "feeding" area. Assuming that the two-way movements are age-dependent adds biological realism and highlights their influence on whether or not the AAF selectivity curves revert to the underlying gear selection. It is important to consider these in relation to the 50% age of gear selection (gear A_{50}). If there is significant movement out of the "spawning" area of fish younger than the gear A_{50}, the extent of the AAF dome in this area is reduced and more closely follows the underlying gear selectivity. The opposite occurs when the fish "delay" their migration out of an area such the AAF selectivity curve in the spawning area becomes quite domed. It is important to note that the predominance of domed selectivity in the S area (and a lack of domes in the N area) is due to the assumption of a positive relationship between age and the probability of moving north in spring, a life history pattern that is well substantiated for Atlantic menhaden. However, if a species had the opposite relationship between age and migration (i.e. younger fish were more likely to migrate), then the opposite AAF selectivity conditions would prevail: flat-topped in the south and domed in the north (Figure 7).

Information on age-specific movement rates is generally limited and analyses to explore these often confront the confounding effects of age-specific fishing mortality and sample coverage (e.g. Atlantic menhaden, SEDAR, 2015). This highlights the need for better understanding of age-specific migration rates, a gap which has increasingly been filled by new tagging technologies (e.g. Campana *et al.*, 2010). It is interesting that the timing of the migrations in either direction did not induce significant changes—relative to the base case—in the AAF selectivity patterns in either area, except when large and biologically unrealistic changes were assumed. This suggests that it is the age-specific movement patterns in relation to gear selectivity that is the more important stock process to consider.

In scenarios not described above, it was determined that assumptions on the month and area in which recruits entered the population did not appear to have as great an impact on the population and AAF selectivity curves as might be expected from previous work. Waterhouse *et al.* (2014) had observed that having non-uniform (by area) recruitment produced more exaggerated population and AAF selectivity curves compared with uniform distribution (their scenarios 1a, 3a, and 4a). However, these findings are confounded with changes in movement rates (none, 5% non-directional and 5% directional) which may be the source for this difference with the current study.

When large, two-way movements are considered, both the overall level of fishing mortality and its areal distribution appeared to have little influence on the population and AAF selectivity curves. These results are in contrast to those of Waterhouse *et al.* (2014) who noted more extreme population and AAF selectivity domes when fishing mortality was increased, either overall or in each area. However, these findings were made under the assumption of no or one-way, relatively small (5 to 20%) directional movements compared with our base case. When larger two-way movements were introduced (50 and 90% age-constant both north and south) to represent the life history of a seasonal migrant, the impact of the areal split in fishing mortality became less significant. This again highlights the importance of considering the results of simulation studies in their proper context. The findings of no and one-way migration studies are pertinent for certain stocks and management situations (e.g. closed areas) and less so for the assessment of seasonal migrating species.

In this context, it is interesting to consider the results of the base case simulation with the findings of the 2015 stock assessment of Atlantic menhaden (SEDAR, 2015). When compared with the observed values from the commercial reduction fishery, the predicted catch-at-age (CAA) from the base case scenario included substantially older ages in all seasons and months (Figure 8). Furthermore, the assessment estimated domed selectivity in the northern area and a more exaggerated dome in the southern area than the base case (Figure 9). Determination of dome-shaped selectivity typically requires convincing auxiliary evidence, beyond improved model fit. In this case, the presence of significantly larger fish in several fishery-independent datasets supported the assessment's finding of dome-shaped fishery selectivity. The discrepancy between the stock assessment and our base case scenario suggests that an additional mechanism beyond migration may be influencing AAF selectivity and that the true gear-specific selectivity pattern for this fishery is more dome-shaped than assumed in the base model. One possible mechanism relates to the process whereby menhaden schools are located by purse-seiners. Spotter planes survey a fishing area and inform the vessels as to the location of large schools. While it remains to be verified, schools located by spotter planes may be made up of the most abundant ages or sizes of fish, which would likely be smaller and younger fish. Thus, although schools of 4- to 6-year-old fish may be present in an area,

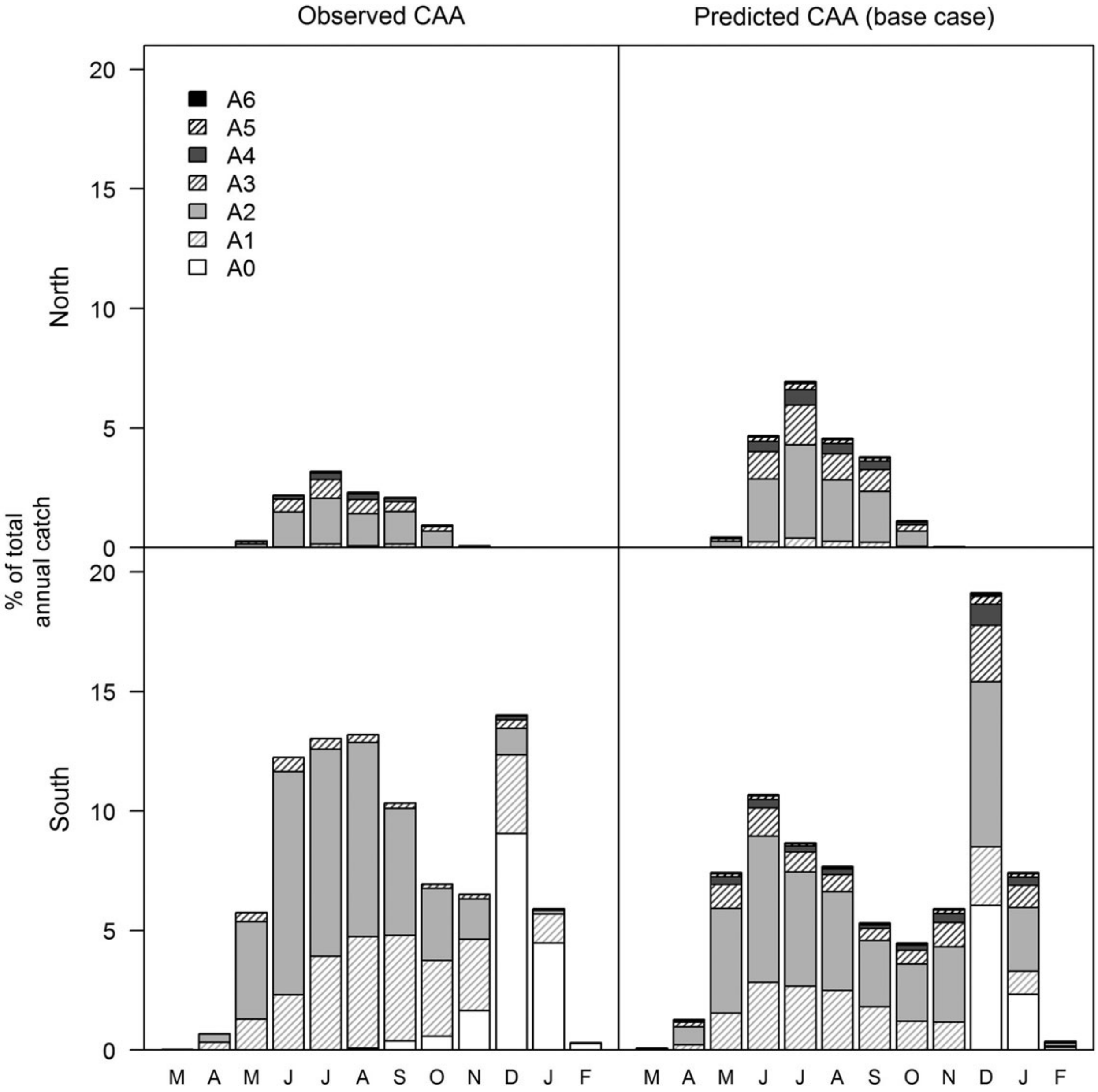

Figure 8. Predicted CAA by month and area from base case scenario, compared with observed CAA from commercial reduction fishery during 1972 – 1993.

the schools are not harvested because they are smaller than the optimum school size for the fishery to set on. Further, there is preliminary analysis which suggests that larger menhaden may be found farther offshore (SEDAR, 2015). These two mechanisms, which require confirmation, would no doubt result in domed gear selectivity.

The central conclusion of this paper is that consideration of biologically realistic movements of a stock has significant implications for the extent to which domed fishery selectivity patterns might be assumed. There are many possible patterns that can be expected both due to different fishing gears (e.g. trawling, longlining, gillnetting), movement patterns, and management interventions (e.g. closed areas). Contemporary assessment models make assumptions on the fishery selectivity patterns, the fitting of which is facilitated by a wide array of analytical tools (e.g. splines) that can define multiple time-varying age and size-specific patterns. Given the correlative structure of these models in which one set of parameters can strongly influence another set, placing priors, or constraints on the resolution of fishery selectivity patterns is of significant benefit. Estimating a less domed selectivity pattern than actually occurs results in an underestimate of stock biomass and overly conservative management advice, with consequences for the fishing industry. Estimating a more extreme domed selectivity pattern than is the case results in the generation of so-called cryptic biomass (Fonteneau, 1996), which can lead to unsustainable harvest and have severe consequences for stock management.

On a final note, given the difficulty of estimating migration rates between areas, it is not clear that increasing the complexity of assessment models for the sake of biological realism of migrating stocks will result in improved accuracy. Errors in estimated or assumed

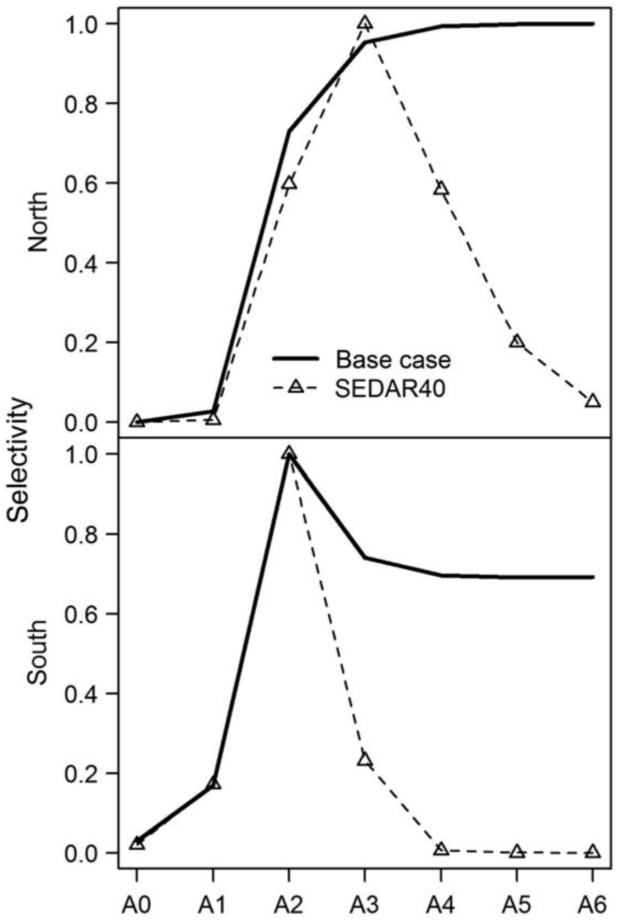

Figure 9. Predicted area-specific AAF selectivity profiles from base case, compared with results of recent AAF stock assessment for the commercial reduction fleet during 1972–1993 (SEDAR, 2015).

migration rates will still cause problems for estimating selectivity. Rather, simulation work as undertaken in the current study can guide assessment efforts by evaluating the effect of a range of plausible scenarios on selectivity patterns, thus assisting the evaluation of model assumptions, particularly whether or not either *a priori* assumed flat-top or domed selectivity at age patterns are appropriate. Building biologically realistic simulations can also be used to explore trade-offs between model complexity and ability to produce reasonable management advice. They can also allow the examination of the implications of uncertainties in stock movements for reference points and harvest projections. The development of such simulations is encouraged as a standard feature of assessment.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript. This includes illustrations of the relationship between selectivity and a given parameter, animated across a series of values of the latter.

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References

Ahrenholz, D. W., Dudley, D. L., and Levi, E. J. 1991. Population biology and life history of the North American Menhadens, Brevoortia spp. Marine Fisheries Review, 53: 3–19.

Cadrin, S. X., and Secor, D. H. 2009. Accounting for spatial population structure in stock assessment: past, present, and future. In The Future of Fisheries Science in North America, pp. 405–426. Ed. by R. J. Beamish, and B. J. Rothschild. Springer Science. ISBN 978-1-4020-9209-1.

Campana, S. E., Joyce, W., and Fowler, M. 2010. Subtropical pupping ground for a cold-water shark. Canadian Journal of Fisheries and Aquatic Sciences, 67: 769–773.

Cochrane, K. L. Ed. 2002. A fishery manager's guidebook. Management measures and their application. FAO Fisheries Technical Paper. No. 424. Rome, FAO. 231 pp.

Cope, J. M., and Punt, A. E. 2011. Reconciling stock assessment and management scales under conditions of spatially varying catch histories. Fisheries Research, 107: 22–38.

Deroba, J. J., Butterworth, D. S., Methot, R. D., Jr., De Oliveira, J. A. A., Fernandez, C., Nielsen, A., Cadrin, S. X., *et al.* 2015. Simulation testing the robustness of stock assessment models to error: some results from the ICES strategic initiative on stock assessment methods. ICES Journal of Marine Science, 72: 19–30.

Dryfoos, R. L., Cheek, R. P., and Kroger, R. L. 1973. Preliminary analyses of Atlantic menhaden, Brevoortia tyrannus, migrations, population structure, survival and exploitation rates, and availability as indicated from tag returns. Fisheries Bulletin, 71: 719–734.

Fonteneau, A. 1996. Why so many very old fishes in the southern bluefin tuna catches? Preliminary modeling of the "cryptic" biomass hypothesis. *In* Proceedings of the Sixth Expert Consultation on Indian Ocean Tunas (Colombo, Sri Lanka, 25–29 September 1995). Indo-Pacific Tuna Development and Management Programme, IPTP Collective Vol. 9, pp. 279–285.

Gordon, G. N. G., Andrew, N. L., and Montgomery, S. S. 1995. Deterministic compartmental model for the eastern king prawn (Penaeus plebejus) fishery in New South Wales. Marine and Freshwater Research, 46: 793–807.

Lorenzen, K. 1996. The relationship between body weight and natural mortality in juvenile and adult fish: a comparison of natural ecosystems and aquaculture. Journal of Fish Biology, 49: 627–642.

Lucena, F. M., and O'Brien, C. M. 2001. Effects of gear selectivity and different calculation methods on estimating growth parameters of bluefish, Pomatomus saltatrix (Pisces: Pomatomidae), from southern Brazil. Fisheries Bulletin. 99: 432–442.

Methot, R. D., and Wetzel, C. R. 2013. Stock synthesis: a biological and statistical framework for fish stock assessment and fishery management. Fisheries Research, 142: 86–99.

Nicholson, W. R. 1978. Movements and population structure of Atlantic menhaden indicated by tag returns. Estuaries, 1: 141–150.

Northeast Fisheries Science Center (NEFSC). 2008. Assessment of 19 Northeast Groundfish Stocks through 2007: Report of the 3rd Groundfish Assessment Review Meeting (GARM III), Northeast Fisheries Science Center, Woods Hole, Massachusetts, 4–8 August 2008. US Dept Commer, Northeast Fish Sci Cent Ref Doc. 08-15; 884 p+xvii.

Rademeyer, R. A., Plaganyi, E. E., and Butterworth, D. S. 2007. Tips and tricks in designing management procedures. ICES Journal of Marine Science, 64: 618–625.

Sampson, D. B. 2014. Fishery selection and its relevance to stock assessment and fishery management. Fisheries Research, 158: 5–14.

Sampson, D. B., and Scott, R. D. 2011. A spatial model for fishery age-selection at the population level. Canadian Journal of Fisheries Aquatic Sciences, 68: 1077–1086.

Sampson, D. B., and Scott, R. D. 2012. An exploration of the shapes and stability of population-selection curves. Fish and Fisheries, 13: 89–104.

SEDAR. 2015. Atlantic Menhaden Stock Assessment Report. SEDAR 40. 643 pp.

Slotte, A., Skagen, D., and Iversen, S. A. 2007. Size of mackerel in research vessel trawls and commercial purse-seine catches: implications for acoustic estimation of biomass. ICES Journal of Marine Science, 64: 989–994.

Stewart, I. 2005. Status of the US English sole resource in 2005. Pacific Fishery Managemnt Council, 7700 NE. Ambassador Place, Suite 101, Portland, Oregon 97220-1384.

Waterhouse, L., Sampson, D. B., Maunder, M., and Semmens, B. X. 2014. Using areas-as-fleets selectivity to model spatial fishing: asymptotic curves are unlikely under equilibrium conditions. Fisheries Research, 158: 15–25.

Warlen, S. M., Able, K. W., and Laban, E. H. 2002. Recruitment of larval Atlantic menhaden (Brevoortia tyrannus) to North Carolina and New Jersey estuaries: evidence for larval transport northward along the east coast of the United States. Fishery Bulletin, 100.3: 609–623.

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