



"So, where do you come from?" The impact of assumed spatial population structure on estimates of recruitment

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ABSTRACT

Understanding population dynamics is essential for achieving sustainable and productive fisheries. However, estimating recruitment in a stock assessment model involves the challenging task of identifying a self-sustaining population, which often includes representing complex geographic structure. A review of several case studies demonstrated that alternative stock assessment models can influence estimates of recruitment. Incorporating spatial population structure and connectivity into stock assessment models changed the perception of recruitment events for a wide diversity of fisheries, but the degree to which estimates were impacted depended on movement rates and relative stock sizes. For multiple population components, estimates of strong recruitment events and the productivity of smaller population units were often more sensitive to connectivity assumptions. Simulation testing, conditioned on these case studies, suggested that accurately accounting for population structure, either in management unit definitions or stock assessment model structure, improved recruitment estimates. An understanding of movement dynamics improved estimation of connected sub-populations. The challenge of representing geographic structure in stock assessment emphasizes the importance of defining self-sustaining management units to justify a unit-stock assumption.

1. Introduction

Understanding population dynamics, including growth, survival and recruitment, is fundamental to managing sustainable and productive fisheries (Beverton and Holt, 1957). Estimating recruitment (the initial abundance of a year-class, size cohort, or other group of young fish in a population) in stock assessment typically involves a population dynamics model that assumes a 'unit stock', a reproductively distinct, self-sustaining population (Secor, 2014). More specifically, stock assessments often assume that the available data (e.g., observed catch, abundance indices, size or age composition, etc.) reflect recruitment from within the stock rather than immigration from adjacent stocks, and that mortality of fish after recruitment is from internal processes (fishery removals, predation, etc.) rather than emigration to other areas (Ricker, 1958; Hilborn, 1985). Many integrated stock assessment models and management reference point models often include the additional assumption of a stock-recruitment relationship in which all recruits in a management area are produced by spawning in the same area (Ricker, 1958; Hilborn, 1985).

Considering new information on stock identity and new paradigms

of stock structure is a challenge for stock assessment and fishery management. Application of advanced stock identification technologies commonly reveals that fishery resources are more spatially complex than assumed in conventional stock assessment models, with multiple population components contributing to fisheries and considerable movement among fishery management units (Kritzer and Sale, 2004; Ciannelli et al., 2013; Kritzer and Liu, 2014). Ignoring spatial structure and connectivity among population components in stock assessment can impact the ability to accurately represent population productivity, because violation of the unit stock assumption results in misinterpreting movement among populations as either additional recruitment or losses due to mortality (Goethel et al., 2015b; Berger et al., 2017; Truesdell et al., 2017). Therefore, misrepresenting spatially complex populations in stock assessment can provide misleading information for fishery management (Reiss et al., 2009; Ying et al., 2011; Kerr et al., 2016), but advanced stock assessment models have now been developed to account for many types of spatial structure (Punt et al., 2000; Cadrin and Secor, 2009; Fay and Tuck, 2011; Goethel et al., 2011; Punt, 2017), despite limited application for providing management advice (Berger et al., 2017).

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Although methods exist for performing spatially-structured stock assessments, reliable parameter estimation remains a challenge for complex stock assessment models (Maunder and Punt, 2013; Punt, 2017). Stock assessment models that account for complex population structure require identification of self-sustaining populations (termed stock identification) as well as information on movement or mixed stock composition. Unfortunately, definitive stock identification, stock composition or spatially-explicit data, and information on movement are not available for many fisheries. As a result, data limitations are often the critical impediment to developing and applying spatially structured stock assessment models (Berger et al., 2017). Some simplification is usually needed to represent the major patterns of spatial population structure with the information available. Although not all spatial population structures can be accurately reflected by stock assessment models (e.g., fine-scale sub-population structure), many general and persistent patterns can be accurately modeled (e.g., Goethel et al., 2011).

Simulation testing has proven to be a valuable tool for determining the optimal complexity for stock assessment models (Hilborn and Walters, 1992; Plaganyi et al., 2012; Kerr and Goethel, 2014), and has been used to determine if the added complexity of a spatial assessment improves estimation performance over conventional, spatially-aggregated models. A spatial version of the operating model concept involves a sequential process in which a spatially-complex operating model (or models) is developed to represent plausible population structure and is conditioned by fitting the model(s) to the information available for the fishery of interest. The operating model is then used to simulation test the performance of alternative estimation models (including relatively simple models) by fitting the estimation models to pseudo-data generated from the operating model (Goethel et al., 2016).

Examples of spatial stock structure hypotheses that have been simulation tested to evaluate assessment performance include a single population with spatial fishing patterns (Cope and Punt, 2011), post-recruit dispersal patterns (Punt et al., 2018), ontogenetic movement in a single population (Hulson et al., 2011, 2013; Carruthers et al., 2015; Lee et al., 2017), metapopulation structure (Fay et al., 2011; Ying et al., 2011; Goethel et al., 2015b; Fay and Cadrin, 2016), natal homing (Vincent et al., 2017; Morse et al., 2017b) and spatial structure resulting from marine protected areas (Pincin and Wilberg, 2012; McGilliard et al., 2015). Previous performance evaluations suggest that spatially-explicit stock assessments are relatively robust to alternative hypotheses of spatial population structure and movement patterns (Berger et al., 2017; Punt, 2017). For example, spatially-explicit models can account for isolated population components by estimating negligible movement rates, but spatially aggregated models cannot accurately account for movement (Carruthers et al., 2015; Goethel et al., 2015b). Conversely, spatial models can be hampered by incomplete knowledge regarding critical population dynamics, particularly the parameterization of movement, which can lead to parameter estimates that are equally or more biased than nonspatial models (Porch et al., 1998; Goethel et al., 2015b; Lee et al., 2017).

Although spatially-aggregated stock assessment models can be robust to spatial population structure in some situations (Cao et al., 2014; Benson et al., 2015), bias often remains when interpreting regional recruitment dynamics (Goethel et al., 2015b; Berger et al., 2017). We

explore how assumed spatial population structure in stock assessment models can influence estimates of population productivity through review of applications and simulation tests of spatial assessment models. We summarize the interdisciplinary stock identification for each case study to illustrate how the spatial population structure was determined. We then outline the development of spatially-explicit operating models for each case study and the simulation testing of alternative stock assessment estimation models. These case studies demonstrate a process of testing spatial models that can be implemented for other fisheries and identify common findings for estimating recruitment. Although estimates of recruitment are commonly biased (e.g., National Research Council (NRC, 1998), these biases are often overlooked. Understanding potential sources of bias in estimates of resource productivity is essential for providing accurate scientific advice for harvest strategies and fishery management actions. The purpose of this review is to demonstrate the impact of ignoring spatial population structure on estimates of recruitment and productivity from stock assessment models.

2. Review of case studies

We explore the impact of spatial population structure hypotheses on estimates of recruitment and population productivity by summarizing results from studies that employed a sequential process of identifying plausible population structure, developing spatially-explicit operating models, and simulation testing alternate stock assessment models. We were directly involved in the process of stock identification and model development for the three primary case studies (New England yellowtail flounder, mid-Atlantic black sea bass, and Atlantic bluefin tuna; Section 2.1), with additional support from a literature review of studies that used a similar approach (Pacific bluefin tuna, Bering Sea walleye pollock, and Great Lakes walleye pollock; Section 2.2). These case studies represent a range of population structures, movement patterns, spatial scales and data availability scenarios. Each case study applied the same general approach and analytical design involving:

- 1) an interdisciplinary evaluation of the most plausible geographic stock structure (Table 1);
- 2) development of a spatially-explicit estimation model based on the most plausible spatial structure and available stock assessment data, including ancillary data where available;
- 3) conditioning operating models on either the complex estimation model or perceptions of stock development and exploitation history from accepted stock assessments and ecological knowledge of the resource (Table 2);
- 4) simulation testing of alternative estimation models (Tables 3 and 4).

Our review describes the process of identifying spatial population structure, developing simulation and assessment models that account for spatial dynamics, and how the assumptions of various estimation models impact recruitment estimation. Based on the review, we offer suggestions on how to refine and account for spatial population structure in assessment and management of marine resources.

Table 1

Characteristics of case studies for investigating the impact of spatial population structure on estimates of recruitment.

Case Study	Spatial Scale (km ²)	Population Structure	Movement Pattern	Life Stages of Movement	Reference
Yellowtail Flounder	1 × 10 ⁵	3 subpopulations (1 much smaller)	Dispersal	egg, larval, juveniles & adults	Cadrin, 2010
Black Sea Bass	2 × 10 ⁵	2 subpopulations	< 100% natal homing with overlap	egg, larval, juveniles & adults	NEFSC, 2017b
Atlantic Bluefin Tuna	1 × 10 ⁸	2 populations (1 much smaller)	Natal homing with overlap	juveniles & adults	ICCAT, 2001
Pacific Bluefin Tuna	1 × 10 ⁹	1 population	Ontogenetic with natal homing	juveniles	Bayliff, 1991
Walleye Pollock	1 × 10 ⁶	1 population	Ontogenetic, seasonal	juveniles & adults	Quinn et al., 2011
Walleye	1 × 10 ⁵	2 subpopulations (2 much smaller)	Natal homing with overlap	adults	Stepien et al., 1998

Table 2
Characteristics of operating models from case studies for investigating the impact of spatial population structure on estimates of recruitment.

Case Study	Conditioned on	Recruitment	Spatial Strata	Movement Patterns	Movement Rates	Reference
Yellowtail Flounder	Tag-integrated, multi-stock estimation model	annual deviations from area mean	3	diffusion	constant (~20% per year) or density-dependent (5–65%)	Goethel et al., 2015b
Black Sea Bass	Tag-integrated, multi-area estimation model	annual deviations from a global stock-recruit with area allocations	2	seasonal with natal homing	~10% per half-year	Fay and Cadrin, 2016
Atlantic Bluefin Tuna	Separate area stock assessments and telemetry	estimated time-series	7	seasonal with natal homing	0–90% per quarter-year, by age and area	Kerr et al., 2017b
Pacific Bluefin Tuna	Single-area stock assessment	annual deviations from stock-recruit	2	ontogenetic movement and natal homing	time-varying, 10%–70% per year by age and area, random or oceanographic process	Lee et al., 2017
Walleye Pollock	Spatially-explicit estimation model	annual deviations from area mean	2	seasonal	0–80% by age and area	Hulson et al., 2011
Walleye	Separate area stock assessments and tagging	annual deviations from area stock-recruit	4	seasonal with natal homing	1–20%	Vincent et al., 2017

Table 3
Characteristics of estimation models from case studies for investigating the impact of spatial population structure on estimates of recruitment.

Case Study	Software	Spatial strata	Estimated Movement	Recruitment Estimation	Age of Recruitment	Assessment Data	Ancillary Data	Other Estimated Parameters	Assumed Parameters	Assumed Error	Reference
Yellowtail Flounder	ADMB	3	1) none, 2) constant, 3) time-varying	annual deviations from area mean	1	fishery yield, age composition, multiple survey indices	recent tagging	year-1 abundance at age, R deviations, fishing mortality, selectivity, catchability	natural mortality, maturity at age, size at age, discard mortality	observation & recruitment process	Goethel et al., 2015b
Black Sea Bass	SS	1 or 2	1) none 2) constant	annual deviations from global stock-recruit relationship with 1) no spatial structure or 2) spatial allocations	0	fishery yield, size composition, age at size, multiple survey and fleet indices, tagging	historical tagging	year-1 abundance at age, R deviations, selectivity, retention, catchability	natural mortality, maturity at age, steepness, recruitment variability, discard mortality	observation & recruitment process	Fay and Cadrin, 2016
Atlantic Bluefin Tuna	VPA-2BOX	1	none	reconstruction of cohort abundance from catch by area and assumed natural mortality	1	fishery yield, age composition, multiple survey and fleet indices	none	catchability, oldest age selectivity	natural mortality, catch-at-age, maturity at age, size at age	observation	Morse et al., 2017b
Pacific Bluefin Tuna	SS	1 or 2	1) none 2) constant 3) time-varying	annual deviations from stock-recruit	0	fishery yield, size composition, multiple fleet indices	none	R0, R deviations, fishing mortality, selectivity, catchability	natural mortality, maturity at age, first year fishing mortality, growth parameters, steepness	observation & recruitment process	Lee et al., 2016
Walleye Pollock	ADMB & ITCAAN	1 or 2	constant and age-dependent	annual deviations from area mean	3	fishery yield, age composition, multiple survey and fleet indices	none or tagging	year-1 abundance at age, recruitment deviations, fishing mortality, selectivity, catchability	natural mortality, maturity at age, size at age	observation & recruitment process	Hulson et al., 2011, 2013
Walleye	ITCAAN	4	constant		2		tagging				(continued on next page)

Table 3 (continued)

Case Study	Software	Spatial strata	Estimated Movement	Recruitment Estimation	Age of Recruitment	Assessment Data	Ancillary Data	Other Estimated Parameters	Assumed Parameters	Assumed Error	Reference
				annual deviations from area stock-recruit		fishery yield effort, age composition, survey index		year-1 abundance at age, stock-recruitment parameters and deviations, fishing mortality, selectivity, catchability, natural mortality	maturity at age, size at age	observation & recruitment process	Vincent et al., 2017

Table 4
General results from case studies for investigating the impact of spatial population structure on estimates of recruitment.

Case Study	Model Fit	Sensitivity to Spatial Structure	Sensitivity to Movement	Recruitment Bias	Comments	Reference
Yellowtail Flounder	some residual patterns	high for dominant yearclass and smaller area	high for dominant yearclass and smaller area	biased, particularly for dominant yearclass; better from models with time-varying movement	recruitment and movement estimates were correlated	Goethel et al., 2015a,b
Black Sea Bass	residual patterns in simple model; no major problems in spatially-structured model	high for dominant yearclass	low	biased from estimation without spatial structure		Fay and Cadrin, 2016
Atlantic Bluefin Tuna	some residual patterns	greater for smaller area	high	substantial bias		Morse et al., 2017b
Pacific Bluefin Tuna	no reported problems	moderate	high	biased for mis-specified movement	correlations of movement and selectivity	Lee et al., 2017
Walleye Pollock	no reported problems	low	high	more biased for spatially-aggregated and mis-specified movement		Hulson et al., 2013
Walleye	no reported problems	high	high	biased for greater movement and different sized stocks	performance was worse with spatial patterns in productivity	Vincent et al., 2017

2.1. Primary case studies

2.1.1. New England yellowtail flounder

The yellowtail flounder (*Pleuronectes ferruginea*) resource is managed as three discrete fishing grounds (Cape Cod/Gulf of Maine, Georges Bank, and southern New England/Mid Atlantic) as part of the New England groundfish fishery (Northeast Fisheries Science Center (NEFSC, 2017b). Yellowtail flounder inhabit shallow sandy bottom including offshore banks (Bigelow and Schroeder, 1953). Movement was once considered to be extremely limited, particularly by deep channels, but electronic tagging documented extensive off-bottom behavior and traditional tag recaptures have demonstrated long distance movement (Cadrin and Westwood, 2004; Walsh and Morgan, 2004; Wood and Cadrin, 2013). Georges Bank and the southern New England/Mid Atlantic continental shelf encompass large areas of yellowtail flounder habitat, and the fisheries and estimated stocks in those areas were historically much larger than in the Cape Cod/Gulf of Maine area (Hart and Cadrin, 2004; Northeast Fisheries Science Center (NEFSC, 2017b).

The Cape Cod/Gulf of Maine stock exhibits distinct differences in growth and maturity rates from the other stock units, while the boundary separating the southern New England/Mid Atlantic stock from the Georges Bank stock is based on regional patterns in abundance (Cadrin, 2010). Despite phenotypic and demographic differences, no genetic differences have been found among U.S. stocks of yellowtail flounder. The lack of genetic differentiation is indicative of reproductive mixing, which is supported by tagging studies that have documented some movement across stock boundaries (Wood and Cadrin, 2013).

The three U.S. yellowtail flounder stocks are assessed as independent, unit populations where the assessment models are fit to time series of catch (landings and discards), several fishery-independent trawl survey indices, and age composition of the fishery and surveys (NEFSC, 2017a). In addition to the information used for stock assessment of New England yellowtail flounder stocks, a tagging study released a total of 45,661 yellowtail flounder from 2003 to 2006 with releases in each stock area proportional to survey biomass, and 3,237 tags were recovered from the fishery with known recapture location (Wood and Cadrin, 2013). Concern over extensive cross-boundary movement of yellowtail flounder based on the tagging study as well as poor model diagnostics for the separate stock assessments (e.g., severe retrospective patterns) prompted the development of a spatially-explicit stock assessment model that could account for the assumed metapopulation structure (Goethel et al., 2015a).

An age-based, tag-integrated, multi-population metapopulation assessment model implemented in Automatic Differentiation Model Builder (Fournier et al., 2012) was developed by Goethel et al. (2015a). The model estimated movement among populations by fitting to the combination of tagging and other assessment data. Results of the metapopulation model, which assumed reproductive mixing among populations, were compared with the outputs from the three independent, unit stock assessment models to highlight differences in the estimates of regional recruitment.

The application of the tag-integrated metapopulation model to the available data provided similar estimates of recruitment as the three independent closed-population models, except for one dominant year-class from the southern New England-Mid Atlantic subpopulation in 1987 that appeared to have moved to adjacent areas (Fig. 1). The 1987 year-class was a strong contributor to fisheries and surveys in all three stock areas, but the estimates of the magnitude of this recruitment event were different between closed population models and the metapopulation model. Closed population models estimated the 1987 year-class to be dominant in southern New England-Mid Atlantic and Cape Cod-Gulf of Maine, and moderate on Georges Bank. The metapopulation model estimated the 1987 year-class to be dominant in southern New England-Mid Atlantic, but only moderate in Cape Cod-Gulf of Maine and below average on Georges Bank. Information from tagging,

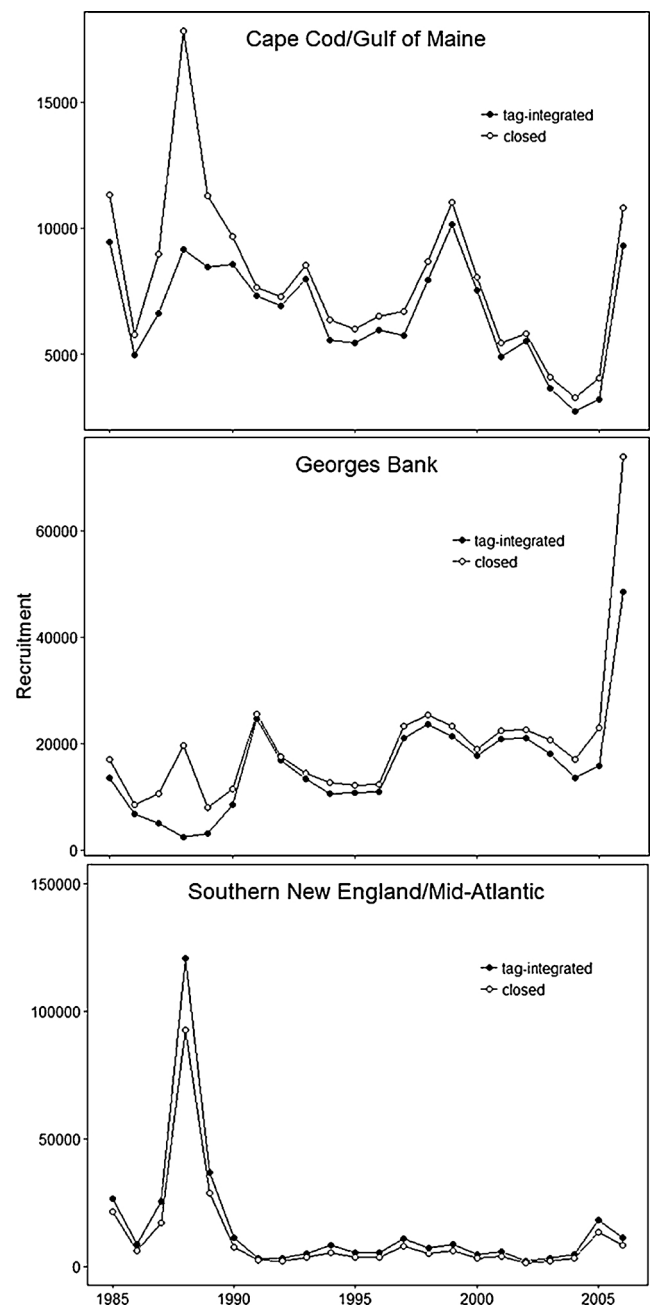


Fig. 1. Recruitment estimates of yellowtail flounder in the Cape Cod-Gulf of Maine (CC), Georges Bank (GB), and Southern New England-Mid-Atlantic (SN) populations from a closed population model (open circles) and a tag-integrated metapopulation model that estimates movement (black solid circles) fit to available data; modified from Goethel, et al. (2015a).

fishery catch, survey trends, and age composition indicated that the 1987 year-class originated from the southern New England-Mid Atlantic stock and moved to other stock areas. The different estimates of recruitment in the Cape Cod-Gulf of Maine stock in the metapopulation model had a large influence on the perceived stock-recruit relationship (and associated biological reference points), because spawning stock biomass for Cape Cod-Gulf of Maine was estimated to be extremely low in 1987 in both models.

Operating models representing different movement parameterizations (e.g., time-invariant and density-dependent time-varying movement) and data uncertainty scenarios were conditioned on the results of the spatially-explicit metapopulation model, with generation of pseudo-datasets representing the available data and possible alternative data

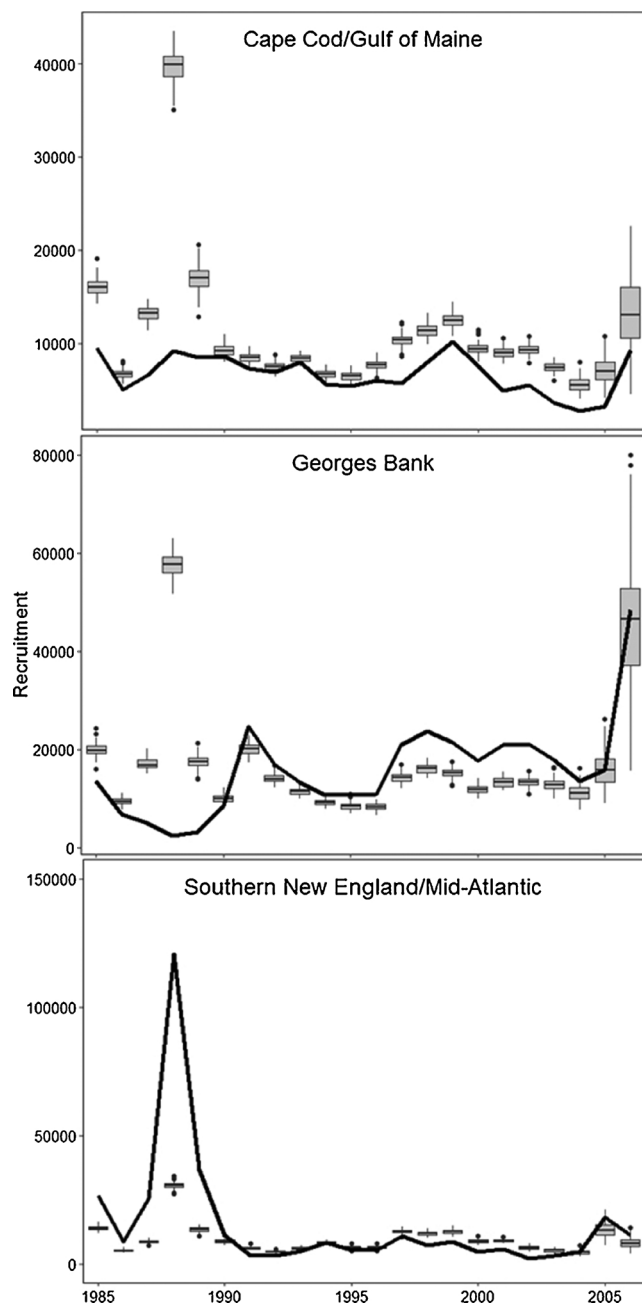


Fig. 2. Time-series of recruitment estimates from a tag-integrated estimation model assuming constant movement of yellowtail flounder in Cape Cod-Gulf of Maine (CC), Georges Bank (GB), and Southern New England-Mid-Atlantic (SN) stocks. True values are from an operating model with time-varying density-dependent movement and indicated by the black line with white dots; modified from Goethel, et al. (2015b).

conditions (Goethel et al., 2015b). The performance of the closed population (i.e., that ignored movement and reproductive mixing) and spatially structured estimation models (including models that differed in approaches for estimating movement, e.g., constant and time-varying) were evaluated by comparing the results of the estimation models to the simulated true dynamics of the operating models.

Simulation testing confirmed that closed-population estimation models estimated recruitment trends well, but many absolute estimates were biased, particularly the simulated dominant year-class (Fig. 2). Without the ability to move fish among areas to fit the observed age composition, the mis-specified closed population model needed to increase recruitment in each of the other areas to account for the

immigration of the dominant southern New England-Mid Atlantic year-class.

Estimates of recruitment from alternative spatial models showed that assumptions about movement among stocks played a strong role in determining the reliability of recruitment estimates (for full details, see Goethel et al., 2015a). Assuming that movement rates were constant over time when movement rates were in fact time-varying in the operating model led to bias in recruitment estimates that was similar in magnitude to that obtained when ignoring connectivity. Results also demonstrated that estimates of recruitment and movement parameters were highly correlated, because the models were able to fit data patterns by either moving fish or creating new recruits. Correctly identifying which mechanism is responsible for population growth is important, because it directly impacts the assumed productivity of the resource and influences perceptions of stock status and management advice relative to reference points. However, even with limited tag-recapture data, spatial models that estimated time-varying movement rates (compared to time-invariant movement) performed well. Despite poorly estimated and imprecise movement parameters in years without tagging data, the models that estimated time-varying movement demonstrated increased robustness to uncertainty in movement dynamics. New England yellowtail flounder populations continue to be assessed as separate unit stocks assuming no mixing (Northeast Fisheries Science Center (NEFSC, 2017a), even though the assumption of closed populations has important implications for potential rebuilding targets (Goethel et al., 2015a).

2.1.2. Black sea bass north of Cape Hatteras

Black sea bass (*Centropomus striata*) is a temperate reef fish distributed from the Gulf of Maine to the Gulf of Mexico, but fish north of Cape Hatteras are managed as a single unit (Northeast Fisheries Science Center (NEFSC, 2017b). Genetic analysis indicates strong differentiation north and south of Cape Hatteras (Roy et al., 2012), with some spatial differentiation between the Mid Atlantic Bight and New England (McCartney et al., 2013). Black sea bass north of Cape Hatteras migrate offshore in autumn and inshore in spring, with some fidelity to inshore summer habitats (Musick and Mercer, 1977; Drohan et al., 2007; Moser and Shepherd, 2009). A multidisciplinary analysis of genetics, tagging, commercial fisheries, trawl surveys, and oceanographic information concluded that the black sea bass stock north of Cape Hatteras includes two spatially-defined components: north and south of Hudson Canyon, and the offshore fishery catches a mixture of fish from both areas in winter (Northeast Fisheries Science Center (NEFSC, 2017b). Tagging data, fishing patterns and survey information suggest that the Hudson Canyon boundary represents a bathymetric, oceanographic and habitat feature that influences the seasonal migration route of fish between inshore, northern areas, and offshore, southern areas (Northeast Fisheries Science Center (NEFSC, 2017b). The Hudson Canyon boundary is also consistent with spatial patterns in genetic variation (McCartney et al., 2013).

A spatial- and age-structured stock assessment model was developed for the northern stock of black sea bass. The model, implemented in Stock Synthesis (Methot and Wetzel, 2013), was fit to available fishery (length composition) and survey data (abundance indices, length composition, and age-at-length composition), as well as tag recapture data (Fay et al., 2016; Northeast Fisheries Science Center (NEFSC, 2017b). The model assumed a single population with spatial heterogeneity (north and south of Hudson Canyon) in recruitment, growth, and fishing fleets. Seasonal movement of northern fish between northern and southern areas was modeled to represent offshore mixing during the winter, resulting in availability of both northern and southern fish to fishing fleets and surveys in the southern area during this period. Seasonal movement rates were assumed constant for all years and ages. The proportion of recruits to each area was estimated to vary over time.

The tag-integrated Stock Synthesis model fit available fishery,

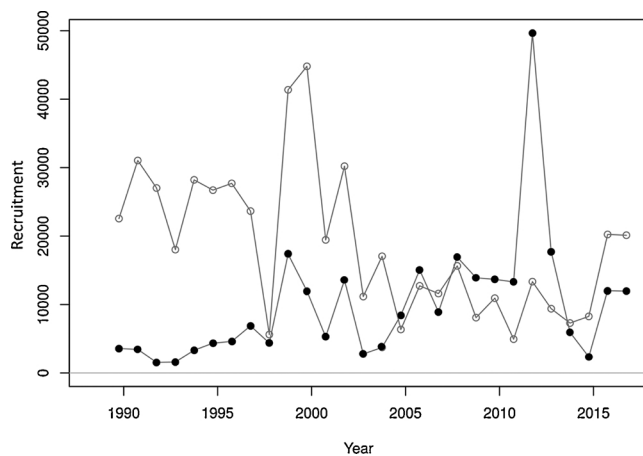


Fig. 3. Estimates of regional recruitment of black sea bass north of Cape Hatteras fit to available data, with regional recruitment estimates north of Hudson Canyon (solid black circles) and south of Hudson Canyon (open circles); modified from Fay et al. (2016).

survey, and tagging data relatively well. By comparison, the spatially-aggregated assessment of the entire resource north of Cape Hatteras could not fit conflicting trends between indices for northern and southern regions, which resulted in strong temporal patterns in index residuals (Northeast Fisheries Science Center (NEFSC, 2017b)). Estimates from spatial models suggest the stock has recently increased, largely due to a strong year-class in 2011 (Fig. 3). However, recruitment trends were different north and south of Hudson Canyon, with an increasing proportion (and number) of the annual recruits to the northern region over time. For example, most recruitment was from the southern area in the early period (1989–2004), but approximately 75% of the strong 2011 year-class was estimated as recruiting from the region north of Hudson Canyon (Fay et al., 2016). Movement rates were estimated to be approximately 10% for each six-month period.

An operating model was conditioned on the spatially complex estimation model to produce pseudo-datasets that were characteristic of the information available for assessment, and alternative stock assessment estimation model configurations were fit to the pseudo-datasets (Fay and Cadrin, 2016; Northeast Fisheries Science Center (NEFSC, 2017b)). The estimation models included a nonspatial single stock ('1 area') model that did not assume spatial structure in population dynamics (but retained disaggregation in data sources), regional structure with no movement ('no move'), and regional structure with movement ('2 area'). The estimation models with regional structure included the same specification for the seasonal and spatial structure.

Simulation testing suggested that the single-stock model with no spatial structure ('1 area') did not perform well for estimating the magnitude of the strong 2011 year class (i.e., combined recruitment, north and south of Hudson Canyon), because the distribution of estimates over simulations did not overlap the true value from the operating model, and median relative bias was -20% (Fig. 5). By comparison, the '2-area' estimation model, with regional structure and seasonal movement, performed better than simpler alternatives, but the regionally structured model that assumed no movement ('no move') performed almost as well as the correctly specified model. Estimates of 2011 recruitment from both spatially structured models ('2 area' and 'no move') overlapped the true value from the operating model, and median relative bias was < 10% (Fig. 4). The simulation results suggest that accurate recruitment estimation required a spatially-structured stock assessment. By comparison, accounting for seasonal movement and mixing during the offshore winter season was less important for recruitment estimation.

Based on results from simulation testing, the benchmark assessment method used as the basis for scientific advice to manage black sea bass

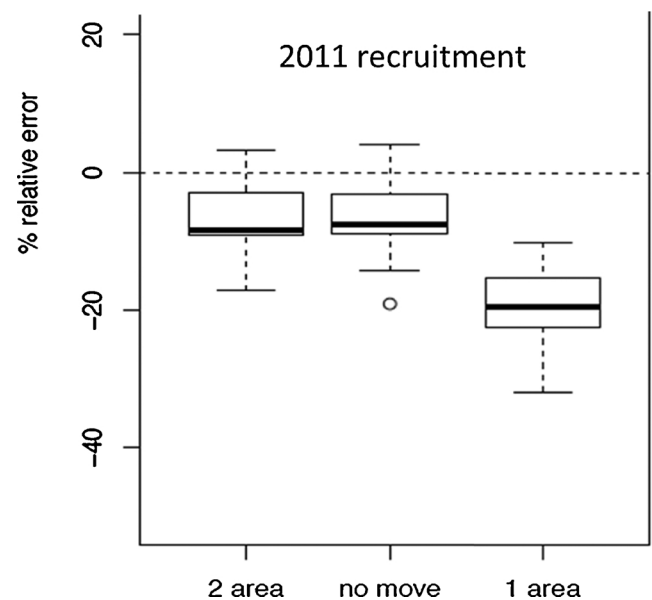


Fig. 4. Distribution for the percent relative error of 2011 yearclass abundance estimates for black sea bass north of Cape Hatteras fit to pseudo-data generated from the 2 area operating model. '2 area' is the self-test with the estimation model equivalent to the operating model, 'no move' is the 2 area estimation model but with no movement between the north and south areas. The estimation model '1 area' is a single area model, but with fleets and seasons modeled separately. Modified from Fay and Cadrin (2016).

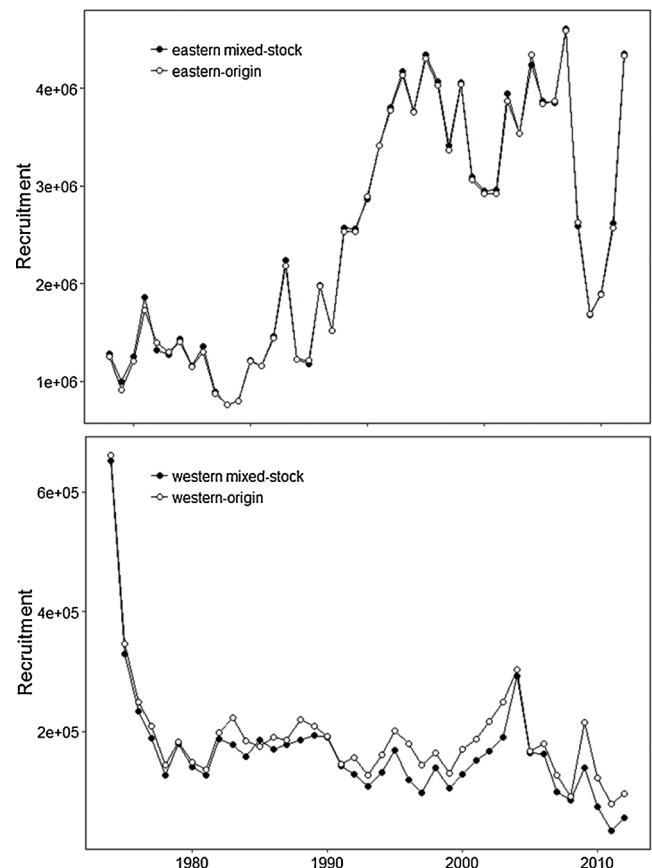


Fig. 5. Estimates of Atlantic bluefin tuna recruitment from the ICCAT (2017) VPA of eastern Atlantic (top) and western Atlantic (bottom) Atlantic mixed-stock fisheries, separated at 45° Longitude, and the VPA of eastern-origin (top) and western-origin (bottom) Atlantic bluefin tuna fit to available data, modified from Morse et al. (2017a).

fisheries now involves separate statistical catch-at-age models for north and south of Hudson Canyon (NEFSC 2017b). Similar to the tag-integrated Stock Synthesis model, the benchmark stock assessment estimates that most recruitment was from the south in the early years, but the strong 2011 year-class was dominated by fish in the north. The new information on regional abundance provided by the spatially-structured stock assessment prompted the Atlantic States Marine Fisheries Commission to implement regional allocation of fishery catch limits (Atlantic States Marine Fisheries Commission (ASMFC, 2017).

2.1.3. Atlantic Bluefin Tuna

Atlantic bluefin tuna (*Thunnus thynnus*) is a highly migratory species that is distributed across the North Atlantic Ocean and Mediterranean Sea. Atlantic bluefin tuna fisheries are assessed and managed by the International Commission for the Conservation of Atlantic Tunas (ICCAT) as two separate stocks, east and west of 45 °W longitude (International Commission for the Conservation of Atlantic Tunas (ICCAT, 2017). Information from genetics, tagging, otolith chemistry, and other chemical tracers have identified two spawning populations, one in the Mediterranean Sea and the other in the Gulf of Mexico, that overlap extensively in the North Atlantic Ocean to feed outside of the spawning season (International Commission for the Conservation of Atlantic Tunas (ICCAT, 2001; Carlsson et al., 2007; Boustany et al., 2008; Rooker et al., 2008a, 2008b; Dickhut et al., 2009). Spawning may also occur in the Slope Sea (Richardson et al., 2016), and there may be separate eastern and western Mediterranean populations (Carlsson et al., 2004).

Atlantic bluefin tuna were initially assessed and managed as a single stock, but recognition of stock structure led to separate assessments of eastern and western Atlantic fisheries since 1982 (Porch et al., 1998). The current stock assessment is based on separate stock assessments of eastern and western Atlantic fisheries (International Commission for the Conservation of Atlantic Tunas (ICCAT, 2017), which estimate that the western stock is much smaller than the eastern stock.

Porch et al. (2001) developed the VPA-2BOX model, which is a tag-integrated and calibrated Virtual Population Analysis of two populations. The initial version of VPA-2BOX and other analyses of Atlantic bluefin tuna applied Beverton and Holt's (1957) box-transfer model to account for movement of tuna between eastern and western Atlantic areas (Butterworth and Punt, 1994; National Research Council (NRC, 1994; Porch, 1995). However, this form of movement assumes that fish from one area move to another and spawn there, which does not conform to the population structure paradigm for Atlantic bluefin tuna. An alternative form of mixing termed 'overlap' assumes that bluefin from one area move to another but return to their natal area to spawn (Porch, 2001). The 2-stock 'overlap' model was applied to Atlantic bluefin tuna for several years but is not the primary basis for management advice.

More recently, the multi-stock age-structured tag-integrated (MAST) assessment model was developed to account for natal homing dynamics and overlap of fish from two spawning populations in five geographic areas within a statistical catch-at-age framework. An alternative assessment approach was also developed to account for annual estimates of stock composition that were used to partition mixed-fishery catch-at-age and relative abundance indices into derived data sets representing population of origin (Morse et al., 2017a; International Commission for the Conservation of Atlantic Tunas (ICCAT, 2017). Closed population stock assessments of eastern-origin and western-origin fish were then run with these updated data and compared to the original assessments of mixed-stock fisheries in the eastern and western Atlantic to evaluate the sensitivity of results to stock mixing.

Several simulation experiments have been developed to explore the performance of various assessment approaches and population structure assumptions. Porch et al. (1998) utilized an advection-diffusion movement model to simulate population dynamics of the two populations of bluefin and applied two population VPA models to the simulated data that assumed either closed populations or estimated

movement. More recently, a spatially-explicit operating model was conditioned on the MAST model that assumed natal homing (i.e., populations could overlap in space, but did not reproductively mix; Taylor et al., 2011; Kerr et al., 2017a).

Estimates of recruitment from the VPAs that accounted for natal origin (population of origin) were generally similar to the ICCAT assessment estimates based on eastern and western Atlantic mixed-stock fisheries (Fig. 5). However, estimates of western recruitment were more sensitive to the assumption of no stock mixing than estimates of eastern recruitment, suggesting that stock mixing with the smaller western stock does not have much influence on population dynamics of the larger eastern stock. Estimates of western recruitment were also nearly identical for early years of the assessment time series but were considerably different for most year-classes since 1983. These results reflect the assumed stock composition in early years and sufficient information for annual stock composition in recent years. These results contributed to the determination of stock status by showing that general trends and magnitude of population-of-origin estimates were similar to mixed-stock assessments (International Commission for the Conservation of Atlantic Tunas (ICCAT, 2017).

After finding that estimates of recruitment and fishing mortality were relatively robust to stock mixing (Morse et al., 2017a; International Commission for the Conservation of Atlantic Tunas (ICCAT, 2017), the operating model was revised to reflect estimates of recruitment and fishing mortality from ICCAT assessments (International Commission for the Conservation of Atlantic Tunas (ICCAT, 2014) as well as fishery-independent estimates of movement from telemetry (Galuardi et al., 2017) to represent current perceptions of stock dynamics, exploitation history, and seasonal movement (Kerr et al., 2017b). Pseudo-data with lognormal observation error were generated from the operating model with the patterns, quantity, and quality of data available for the 2014 stock assessment of Atlantic bluefin tuna (ICCAT, 2014). Separate assessments of eastern and western fisheries (similar to those applied to Atlantic bluefin tuna by ICCAT since 1982) were applied to the generated pseudo-data using VPA-2BOX (Porch et al., 2001) as the estimation model, and model performance was assessed based on the accuracy, precision, and bias of VPA-2BOX outputs relative to the operating model (Morse et al., 2017b).

Simulation analyses suggested that models with and without mixing estimated recruitment trends well, but estimation models that included mixing performed better than separate assessments of each area when relatively high movement rates were simulated (Porch et al., 1998). Simulation testing from the operating model with mixing suggests that recruitment estimates are sensitive to spatial model structure, particularly for the smaller western stock component (Fig. 6). The mis-specified VPA-2BOX estimation model without movement tends to overestimate the magnitude of many western year-classes. The results suggest that separate stock assessments of eastern and western fisheries reflect general trends, but that absolute estimates of recruitment are biased and may provide misleading perceptions of the western population, because productivity of the western population is overestimated from subsidies of eastern-origin fish. ICCAT is currently developing a Management Strategy Evaluation using spatially explicit operating models to determine management procedures that may be robust to such uncertainties (Kell et al., 2012; Carruthers and Butterworth, 2018).

2.2. Other case studies

2.2.1. Pacific Bluefin Tuna

Pacific bluefin tuna (*Thunnus orientalis*) is a highly migratory species that is considered to be a single population, distributed across the North Pacific Ocean (Sund et al., 1981), but spatial heterogeneity within the stock is recognized. A synthesis of information from reproductive biology, ichthyoplankton, fishing patterns, demographics, and tagging supports a population paradigm for Pacific bluefin tuna in which

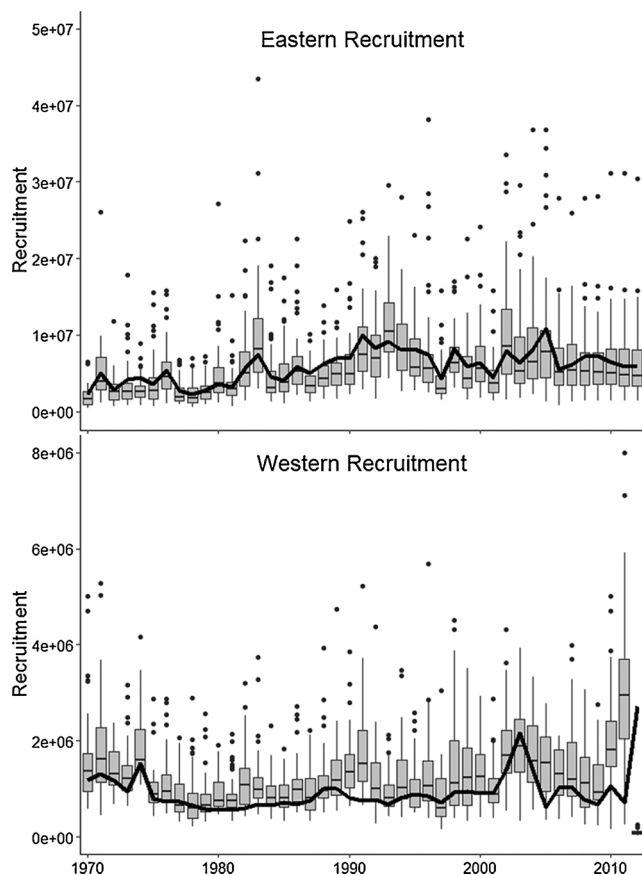


Fig. 6. Atlantic bluefin tuna recruitment series from a spatially-explicit operating model (black lines) to results of VPAs of pseudodata with measurement error (box plots) for eastern (top) and western (bottom) Atlantic bluefin tuna, modified from Morse et al. (2017b).

spawning occurs in spring and summer in the western Pacific Ocean, the larvae, postlarvae, and juveniles are transported northward by the Kuroshio Current toward Japan, some juveniles remain in the western Pacific Ocean and others migrate to the eastern Pacific to feed during their first two years of life, then return to the western Pacific to spawn (Bayliff et al., 1991; Bayliff, 1994). There are multiple nursery grounds in the western Pacific (Rooker et al., 2001), juveniles can cross the north Pacific in one season (Itoh et al., 2003), and decadal variation in ontogenetic trans-Pacific migrations may be associated with temperature, prey and maturation (Polovina, 1996).

In recognition of this perception of a single population in the North Pacific, Pacific bluefin are assessed as single stock and managed by two international organizations, the Inter-American Tropical Tuna Commission (IATTC) and the Western and Central Pacific Fisheries Commission (WCPFC). The integrated, age-structured stock assessment implemented in Stock Synthesis has fleet structure, but no explicit spatial structure because movement rates are uncertain (ISC, 2014). The stock assessment model is fit to catch, catch rate and size composition data from fourteen fisheries. The most recent stock assessment could not identify a model that fit all available data and recommended further model development (ISC, 2014).

Lee et al. (2017) emulated the Pacific bluefin tuna population structure paradigm with an operating model in which a variable proportion of juveniles migrate from the western Pacific Ocean to the Eastern Pacific Ocean where they reside for up to four years, then return to the western Pacific Ocean prior to spawning and remain there. The operating model was conditioned to reflect the general stock development and exploitation pattern from the spatially-aggregated stock assessment (ISC, 2014) but included spatial structure (eastern and

western Pacific), recruitment in the western Pacific Ocean, and movement of some juveniles to the eastern Pacific. A variety of movement scenarios were assumed, including time-varying random movement and movement associated with the Pacific Decadal Oscillation (as hypothesized by Polovina, 1996). A wide range of estimation models (including fleets-as-areas, two-area, constant movement, and time-varying movement) were fit to pseudo-data generated from operating models.

Results indicated that estimation models with mis-specified spatial dynamics produced biased and imprecise estimates of abundance but estimates from correctly specified estimation models were unbiased and more precise. For this system of spatial structure and movement, approximating spatial structure and movement by modeling fleets-as-areas performed better than estimation models with spatial structure and constant movement rates. Lee et al. (2017) conclude that the stock assessment of Pacific Bluefin could be improved by investing in well-designed studies to inform movement in a spatially-structured estimation model.

2.2.2. Walleye Pollock in the Eastern Bering Sea

Walleye pollock (*Theragra chalcogramma*) is a semipelagic schooling fish widely distributed in the North Pacific with the highest concentrations in the eastern Bering Sea supporting one of the world's largest fisheries (Hulson et al., 2011). Interdisciplinary syntheses of information on genetics, ichthyoplankton, spatio-temporal fishing patterns and resource surveys concluded pollock in the Bering Sea and the Gulf of Alaska are separate genetic populations, but there is some spatial structure within the Bering Sea (Bailey et al., 1999; Quinn et al., 2011). The conceptual model includes winter spawning from three areas of the eastern Bering Sea (Hinckley, 1987), advection of eggs and larvae producing a spatial distribution of one-year old pollock, and regular spatial distributions by season that reflect seasonal movement between northwest and southeast areas of the Bering Sea (Quinn et al., 2011).

The stock assessment of walleye pollock in the Eastern Bering Sea is based on an integrated age-structured assessment model implemented in Automatic Differentiation Model Builder (Ianelli et al., 2017). The stock assessment model is fit to fishery catch, catch rate and age composition data as well as fishery-independent indices. The stock assessment has no explicit spatial structure and models the fishery as a single fleet. However, the fishery is managed as two seasonal components: one from January to April primarily in the southeast region that produces highly valued roe, and another from June to November with some area restrictions. The stock assessment model has considerable retrospective inconsistencies that may result from movement patterns (Quinn et al., 2011).

Miller et al. (2008) developed a spatial assessment model that was consistent with the paradigm of population structure, assuming a single population of walleye with seasonal age-specific movement between the northwestern and southeastern eastern Bering Sea. The spatially-structured assessment produced abundance estimates that were similar to those from the spatially-aggregated stock assessment, but some parameters were not well estimated, and tagging data was recommended. Hulson et al. (2011) then developed an operating model that mimicked these dynamics using parameters from the applied spatial assessment. The model was further extended to include climate-driven recruitment and movement patterns in the operating model (Hulson et al., 2013). These two simulation-estimation frameworks then compared the estimation performance of spatially-aggregated and spatially-structured estimation models.

Estimates from models with and without tagging data were unbiased, but precision was greater with tagging data (Hulson et al., 2011). When climate impacts were simulated the biased estimates from spatially-aggregated estimation models were attributed to unaccounted for process errors, and estimation models that mis-specified ontogenetic movement were also biased. A review of the spatial modeling

recommended the continued development of seasonally and spatially disaggregated models for Eastern Bering Sea walleye pollock and concluded that tagging data would be valuable for estimating movement and spatial structure.

2.2.3. Walleye in Lake Erie

Walleye (*Sander vitreus*) is a freshwater predatory fish that supports commercial and recreational fisheries in North America (Scott and Crossman, 1998) and is a relatively ‘population rich species’ that has distinct genetic variation among areas (Sinclair, 1988; Haponski and Stepien, 2014). Lake Erie has distinct subpopulations of walleye in the western, central, and eastern basins, with more abundant subpopulations in shallower basins, and a moderately abundant population in Lake Huron (McParland et al., 1999; Brenden et al., 2015). After spawning in early spring, walleye move throughout both lakes but return to natal spawning grounds (Stepien and Faber, 1998).

Walleye in Lake Erie Basins and Lake Huron are separately assessed (Vincent et al., 2017) and managed independently in each jurisdiction (Wills et al., 2018). Separate statistical catch at age models are used to model walleye populations in west-central Lake Erie (Wills et al., 2018), east basin of Lake Erie (although it is considered a mixed stock, Zhao et al., 2011), and Lake Huron (Fielder and Bence, 2014). The stock assessment models are fit to fishery catch, fishing effort, and age composition data as well as fishery independent survey indices. Berger et al. (2012) developed a spatially-implicit fleets-as-areas model to account for observed spatial structure without the need to account for unknown movement rates. Using spatially-referenced parameters provided a statistically better fit to several data sources and led to decreased estimates of abundance and greatly increased fishing mortality rates, which indicated that spatial dynamics and population structure assumptions of the single population assessment model used for management needed to be more closely examined (Berger et al., 2012).

Vincent et al. (2017) conditioned an operating model on stock assessments of each subpopulation and simulated a range of movement rates and productivities among subpopulations to test a range of alternative tag-integrated estimation models. Simulations assuming the four populations with natal homing indicated that the more complicated spatial models (i.e., those with spatial variation in natural mortality) had less accuracy and precision in recruitment estimates, particularly from scenarios with fewer tag releases. Bias also increased when the simulated movement rates were greater and when productivities varied among subpopulations. Spatially-complex estimation models performed better for similarly sized populations than simpler models (i.e., with constant natural mortality among areas). The Great Lakes Fishery Commission is currently in the process of exploring the extent to which lake-wide assessment programs could be combined across jurisdictions to improve stock assessment and fishery management (Wills et al., 2018).

3. Discussion

Results from these case studies and others (e.g., Ying et al., 2011; Pincin and Wilberg, 2012; Carruthers et al., 2015; Li et al., 2015, 2018; McGilliard et al., 2015; Punt et al., 2015, 2016, 2018) demonstrate that the spatial structure assumed in a stock assessment model influences the estimation of recruitment and that accounting for the most plausible stock structure can improve the accuracy of recruitment estimates. These results demonstrate the importance of determining biological population structure and adequately representing that structure in estimation models. However, the unit stock assumption can be a useful model simplification of more complex dynamics and can improve tractability of parameter estimation in stock assessment models (Goethel et al., 2016). For some situations, the fleets-as-areas approach also performs well for informing fishery management despite biased estimates of recruitment (e.g., Lee et al., 2016; Punt, 2017).

Conclusions from simulation testing depend on the plausibility of

the operating models, which imposes a challenge for spatially complex fisheries and resources (Kerr and Goethel, 2014). Testing the performance of estimation models using operating models that do not accurately represent population structure may be misleading. The approach developed by Goethel et al. (2016) can determine the consequences of a new paradigm before initiating the transition costs of a new assessment-management framework. The approach attempts to answer the question, “If the new paradigm of stock structure is true, how does the current assessment approach perform relative to alternatives?” Although the case studies we reviewed were tailored to answer that question for each fishery, some common results may be general features of spatially structured populations. For example, sensitivity of recruitment estimates in smaller stocks to mixing with a larger stock was a common feature in case studies (e.g. Cape Cod-Gulf of Maine yellowtail flounder and western Atlantic Bluefin tuna). Taylor and Woilwod (1982) found greater relative variability of the size of smaller subpopulations in metapopulations of insects and birds, and similar results were found in metapopulations of fishes (Anderson et al., 2012). Similarly, Vincent et al. (2017) demonstrated that estimates of recruitment and other population parameters for less productive populations tended to be more biased in the Lake Erie walleye simulations. Assessment model estimates for relatively abundant year-classes may demonstrate similar bias in spatial models, as illustrated by the 1987 year-class of yellowtail flounder and the 2011 year-class of black sea bass, because the models have difficulty deciphering the signals in the age composition data as either movement or recruitment. The rapid advancement and application of stock identification studies is expected to continue with the development of new technologies and methodologies (Cadrin et al., 2014). Therefore, we expect that new information on spatial population structure will continue to emerge for consideration in many stock assessments. These results demonstrate that spatial modeling and simulation testing are valuable tools for strategic decision making in the context of new information on stock structure.

Simulation testing is well suited to help determine the most important complexities that are needed to develop assessments that meet the needs of fisheries management (Kerr and Goethel, 2014; Goethel et al., 2016). The most complex spatial models were not always necessary. When estimation models had accurate spatial structure, and movement rates were relatively low, accounting for movement or mixing did not always improve estimates (e.g., Fay and Cadrin, 2016), except during strong recruitment events or for the smaller of connected subpopulations (e.g., Goethel et al., 2015b). Conversely, when spatial structure was ignored and a spatially-aggregated model applied when spatial structure was in fact present (e.g., the ‘1 area’ black sea bass model), assessment bias increased substantially (e.g., Fay and Cadrin, 2016). Bias in assessment outputs associated with this mis-specification may lead to inappropriate management advice (e.g., Ying et al., 2011; Kerr et al., 2014; McGilliard et al., 2015).

Similar to our conclusions about assumed stock structure, accounting for connectivity among population units can also improve model estimates and management advice (Goethel et al., 2015b; Punt, 2017). However, inappropriate parameterization of movement dynamics can be as detrimental as ignoring movement (Goethel et al., 2015b; Lee et al., 2017). The data signals provided by movement and recruitment are closely intertwined, because they both can lead to apparent increases (immigration or strong year-classes, respectively) or decreases (emigration or weak year-classes, respectively) in relative abundance of a given age class and can also be correlated with mortality (Berger et al., 2017). Disentangling recruitment and movement events is difficult, so spatial models may need to emulate multiple plausible movement scenarios. When there is a paucity of data available on movement patterns or to inform movement rates (e.g., tag-recapture information), spatially implicit models (e.g., areas-as-fleets models) or multiple closed-population stock assessments (i.e., that model unit stocks within areas) may perform reasonably well (e.g., Punt et al., 2015; Lee et al., 2017). However, Carruthers et al. (2015) found that

movement rates can sometimes be well estimated from limited data (e.g., age composition and abundance indices) and despite the potential for overparameterization, freely estimating movement parameters (e.g., annual or age-specific instead of time- and age-invariant) can lead to less biased population estimates even though movement estimates may be imprecise (Goethel et al., 2015b; McGilliard et al., 2015; Punt, 2017).

Stock assessments cannot account for all complexities in fisheries and fish populations, and simplifications are needed to support parameter estimation with the information available. The case studies we reviewed demonstrate that simulation testing is a useful tool for considering how new information on stock structure or new paradigms of stock identity can be considered in stock assessment and fishery management. Transition costs, management constraints (e.g., catch allocations), or data limitations limit the ability of stock assessment and fishery management processes to adapt to new information (Kerr et al., 2016). Recognizing that such strategic changes need to be justified, simulation testing provides an evaluation of the implications of assumed spatial structure on stock assessment results (Kerr and Goethel, 2014). Compelling evidence of spatial structure may not be sufficient to justify a paradigm-shift in stock assessment methods or management strategy. However, if status-quo assessment methods do not perform as well as spatially-structured models when fit to representative pseudo-data from a spatially structured operating model, revising the assumed spatial structure of the stock assessment method may be justified.

These case studies demonstrate that simulation testing can be valuable within an iterative stock assessment process, and the role of simulation in analytical decision making should be considered in model specifications. Results from simulation testing are typically used to make major model decisions (e.g., spatial model structure), but the process is iterative and time consuming. As a result, the final stock assessment model usually has some differences from the estimation models used in simulation testing. For example, simulation results for Atlantic Bluefin tuna were presented at the 2017 benchmark assessment meeting, but simulations were conditioned on the 2014 stock assessment results, and estimation models were based on the most recent refinements that were decided before the stock assessment meeting rather than the final accepted base run that was completed after the benchmark assessment meeting. Similarly, the yellowtail flounder and black sea bass simulations were based on different estimation models than the stock assessments that were used for fishery management advice. This practical aspect of simulation testing can be accommodated if operating models and estimation models are conditioned to represent the general exploitation history, stock development and available information for the population of inference so that the results are applicable to similar estimation models. Berger et al. (2017) recommended an open dialogue among assessment scientists, field samplers, ecologists and stakeholders about feasibility of various spatial model types. Effective communication and engagement with and between stock assessment scientists, simulation analysts, and decision-makers is paramount at the design stage to help fishery managers and stakeholders view the value of complementary analyses, rather than viewing alternative assessment models as competing methodologies.

The usefulness of a spatial model depends on the assessment-management framework that it is applied to (Berger et al., 2017). Even if spatial heterogeneity is present in resource distribution or fishing effort, broad-scale management advice may be adequate and spatially aggregated models sufficient (Punt et al., 2015; Li et al., 2015; Punt et al., 2017). However, if spatial management is desired (or mandated), then developing assessment models that can provide results as close to the scale of management as possible while also representing the spatial population structure is desirable (Cadrin and Secor, 2009; Kerr et al., 2016; Berger et al., 2017). Under such circumstances, spatially-explicit models tend to provide the most robust management advice, but care must be taken when determining the spatial scale of the model and the parameterization of movement dynamics (Ying et al., 2011; Goethel

et al., 2015b). Although movement models and non-movement models may produce similar results, even slight differences in estimates of stock-recruit parameters, underlying population structure assumptions, or movement parameterization can affect estimates of sustainable harvest levels and potential rebuilding targets (Goethel and Berger, 2017). Therefore, careful consideration must be taken when choosing the underlying spatial population structure of an assessment model. Even if assessment model outputs do not differ widely among underlying population structure assumptions, the chosen population dynamics may lead to different advice for fishery management if assumptions are carried through to management reference point models (Wilberg et al., 2008; Ying et al., 2011; Carruthers et al., 2015; Goethel and Berger, 2017). Ideally, Management Strategy Evaluation would be implemented to determine the model complexity necessary to achieve management goals, and the data that would be required to support these analyses (e.g., Li et al., 2015; Punt et al., 2017).

4. Conclusions

Results from the case studies we reviewed indicate that recognizing population structure, either in management unit definitions or estimation model structure, improves estimation of recruitment. Recruitment estimates for the smaller of multiple connected population components were more sensitive to connectivity (e.g., western Atlantic bluefin tuna and Cape Cod-Gulf of Maine yellowtail flounder). Movement rates can be estimated from high quality catch and survey data, especially for the movement of strong year-classes, as demonstrated for the 1987 year-class of yellowtail flounder and the 2011 year-class of black sea bass. However, estimating movement with spotty ancillary data provided limited improvement in the performance of estimation models when assessments were performed on essentially self-sustaining units (yellowtail flounder and black sea bass). The challenges of accounting for spatial structure and movement in stock assessment models often justify the delineation of self-sustaining stocks whenever possible.

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