Chapter 22
Accounting for Spatial Population Structure in Stock Assessment: Past, Present, and Future*

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Abstract Stock identification has been an important prerequisite for stock assessment throughout its history. The earliest evaluations of recruitment variability recognized that understanding the spatial scale of a fishery resource is essential for studying population dynamics. A paradigm of stock structure was based on closed migration circuits and geographic variation of phenotypic traits and formed a premise for fishery modeling conventions in the mid-1900s. As genetic techniques developed in the late 1900s, the "stock concept" was refined to include a degree of reproductive isolation. Realization that there was no single method that addressed the various assumptions of stock assessment and needs of fishery management prompted a more holistic view of population structure that called for multiple sources of demographic and genetic data. Recent applications of advanced techniques challenge the traditional view of populations as geographically distinct units with homogeneous vital rates and isolation from adjacent resources. More complex concepts such as metapopulations and "contingent theory" may be more applicable to many fishery resources with sympatric population structure. These more complex patterns of population structure have been incorporated into some advanced stock assessment techniques and metapopulation models that account for movement among areas and sympatric heterogeneity. Wider application of spatially explicit models in future stock assessments will require clear identification of stock components, evaluating movement rates and determining the degree

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of reproductive isolation. Because spatial structure affects how populations respond to fisheries, incorporation of heterogeneous patterns and movement in stock assessment models should improve advice for fishery management.

Keywords Mixed-stock fisheries · migration · spatial heterogeneity · stock assessment · stock identification

> "The theory of exploitation of homogeneous stocks of a fish species has had considerable attention in recent years"
>
> W.E. Ricker (1958)

22.1 Introduction

Stock assessment of fishery resources is an exercise in simplification of complex population processes and patterns of variation (Hilborn and Walters 1992; Quinn and Deriso 1999). Even the most elaborate population models are gross abstractions that hopefully retain the general properties of the population while avoiding many subtle complications. Stock assessment modeling can be viewed as a progression of increasing demographic complexity, with successive extensions incorporating information on size, age, gender, and maturity. Despite some compelling demonstrations of the importance of spatial structure for population dynamics (e.g., Ricker 1958; Sinclair 1988; MacCall 1990; NRC 1994), spatial aspects of demographic structure have been relatively ignored.

The history of stock identification of fishery resources is marked with technological milestones that represent advances in methodologies, providing new perspectives on what defines a "stock" and revised concepts of stock structure (Cadrin et al. 2005). However, depicting the historical development of population structure concepts as an overly simplistic beginning and a gradual modification to more and more complex views would be a revisionist history. A more accurate review would recognize that recent advocacy for more complex views of population structure revive concepts from some of the earliest research on the subject (Secor 2005). Similarly, some of the pioneering work on stock assessment modeling explicitly considered spatial structure. For example, spatial variation of parameter values and movement of fish are two "extensions of the simple theory of fishing" offered by Beverton and Holt (1957).

We review the historical development, state of the art, and future considerations of population structure in the context of stock assessment modeling. This summary is neither a comprehensive history of stock identification research nor a complete review of spatial models for other applications like general ecology or conservation biology. Our objectives are to describe the mutual relationship between the disciplines of stock assessment and stock identification by presenting their parallel histories and to discuss the research needed to advance spatial aspects of population modeling.

22.2 The Past: Coevolution of Stock Assessment and Stock Identification

A convenient and common starting point for a retrospective review of population structure is the late nineteenth century, when the Platonic paradigm of typology was being replaced with a more dynamic view of populations and greater appreciation of variability among populations (Lebedev 1969; Sinclair 1988; Sinclair and Smith 2002). The typological concept emphasized homogeneity, so much so that populations were represented by a single "type specimen," and variability within populations was considered developmental noise that obscured perceptions of the underlying type (Mayr 1982). In the context of population genetics, homogeneity is associated with panmixia (i.e., random mating of individuals within a population). Although such essentialist views of natural populations have been largely abandoned, vestiges of typology persist in the form of parametric statistics (Gould 1981), which describe populations using simple means and test for differences among populations by comparing differences in group means in the context of variability within groups (e.g., Fisher 1932). Similar vestiges of typology also pervade stock assessment modeling despite the advancement of stochastic methods.

Population structure was a central theme in the overfishing debate at the turn of the twentieth century (Smith 1994). Homogeneity and panmixia are often inferred as a corollary of the nineteenth-century perceptions that some abundant fishery resources were "inexhaustible" (Huxley 1882) and not vulnerable to local depletions. The "migration theory" explained local fluctuation in fishery yields as the result of large-scale movements of a single, expansive population of each species. However, the migration theory and the implicit panmictic view of fish populations were not consistent with the distinct patterns of geographic variation in morphology among local groups of Atlantic herring observed by Heinke (1898; reviewed by Sinclair, 1988). Early explorations of phenotypic variation eventually refuted the single-population migration theory, and supported the recognition of population structure and local recruitment patterns for explaining local fluctuations in fishery resources (Smith 1988, 1994). Sinclair and Smith (2002) describe the notion of fish stocks as a component of the paradigm shift from "migration thinking" to "population thinking."

Just as the overfishing debate formed a view of population structure of fishery resources in the northeast Atlantic, a coincident scientific debate over the "parent stream theory" of Pacific salmon was a significant development for understanding stock structure and had many common elements (Secor 2005): a premier biologist described migration patterns as random dispersion (Jordan 1905), but a field-oriented fishery scientist observed local phenotypic variation and natal homing (Gilbert 1914) that challenged this Pacific version of the migration theory. Unlike the coastal fishery resources in the eastern Atlantic, that could effectively be described with allopatric population structure (i.e., spatially distinct components), Pacific salmon populations exhibited sympatry (i.e., spatially overlapping components) of oceanic stages and philopatry (i.e., natal homing). Resolving the parent stream theory required nearly a century of research on oceanic migrations (Royce et al. 1968),

and many aspects remain unresolved. In the context of stock structure and stock assessment, the overfishing issue and parent stream theory demonstrated that determining the appropriate geographic scale is necessary for understanding population dynamics (Secor 2005).

22.2.1   Phenotypic Stocks

Continued research on morphological variation and local movements set the stage for definition of phenotypic stocks and the development of conventions in fish population dynamics to model groups of fish with similar vital rates. When Russell (1931) addressed the issue of overfishing by expressing sustainable yield as the sum of recruitment and individual growth minus mortality (Fig. 22.1), "he effectively defined the field of fisheries biology as one concerned primarily with defining unit stocks and fisheries and their sizes" (Pauly 1986). The characters used to define local "races" in early studies were particularly suited for the operational definition of stock needed to apply Russell's equation. Hjort (1914) defined groups of Atlantic herring, Atlantic cod, and haddock, and Gilbert (1914) classified sockeye salmon to spawning location using growth patterns recorded on fish scales. Groups of fish with different circuli patterns on their scales had different individual growth rates. Furthermore, scale annuli could be used to determine age, and were used to study geographic patterns of recruitment and to estimate mortality rates. Therefore, each of Russell's components of production (growth, recruitment, and mortality) was indicated by fish scales, and scale patterns were effectively used to identify stocks that could be accurately modeled using Russell's harvest equation.

In the early 1900s, fish populations were considered to have homogeneous genetic constitutions, and variations in vital rates or morphology among stocks were regarded as a result of varying environments (Ricker 1972). This phenotypic stock definition was the context in which Thompson and Bell (1934) developed yield-per-recruit, Graham (1935) derived maximum sustainable yield, and Ricker (1954) and Beverton and Holt (1957) quantified stock–recruit relationships and many other
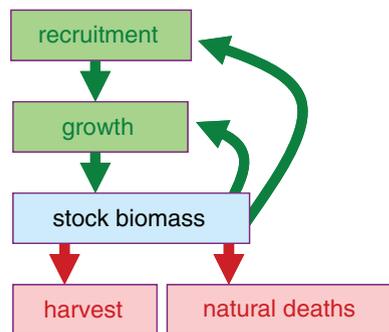

Fig. 22.1 Schematic depiction of the components of population growth, renewal, and fishery production as described by Russell (1931) (Modified from Pauly 1986)

foundations of stock assessment. These advances in assessment modeling were accompanied by the development of conventions for defining phenotypic stocks, as described in Marr's (1957) comprehensive review of stock identification methodology. However, such conventions were most appropriately applied to allopatric groups that could be effectively delineated in space and time.

The paradigm of allopatric structure was reasonable for some marine populations that inhabit distinct estuaries, continental shelves, offshore banks or open ocean basins. However, anadromous populations presented a challenge to this view of population structure. Ricker (1958) and others recognized the challenge of monitoring and managing fisheries that harvest mixed stocks, illustrating how less-productive components are vulnerable to depletion by mixed-stock fisheries. Despite the clear reproductive isolation of anadromous populations, the sympatric nature of their oceanic stages continues to be a challenge for considering stock composition in stock assessment models.

22.2.2   The Migration Triangle

Definition of phenotypic stocks for population modeling helped to determine the appropriate spatial scale for studying population processes, allowing fishery scientists to explain fluctuations in fishery yields primarily as the result of variable recruitment. That consensus prompted another thrust in fisheries research toward explaining the causes of recruitment variability. Research on recruitment dynamics included advances in fisheries oceanography, climate effects, reproductive processes, and most importantly for the subject of population structure, early life-history stages (Sinclair 1988). One question raised in this research agenda was "why do fish spawn where they do?" Information on spawning migrations and distributions of early life stages was depicted by Harden Jones' (1968) migration triangle (Fig. 22.2a), which illustrates "denatant" drift of planktonic stages to nursery habitat, ontogenetic "recruitment" to adult habitat, and seasonal migrations to spawning grounds. Although this frequently used form of the triangle represents a single migration circuit, Harden Jones also presented a more flexible schematic to allow a diversity of patterns, including the overlapping circuits of spring-spawning, autumn-spawning, and winter-spawning herring in the North Sea (Fig. 22.2b).

The migration triangle has been adopted widely in the fisheries literature, in most instances with greater emphasis on life-cycle closure (i.e., the maintenance of a population from one generation to the next) than Harden Jones initially intended. For example, concepts related to the recruitment problem formulated by Cushing (the match–mismatch concept; 1982) and Sinclair (the member-vagrant hypothesis; 1988) were entirely dependent upon life-cycle closure, yet Harden Jones recognized that straying was a necessary form of "biological insurance" against environmental change (Secor 2002). The simple version of the triangle (Fig. 22.2a) has become somewhat iconic in that researchers assume that a single migration circuit represents all populations. For example, tagging studies proliferated in the late
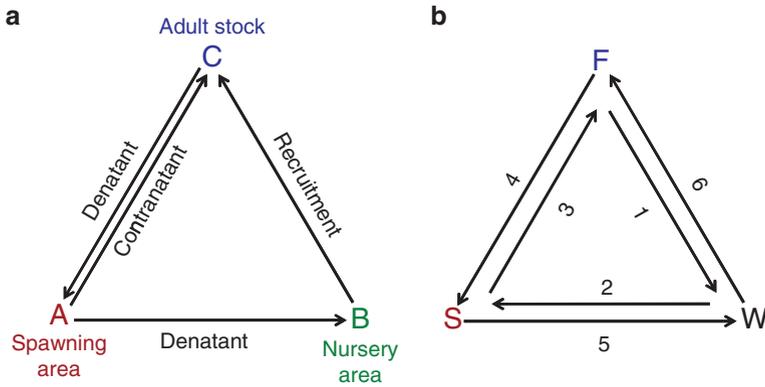
Fig. 22.2 Two forms of the migration triangle depicted by Harden Jones (1968): (**a**) a simple migration circuit involving passive drift of pelagic phases from the spawning area to the nursery area with the prevailing current (denatant), recruitment to the adult stock and seasonal migration to and from the spawning area; and (**b**) a flexible schematic for more complex movement patterns among spawning (S), feeding (F), and wintering (W) habitats, describing sympatric groups with different movement patterns (e.g., spring, autumn, and winter spawning herring in the North Sea)

1900s (Jakobsson 1970; Thorsteinsson 2002), many aimed at describing a single migration circuit for each population. Ironically, the migration triangle became an icon for allopatric stock structure, despite its original intent to illustrate a diversity of patterns, including sympatric structure.

22.2.3 The Stock Concept

Formal definition of the term "stock" is commonly attributed to the "Stock Concept Symposium" (STOCS), which was organized to address the concern that hatchery-based stocking of fish in the Great Lakes was altering genetic diversity and fitness of wild populations (Fetterolf 1981) and included some of the first direct observations of fish genotypes. However, a decade earlier in Seattle, a workshop on "The Stock Concept in Pacific Salmon" identified the need to understand the genetic basis of variability among salmon stocks (Larkin 1972). Despite an absence of genotypic observations, Ricker (1972) summarized information on philopatry, patterns of variation, and breeding experiments to support a compelling argument that phenotypic differences are heritable.

The development of electrophoretic methods to study allozyme frequencies allowed researchers to test genetic differences among stocks and shifted the emphasis of stock identification from phenotypic to genotypic methods. Booke's (1981) definitions of "genetic stock" and "phenotypic stock" gave clear preference to genetics, allowing that phenotypic stock identification could be used when genotypic stock characterization was not possible. Ihssen et al.'s (1981) methodological review

included a wide range of traditional and newly developed techniques, but awarded electrophoresis the "primary position among methods used for stock identification." Redefinition of stocks and advocacy for genetic methods prompted a proliferation of electrophoretic studies of fish stocks (e.g., Hedgecock 1984; Utter 1991). However, unlike the distinct patterns of genetic variation among anadromous salmon stocks, allozymes indicated little intraspecific variation of most marine species and supported the previous concept of genetically homogeneous populations (Wirgin and Waldman 2005).

Perhaps as a result of the different electrophoretic results between anadromous and marine species, stock assessment and management of salmon explicitly recognized sympatric population structure, but population modeling of other fishery resources generally continued an allopatric, phenotypic approach (e.g., Brown et al. 1987). The last few decades of the 1900s have been described as the "golden age" of fisheries stock assessment (Quinn 2003). With the foundations for stock assessment modeling laid in the mid-twentieth century, applications of basic models proliferated, and estimation techniques advanced through developments in computers and statistics. Formal definition of the stock concept represented a milestone in considering population structure for fishery management, but impact of the stock concept was limited to populations that demonstrated genetic divergence (e.g., Pacific salmon). For many other fishery resources with apparently less genetic variation (or a lack of information on genetics), the earlier view of phenotypic stocks and allopatric structure persisted. Despite advances in modeling and development of new stock identification techniques, there was little progression in stock concepts in the northeast Atlantic and elsewhere during the last half of the twentieth century (Stephenson 2002). Unlike the earlier coevolution of stock identification and stock assessment, population modeling has been slow to adapt to the recognition of complicated population structures.

22.2.4 An Interdisciplinary Approach

Since the application of electrophoresis to stock identification in the early 1980s, a series of technological advances further changed the approach to identifying stocks (and associated definition of "stock"). A series of molecular genetic markers, including mitochondrial DNA, minisatellites, microsatellites, random amplified polymorphic DNA, amplified fragment length polymorphisms and single nucleotide polymorphisms were developed, each having potentially greater sensitivity to genetic variation (Wirgin and Waldman 2005). Similar to the advocacy for allozymes as the "primary" method to detect reproductive isolation in the 1980s, each newly developed technique was claimed to be the next best thing for determining stock structure. As new data on genetic variation became available, there was a desire to reconcile new results with previous information from traditional techniques like tagging or morphology (Waples 1998). When results from multiple stock identification approaches were compared, interdisciplinary perspectives emerged (e.g., Waldman et al. 1997; Waldman 1999).

Begg and Waldman (1999) reviewed the various techniques used to identify stocks and advocated a method that integrates results from different approaches. Information from genetic, phenotypic, and environmental approaches can be complementary, because the definition of a stock includes all three components (Dizon et al. 1992; Coyle 1998). Using information from multiple methods also increases the likelihood that stocks are correctly identified (Hohn 1997). In addition to the advances in molecular genetics, other technological advances such as image analysis, microchemistry, electronic tags, and geostatistics have improved the ability to detect population structure. The state of the art in stock identification is to apply multiple approaches to stock identification, ideally on the same samples, and compare all results to achieve an interdisciplinary perspective (e.g., Abaunza et al. 2004; Hatfield et al. 2005). A recent development in stock identification that involves interdisciplinary synthesis of genetic and phenotypic approaches is the definition of management units on the basis of demographic independence (Palsbol et al. 2006; Waples and Gaggiotti 2006).

Recent application of advanced technologies and interdisciplinary approaches reveal complex patterns of spatial structure of many marine populations, similar to the complex patterns of anadromous species detected much earlier (Conover et al. 2006). These heterogeneous, sympatric patterns present challenges to stock assessment modeling. New conventions in sampling fish populations, fishery monitoring, population modeling, and fishery management are needed to account for new perspectives on population structure.

22.3   The Present: Rethinking "Population Thinking"

Despite the successive advances in theory and practice regarding population structure, problems with stock definition are common. For example, Stephenson (2002) reported a mismatch between population structure and management units for approximately one third of the stock units in the northeast Atlantic, and many of these problems involved subunits within stocks. Apparently, sympatric structure is a problem for the current "stock concept."

22.3.1   Alternative Concepts of Population Structure

Ironically, the "population thinking" that replaced typological perspectives of biological species still has inaccurate vestiges of typology in the common assumption of homogeneity within allopatric stocks. Although the migration triangle can be used to represent a single migration circuit, Harden Jones (1968) doubted that a single migration pattern would persist over many generations, and speculated that a "level of straying and multiplicity of spawning grounds" provide insurance against unfavorable conditions. Harden Jones's discussion on multiple behavioral groups was prescient of the complex patterns currently revealed by advanced technologies (Secor 2005).

In an attempt to reconcile the spatial structure of Atlantic herring spawning groups and management of a coast-wide fishery, Stephenson et al. (2001) advocated a schematic depiction of spatial patterns for each life-history stage that allows for a range of reproductive patterns, from philopatry to mixing (Fig. 22.3). The approach was generalized by Smedbol and Stephenson (2001) to be applied to any species with spatial structure. For example, Hare (2005) illustrated the spatial patterns of weakfish reported by Thorrold et al. (2001) using the schematic approach to visualize population structure. This simple visualization offers an important conceptual break from the single circuit of ontogenetic movements depicted by the migration triangle (Fig. 22.2a), because it allows for heterogeneous patterns and groups within a population and a fishery.

The high rate of straying among local groups and the general lack of genetic variation observed in most marine species from electrophoresis prompted challenges to the widespread application of the stock concept (Smith and Jamieson 1986; Smith et al. 1990). Although these authors recognized spatial heterogeneity, a
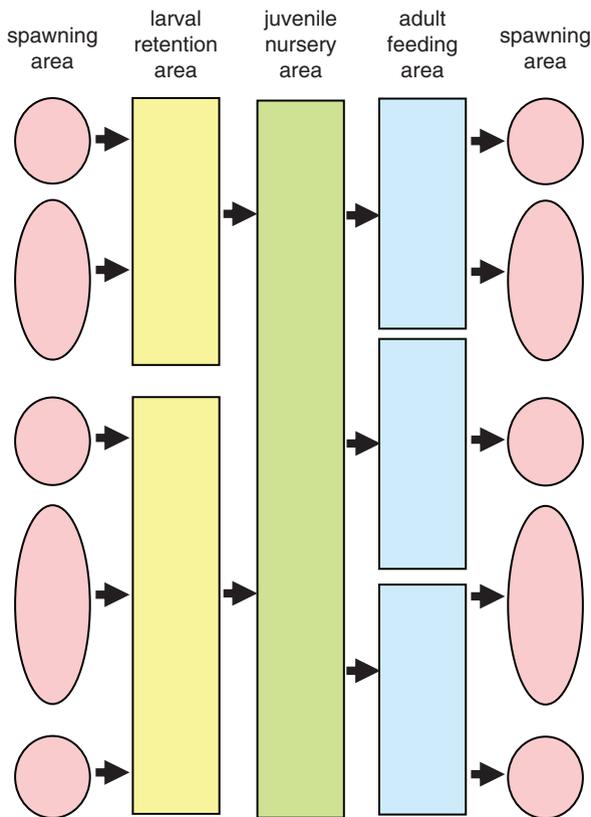

Fig. 22.3 Spatial patterns of Atlantic herring (Modified from Stephenson et al. 2001)

mechanism for maintaining spatial structure was not presented (McQuinn 1997). Several fishery scientists have since applied metapopulation concepts developed for terrestrial populations (Levins 1968) to explain persistence of local spawning groups and extensive mixing of marine populations (McQuinn 1997; Policansky and Magnuson 1998; Smedbol and Wroblewski 2002; Smedbol et al. 2002). However, the local extinctions and recolonizations implicit in the theoretical metapopulations described by Levins (1968) may not apply to many marine populations, and applying metapopulation models may not be appropriate (Smedbol et al. 2002). Still, some suggestions of local extinction and recolonization have been found (e.g., Georges Bank herring, Overholtz and Friedland 2002), and the emphasis on extinction and recolonization may not be necessary (Kritzer and Sale 2004). Perhaps the most important distinction is that the metapopulation concept recognizes spatial distribution of behavioral groups, whereas the discrete stock concept recognizes spatial patterns of genetic variation (McQuinn 1997).

A similar concept of population structure is contingent theory (Secor 1999, 2002, 2005). Hjort (1914) developed the term to describe behavioral groups of Norwegian herring with distinct migration circuits that mix during certain seasons and life-history stages. Contingent theory allows for sympatric structure within populations in which contingents have potentially different life histories (e.g., movement patterns, habitats, and productivity). Advances in methodologies that can determine an individual's environmental history (e.g., otolith microchemistry, parasite assemblages, and electronic tagging) allow researchers to discriminate and track contingents. Clark (1968) revived Hjort's contingent theory to describe groups of striped bass with distinguishable patterns of seasonal movement. Secor (1999) extended the view of population structure depicted by Stephenson, and showed how the simple migration triangle represents one contingent in a sympatric complex of contingents (Fig. 22.4). Contingent theory has been applied to a variety of fishery resources, and much like the term "stock," it may have slightly different definitions for each application. A recent workshop on the role of behavioral groups on population dynamics defined contingents as "groups of fish with different capabilities and life-cycle patterns" (ICES 2007). For our purposes, a contingent is a cohesive group of individuals within a population that share a common migrational pattern. Although these groups are not necessarily distinct genetically, the divergent movement patterns may serve as a mechanism of reproductive isolation, and contingent structure may lead to genetic structure.

An elusive aspect of developing a robust concept of population structure is understanding the mechanisms of natal homing. The intent of the migration triangle was to explain why fish spawn where they do, but the mechanism of philopatry, its primary premise, remains entirely unexplained. Evaluating the relative amounts of fidelity to spawning ground or straying to other spawning grounds is critical to modeling population dynamics of connected subpopulations (e.g., Porch and Turner 1998; Fromentin and Powers 2005).

Despite the long history of stock identification and the many methodological advancements, the definition of management units remains a practical decision,
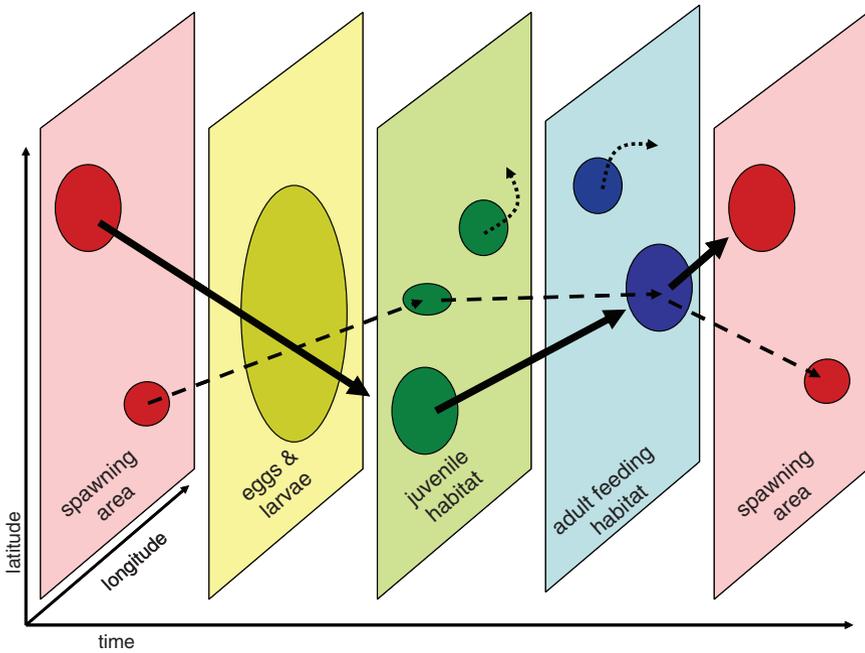
Fig. 22.4 Geographic distributions of successive life-history stages, with one "migration triangle" depicted as solid arrows and, a second contingent depicted as dashed arrows and "vagrants" as dotted arrows (Modified from Secor 1999)

because it depends on the management objective (Cadrin et al. 2007). Managing the recovery of species at risk of extinction requires a different operational definition of a stock than the definition needed for managing sustainable yield. Therefore, conservation biology tends to focus more on long-term reproductive isolation and selective adaptations than stock assessment, which focuses more on demographic independence in the short term.

22.3.2   *Advances in Spatial Population Modeling*

The continuing problems of exploiting sympatric populations, local depletions and recent issues of conserving essential fish habitats and designation of marine-protected areas require new information from stock assessments, and impose new challenges for population modeling (e.g., Field et al. 2006; Tuckey et al. 2007). These new challenges require the incorporation of spatial patterns in sampling and stock assessment modeling. Considering spatial structure in stock assessments takes three general forms: spatial heterogeneity, movement, and reproductive isolation.

22.3.2.1   Spatial Heterogeneity

In their text on stock assessment methods, Hilborn and Walters (1992) describe spatial models as one of the four typical extensions to simple biomass dynamics models. For sessile or sedentary invertebrates, spatial heterogeneity can be incorporated relatively easily. As demonstrated for Tasmanian abalone, conventional relationships, like Baranov's catch equation (that equates abundance, N, at time t as a function of catch, C, fishing mortality, F, and natural mortality, M) can be decomposed into spatial units (i):

$$N_{t,i} = \frac{C_{t,i}\left(F_{t,i} + M_i\right)}{\left[1 - e^{-(F_{t,i} + M_i)}\right]F_{t,i}} \tag{22.1}$$

All components of biological or fishery production (fishing mortality, natural mortality, individual growth, and recruitment; Fig. 22.1) can be similarly partitioned into discrete spatial units. For example, survival of a cohort over time can be spatially explicit:

$$N_{t+1,i} = N_{t,i}e^{-Z_{t,i}} \tag{22.2}$$

where total mortality (Z) is allowed to vary in time and space. Assuming homogeneity in vital rates, when spatial patterns exist, results in biased estimates from conventional dynamic pool models (e.g., yield-per-recruit, biomass-per-recruit, and age-based production models). In a spatial analysis of Atlantic sea scallop, Hart (2001) recommended calculating per-recruit expectations in sub-stock areas and weighting expectations by local recruitment.

A milestone in spatial modeling was the consideration of heterogeneous environments by MacCall (1990), who modified a conventional biomass dynamics model to include realized population growth rate for each habitat. Density-dependent habitat use was depicted as a basin, in which relatively large populations expand their geographic range, inhabiting less-productive "fringe" habitats (Fig. 22.5). MacCall's simulations of the basin model suggest that the optimal harvesting strategy is to fish the less-productive, fringe habitats. However, one critical assumption of the model is conformance to an ideal free distribution, in which distribution of individuals equalizes the net rate of growth rate of the entire population. Shepherd and Litvak (2004) warn that many populations may not conform to the ideal free distribution. Furthermore, the basin model implicitly assumes no barriers or restrictions to movement or mating.

22.3.2.2   Movement

Modeling spatial patterns of mobile populations requires reliable observations and estimates of movement rates. The cohort model described above (Equation 22.2) can be modified to include movement:
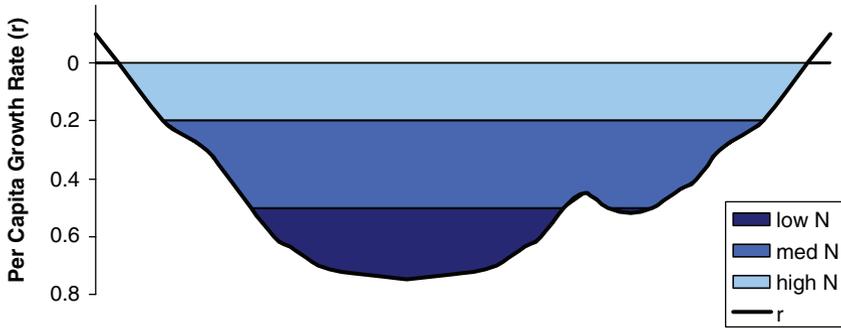
Fig. 22.5 MacCall's (1990) basin model of density-dependent habitat use, depicting three levels of population abundance (N), where r is intrinsic rate of increase

$$N_{t+1,i} = \left(\sum_j N_{t,j} \alpha_{ji} \right) e^{-Z_{t,i}} \qquad (22.3)$$

where α_{ji} is the proportional movement of fish from area j to i (or the probability of movement [Hilborn 1990]). All possible movements among k areas can be considered a matrix, in which diagonal elements are proportional residence, off-diagonal elements are movements, and rows sum to 1:

$$A = \begin{bmatrix} \alpha_{1,1} & \alpha_{1,2} & \dots & \alpha_{1,k} \\ \alpha_{2,1} & \alpha_{2,2} & \dots & \alpha_{2,k} \\ \dots & \dots & \dots & \dots \\ \alpha_{k,1} & \alpha_{k,1} & \dots & \alpha_{k,k} \end{bmatrix} \qquad (22.4)$$

Among the first quantitative approaches to evaluating movement rates of fishery resources was that of Beverton and Holt (1957), who extended their framework for stock assessment models by considering fish movement as diffusion (D) in dimensions x (e.g., latitude) and y (e.g., latitude):

$$\frac{dN}{dt} = \frac{d}{dx}\left(D \frac{dN}{dx} \right) + \frac{d}{dy}\left(D \frac{dN}{dy} \right) \qquad (22.5)$$

This continuous model was used to derive movement across discrete boundaries, termed the "box-transfer model." This pioneering work on modeling movement was extended by including directional movement (u and v, in the same dimensions) and total mortality (Z; Sibert et al. 1999):

$$\frac{dN}{dt} = \frac{d}{dx}\left(D \frac{dN}{dx} \right) + \frac{d}{dy}\left(D \frac{dN}{dy} \right) - \frac{d}{dx}(uN) - \frac{d}{dy}(vN) - ZN \qquad (22.6)$$

Movement parameters D, u, and v can be estimated from tagging data, if area and time are discretized, and the number of recaptures in each period and area ($r_{t,i}$) can be predicted by rearranging Equation 22.1, replacing total abundance with number of marked fish (n) and including a reporting rate (β):

$$r_{t,i} = n_{t,i} \left[1 - e^{-\left(F_{t,i} + M_i\right)} \right] \frac{F_{t,i}}{\left(F_{t,i} + M_i\right)} \beta_{t,i} \qquad (22.7)$$

Movement rates can be estimated using a series of continuous and discrete models (Hilborn 1990; Schwarz 2005).

As the number of areas and the possibility of local extinction within an area increase, these movement models approach the structure and behavior of meta-population models. Levins (1968) developed a simple metapopulation model, and Smedbol and Wroblewski (2002) modified the model to include the natural rate of extinction and the added effect of fishing. However, their applications to Atlantic cod were limited by the inability to distinguish "commercial extinction" from true extinction, recolonization from rebuilding of a remnant subpopulation, and large subpopulations from small subpopulations. Quantitative models of metapopulations have diversified to the extent that Smedbol et al. (2002) advocate a clear definition of terms and assumptions when using the term "metapopulation." Kritzer and Sale (2004) describe more complex metapopulation models that are more relevant to fishery resources (e.g., allow changes in population size). Complex metapopulation models can also include demographic structure (e.g., age, maturity) and age-dependent movement rates among subpopulations. Application of an age-based metapopulation model to yellowtail flounder showed that population dynamics of some stocks were highly sensitive to rates of planktonic drift and directed movements at older ages (Fig. 22.6; Hart and Cadrin 2004).

22.3.2.3 Reproductive Isolation

MacCall's (1990) basin model, which implicitly assumes that mating occurs among individuals from all areas, suggests that the optimal harvest strategy is to fish the less-productive, fringe habitats. In contrast, Ricker's (1958) modeling of a mixed fishery of reproductively isolated components supports the opposite conclusion (i.e., conserve the least productive components), illustrating the importance of determining the degree of reproductive isolation for spatial modeling. Unfortunately, all of the spatially explicit models described above are essentially allopatric, and consideration of sympatric groups requires information on stock composition of mixed harvests and samples.

Incorporation of movement patterns in the stock assessment of Atlantic bluefin tuna demonstrates the importance of reproductive isolation for population dynamics (NRC 1994). Porch (2003) reviews the development of age-based methods for
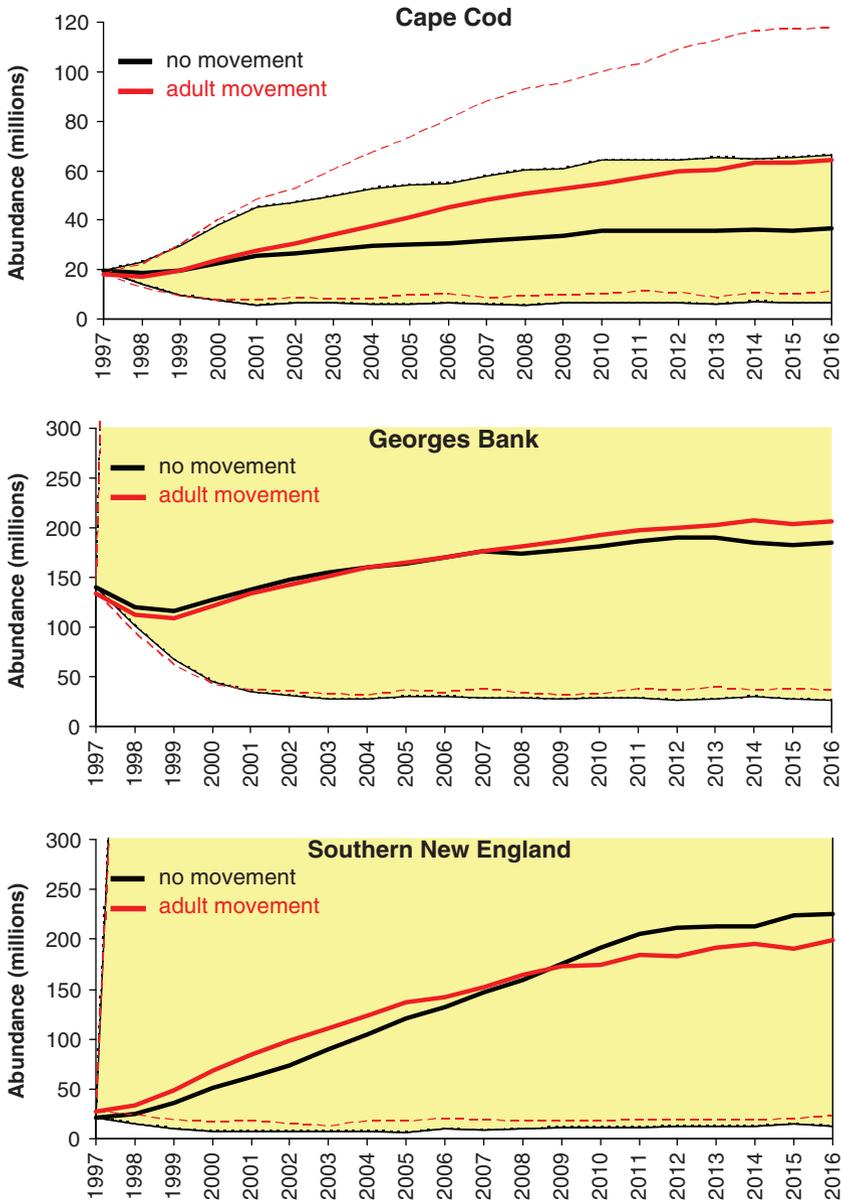
Fig. 22.6 Projected stock abundance of yellowtail flounder in three subpopulations (Cape Cod, Georges Bank, and southern New England), assuming a fishing mortality rate of $F_{0.1}$ for all subpopulations with no movement (black line and shaded confidence region) and adult movement (red line and dashed confidence region) illustrating the sensitivity of including movement for the smaller Cape Cod subpopulation (projections from Hart and Cadrin 2004)

two intermixing stocks using Beverton and Holt's (1957) box-transfer model (Equation 22.5). Simulation analyses showed that stock assessment models that included movement among eastern and western management areas performed better than separate assessments of each area (Porch et al. 1998). Subsequent model developments included two assumptions of reproductive isolation:

- *Diffusion*: Fish from one area move to another and spawn there (i.e., reproductive mixing). The process defined by the cohort model with movement (Equation 22.3) is used to model "diffusion."
- *Overlap*: Fish from one area move to another, but return to their natal area to spawn (i.e., complete philopatry, sympatry). Overlap involves a different process for tracking cohort abundance:

$$N_{t+1,i} = \left(\sum_s N_{t,s} P_{s,i,t} \right) e^{-Z_{t,i}} \tag{22.8}$$

where $P_{s,i,t}$ is the proportion of stock s in area i at time t. Estimation of P requires stock composition analysis in which identifiable differences (e.g., genetic, phenotypic, or environmental signals) in baseline samples of separate stocks are used to determine composition of a mixture (e.g., Prager and Shertzer 2005).

Stock assessment results (e.g., recruitment, spawning stock biomass, and fishing mortality) are quite sensitive to these alternative assumptions of overlap or diffusion. Estimates of Atlantic bluefin tuna abundance were relatively insensitive to movement rates when assuming philopatry, but were sensitive to movement estimates when assuming diffusive movement (Porch and Turner 1999), illustrating the importance of philopatry in modeling spatial dynamics. Indeed, several reviews advocate more elaborate population structure for Atlantic bluefin tuna, such as partial reproductive isolation, contingent structure or metapopulation dynamics (Secor 2001; Fromentin and Powers 2005). Despite the relatively simple two-stock modeling developed for Atlantic bluefin, the model structure (generalized here in Equations 22.3 and 22.10) can be extended to more areas, more stocks, and more complex relationships among stocks (e.g., partial isolation or age-specific movement rates [Powers and Porch 2004]).

A synthesis of current methods for incorporating spatial structure in stock assessment modeling remains somewhat Platonic (i.e., assuming random variability around a population average). Although population dynamics can be disaggregated to account for spatial heterogeneity in vital rates (e.g., Equations 22.1 and 22.2), the processes within subareas (i) are assumed to be homogeneous. Similarly, movement patterns can be incorporated into models (e.g., Equations 22.3–22.7), but movement is expressed as a net rate, assuming homogeneity within areas (α_{ij}), ignoring different behavioral groups within areas that have divergent movement patterns (e.g., contingents). Perhaps the promising development of genetic stock identification, otolith microchemistry, and electronic tagging will support the development of stock assessment models that account for the spatial diversity apparent in many fishery systems.

22.4 The Future: Prospects for Spatial Monitoring and Modeling

Challenges in modeling and managing fishery resources with complex spatial patterns will become increasingly important as migration behaviors are discovered that do not conform to patterns of allopatry in coastal populations (e.g., Block et al. 2005; Kraus and Secor 2005). The recurrent problem posed by sympatric distributions of populations and contingents indicates that improvements in determining the stock composition of mixed samples are needed. The sensitivity of population dynamics to movement and philopatry suggests that research should continue for estimating individual variation in migration and for a better understanding of natal homing.

Stock composition analysis has improved over the last few decades from valuable developments in genetic markers (e.g., Waples et al. 1990) and statistical mixing models (e.g., Prager and Shertzer 2005; Pella and Masuda 2006). The progress made in the recovery of Pacific salmonid stocks (Banks 2005) demonstrates that appropriately designed sampling of mixed-stock fisheries can support accurate estimates of stock composition and provide information for reliable stock assessment and real-time management decisions.

The effective stock composition analysis demonstrated for Pacific salmonids should be applied to more coastal and marine species that support mixed-stock fisheries. As genetic markers or other natural tags of natality (e.g., otolith growth patterns; Campana and Thorrold 2001) become more affordable to analyze, tissue collection should be incorporated into regular fishery and research sampling programs that currently measure biological attributes (e.g., size, gender, maturity, and age). If such programmatic sampling of genetics and other natural tags becomes common, fisheries agencies will need to invest in analytical facilities to process large volumes of tissue samples in support of regular stock composition analyses.

As more elaborate population models are developed to include spatial structure, the dependence on accurate movement rates will also increase. For example, an area-disaggregated, Bayesian state–space model was developed to estimate population parameters for Atlantic sardine, but estimates of movement were too uncertain to provide reliable estimates (Stratoudakis 2006). Similarly, Kritzer and Sale (2004) show how metapopulation models rely on accurate rates of exchange among subpopulations. Most importantly, movement rate is a critical criterion to determine genetically discrete populations (Waples and Gagiotti 2006).

The prospects for advancement in the estimation of movement rates are promising, because of recent developments in tagging technology and statistical estimation procedures. As reviewed by Schwarz (2005), estimation of mortality from tagging models improved substantially in the last decade because of advances in statistical procedures, analytical designs, and the development of conventions for best practices. The likelihood-based mortality estimators that were initially developed to estimate mortality have been extended to include movement,

but further improvements are likely as they are applied to different systems. In addition, electronic tagging can be used to estimate fishing and natural mortality rates (Hightower et al. 2001).

The rapid development of electronic tagging technologies expands the capacity to understand fine-scale movement patterns. Such individual-based observations can be used to estimate movement rates and the mode of movement (e.g., overlap or diffusion). Similar to the trend in genetic techniques, electronic tags are continually becoming more affordable, as well as smaller, more reliable and longer-lasting (Thorsteinsson 2002). Continued advances in the analysis of natural tags (e.g., scale microstructure and otolith microchemistry) also promise to improve the understanding of ontogenetic movement patterns and identification of past spawning and nursery habitats (e.g., birth certificates).

Our focus has been on consideration of spatial structure in stock assessments, but advances in spatial modeling have wide applicability in other aspects of fishery science, such as ecological theory (e.g., population stability, biocomplexity, and climate effects); more effective fishery management plans (e.g., rebuilding and mixed-stock sustainable yield); design, implementation, and evaluation of marine-protected areas, defining the appropriate spatial scale of ecosystem processes and management; designation and protection of essential fish habitat; improved assessment of environmental and economic impacts of management alternatives; and optimization of spatial harvest strategies.

Advances in global positioning, vessel monitoring systems, and geostatistics offer powerful tools for monitoring spatially explicit information from fisheries and research samples. Population concepts have evolved to the point of accepting complex spatial patterns that can accommodate problems related to how mixed-stock fisheries and climate affect recruitment and resource sustainability. The extension of conventional stock assessment methods to incorporate spatial patterns is relatively straightforward and available (e.g., the most recent version of stock-synthesis assessment software allows for spatial heterogeneity and movement; Methot 2005). It appears that the missing link in applying spatially explicit population models is the lack of information on movement rates and patterns, reproductive isolation, and stock composition. Therefore, advancement in modeling spatial population structure for stock assessment requires more extensive sampling of stock composition (genetic sampling of mixed stocks, analysis of environmental signals for contingents), and tagging studies designed to estimate movement rates and patterns of movement with respect to natal homing.

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