




Review Article

Contribution to the Themed Section: 'A tribute to the life and accomplishments of Sidney J. Holt'

Revival and recent advancements in the spatial fishery models originally conceived by Sidney Holt and Ray Beverton

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Sidney Holt and Ray Beverton are primarily recognized for developing the basis of demographic stock assessment modelling, but their enduring legacy continues to influence and guide advancements in many fields of fisheries science. Although largely forgotten, their contributions to spatial modelling laid the foundation for a variety of applications in aquatic and terrestrial populations. Spatial modelling approaches are rapidly evolving beyond even the visionary scope of Beverton and Holt due to advancements in understanding of spatial population structure, collection of spatially explicit data, and statistical parameter estimation. A review of Beverton and Holt's original movement models demonstrates that understanding the origins and basic underlying assumptions can help ensure that current models are consistent with fundamental principles. Additionally, recent simulation studies show that conforming to or revising spatial model assumptions is essential for accurate estimation. As fisheries science transitions to more complex spatial stock assessment models, understanding their conceptual development and the lessons learned by our predecessors is essential for proper model specification and application.

Keywords: Beverton and Holt, ICES history, movement, stock assessment, tagging, connectivity

Introduction

Beverton and Holt's (1957) *On the Dynamics of Exploited Fish Populations* is a timeless contribution to the scientific literature that is constantly being "rediscovered" by scientists when developing state-of-the-art fisheries models (Holden, 1995; Pitcher and Pauly, 1998). Their book continues to be one of the most highly cited fisheries publications (Branch and Linnell, 2016; Figure 1). It covers a breadth of visionary topics, many of which have yet to be fully investigated six decades after its first printing. Daniel Pauly (Fisheries Professor, University of British Columbia) mused in his foreword to the 1993 reprint:

"I wonder what example will be used for illustrating Beverton and Holt's anticipation of ideas when, in a few years or decades, another reprint... is presented to a new generation of fishery scientists?"

Beverton and Holt (1957) recognized that spatial variation and connectivity were primary drivers of population dynamics and sustainable harvest levels. Section 10 of Beverton and Holt (1957), titled *Spatial Variation in the Values of Parameters: Movement of Fish within the Exploited Area*, is relatively brief, composing less than 30 of the more than 500 pages of the original

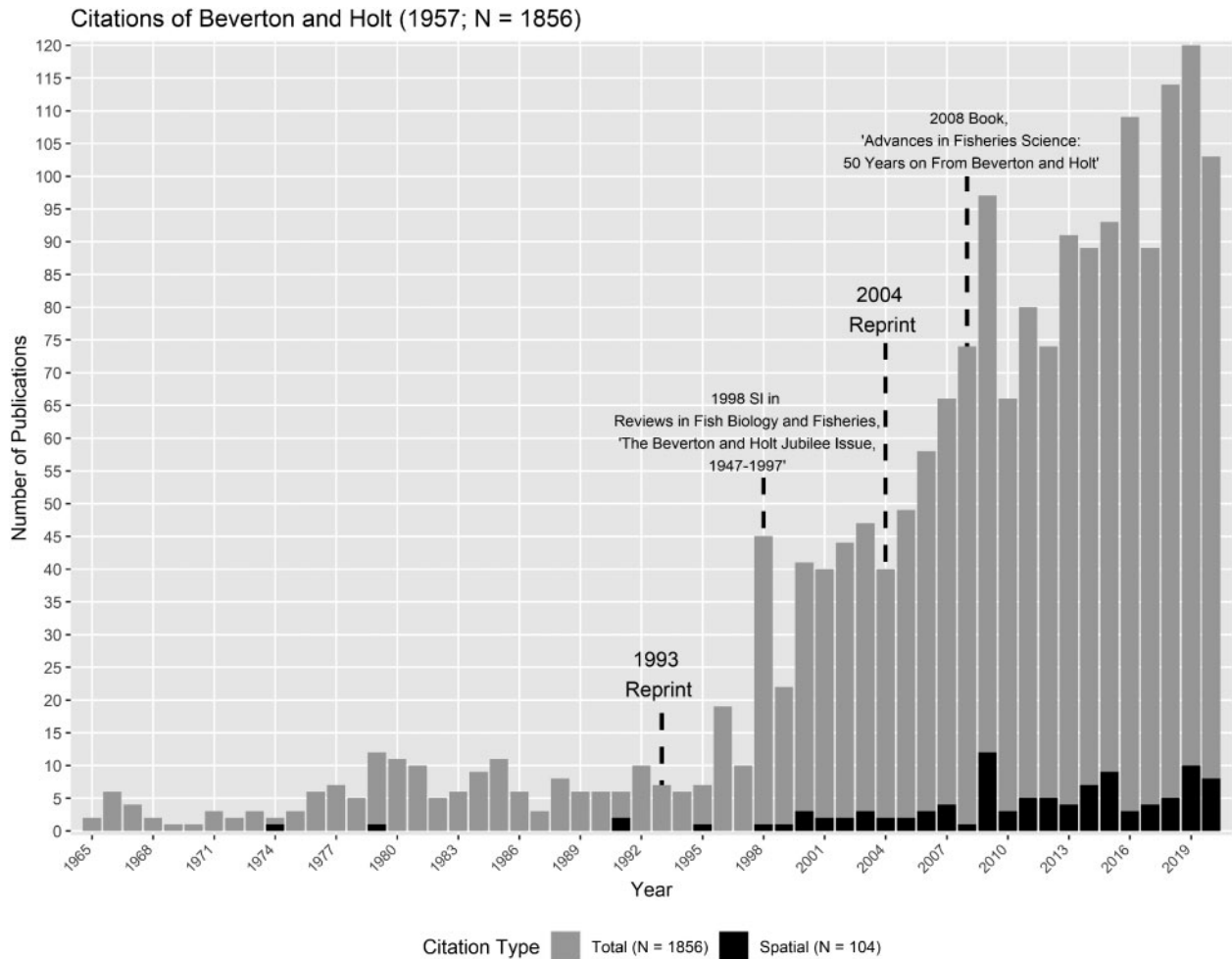


Figure 1. Publications citing [Beverton and Holt \(1957\)](#); grey bars, $N = 1856$ along with the subset of these citations associated with spatial processes (black bars, $N = 104$) and major events (vertical lines) subsequent to publication of [Beverton and Holt \(1957\)](#), including the two reprints, a journal special issue, and an edited book celebrating the publication of the original book. Publications were identified using the Web of Science Core Collection database (October, 2020), which included years 1965–2020. Citations of clear typographical errors of any version of [Beverton and Holt \(1957\)](#), including the 1993 and 2004 reprints, were included.

tome. However, since the early 2000s, citation rates related to spatial components of Beverton and Holt’s models ([Figure 1](#)) have remained consistently high.

The range of citations indicate that their movement models have been adapted across an array of disciplines in both aquatic and terrestrial ecology, including theoretical simulations on the impact of movement dynamics across landscapes and seascapes, tagging analyses, implementation of marine protected areas (MPAs), exploration of larval dispersal and recruitment dynamics, determination of demographic heterogeneity, and spatial population models ([Figure 2](#)). In particular, Beverton and Holt’s original analyses have been incrementally adapted for use in the field of quantitative stock assessment, first as the basis of spatial yield-per-recruit models ([Goethel et al., 2016](#)) and, more recently, spatially explicit length-based or age-based stock assessment models ([Cadrin and Secor, 2009](#); [Goethel et al., 2011](#)).

Several technological developments since [Beverton and Holt’s \(1957\)](#) publication have facilitated the resurgence of interest in the implementation of movement models for use in stock assessment applications. For centuries, fishery catch and effort data

have been reported by fishing grounds (e.g. [Fulton, 1889](#)), and fishery recaptures of tagged fish have informed general movement patterns ([Hall, 2014](#)), but the spatial resolution of fishery data was usually low and accuracy was difficult to verify. The development and application of vessel monitoring systems and other forms of electronic monitoring have improved the spatial resolution and quality of fishery data (e.g. [Van Helmond et al., 2020](#)). Similarly, fishery-independent surveys are widespread, which provide spatially explicit information on relative density for many fishery resources ([Gunderson, 1993](#); [Thorson, 2019](#)). High-resolution information on movement is also available from electronic tagging and “natural tags” (e.g. parasites, otolith chemistry, and genetic stock composition, [Cadrin et al., 2014](#)). Concomitantly, there has been increased recognition that better engagement of stakeholders in both data collection and participatory modelling initiatives can lead to direct incorporation of rich and often spatially resolved local ecological knowledge into assessment and fisheries management frameworks ([Röckmann et al., 2012](#); [Sampedro et al., 2017](#); [Sun et al., 2019](#)). Finally, rapid advances in computing power, statistical parameter estimation techniques,

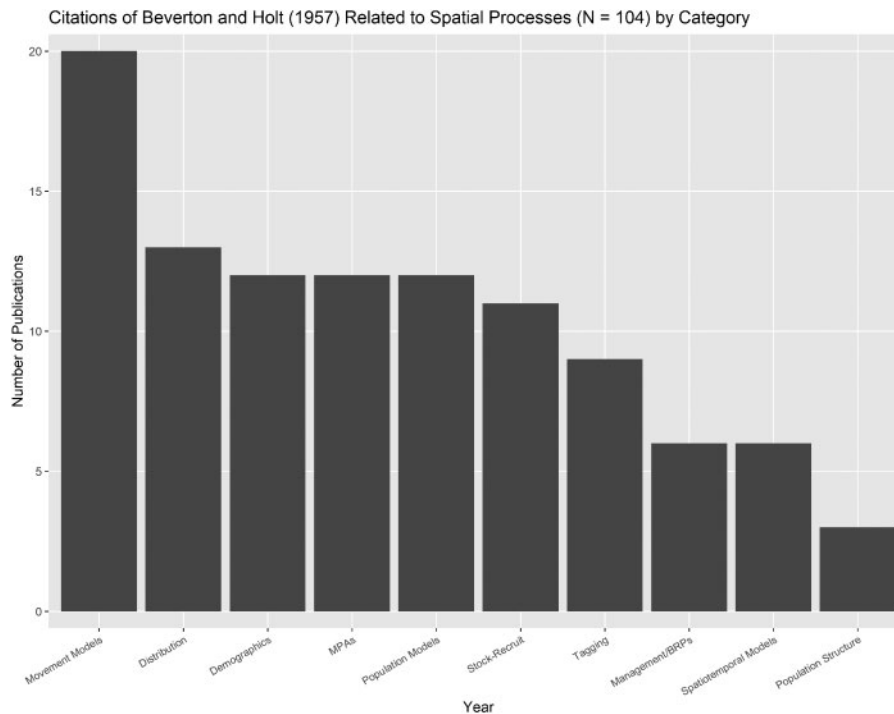


Figure 2. Citations of [Beverton and Holt \(1957\)](#) from [Figure 1](#) related explicitly to spatial processes ($N = 104$) delineated by category. General categories include: development of theoretical movement models (Movement Models; $N = 20$); identifying the spatial distribution of a resource or harvesters (Distribution; $N = 13$); addressing spatiotemporal demographic heterogeneity (Demographics; $N = 12$); implementing and modelling marine protected areas (MPAs; $N = 12$); developing spatially explicit population models (Population Models; $N = 12$); accounting for larval dispersal and spatial recruitment dynamics (Stock-Recruit; $N = 11$); estimating movement from mark-recapture data (Tagging; $N = 9$); including spatial structure in harvest control rules and biological reference points (Management/BRPs; $N = 6$); development of spatiotemporal species distribution models (Spatiotemporal Models; $N = 6$); and exploring spatial population structure and stock identification (Population Structure; $N = 3$).

and integrated modelling approaches ([Maunder and Punt, 2013](#); [Zipkin and Saunders, 2018](#)) support the application of the spatial models initially developed by Beverton and Holt. [Punt et al. \(2020\)](#) illustrate the growing importance of spatial modelling by concluding that the next generation of stock assessment models must incorporate the ability to model spatial structure and connectivity.

Although spatial assessment models are much more complex than Beverton and Holt envisioned, the basic tenets and simplifying assumptions used in these models can be traced back to their 1957 book ([Schwarz, 2005](#); [Goethel et al., 2011](#)). Most scientists recognize that progress is only possible by “standing on the shoulders of giants” ([Hilborn and Liermann, 1998](#); [Anderson, 2011](#)), and understanding those foundations is essential for advancing science. [Quinn \(2003\)](#) observed “. . . a tendency among modern researchers to ignore the historical literature, which results in failure to appreciate the origins of modern fisheries science and reinventions of already published methodology.” In the case of fisheries science, and especially stock assessment, understanding the past necessitates study of [Beverton and Holt \(1957\)](#). As [Holden \(1995\)](#) noted:

“reading [[Beverton and Holt, 1957](#)] will take [you] back not only to the fundamentals upon which all modern work is based but more importantly, might cause [you] to think more about what [you] are doing. It is my experience that too many research workers are prepared to slip the

appropriate disk in their computer, load the program and analyse their data without having the slightest idea of what the program is calculating, whether the method of analysis is appropriate and what the results mean.”

Therefore, we review [Beverton and Holt’s \(1957\)](#) ideas on incorporating spatial structure and connectivity, then provide a brief history of how their simple models developed into current methods and applications for spatially explicit versions of tagging, yield-per-recruit, and stock assessment models. We conclude with a discussion of how the assumptions of their basic models can be adapted to account for the complex spatial population structures often observed in marine resources and how we envision their work being incorporated into the future of spatial population modelling.

Early migration research and the emergence of quantitative fisheries science

Spatiotemporal changes in fish abundance resulting from larval dispersal, foraging behaviour, and temporary or permanent migrations have intrigued scientists since the field of ecology emerged. [Anderson \(1746\)](#) presented the premise that panmictic stocks undergoing large-scale migrations could explain fluctuations in fishery production. He hypothesized that herring migrate from their “home” under the polar ice cap in search of food when the population outgrew the available prey and arrived at various fishing grounds at different periods during this migration

(Wegner, 1996; Chambers and Trippel, 1997; Sinclair 2009). The “migration” theory remained a prominent viewpoint well into the early part of the 20th century, when research on herring (Heincke, 1898) and cod (Hjort, 1914) demonstrated that different spawning “races” or populations existed within a given species, which underwent small-scale spawning and feeding migrations. In contrast to the migration hypothesis, “population thinking” posed that fishery fluctuations were caused by year-class variability within geographically distinct populations (Sinclair, 1988; Chambers and Trippel, 1997; Secor, 2002; Sinclair, 2009). However, the cause of fishery fluctuations was still very much under debate when the 1902 inaugural International Council for the Exploration of the Seas (ICES) delegation met, which was demonstrated by the corresponding vote to form “Committee A” to investigate the role of migration theory compared to population thinking for explaining variability (Smith, 1994; Sinclair, 1997; Anderson, 2002; Rozwadowski, 2002). As the fledgling field of fisheries science began to develop in the early 1900s, understanding the implications and scales of fish movement continued to be a primary goal.

In the early 1900s, ecology slowly began to turn towards mathematics in order to develop modelling tools to predict and understand nature (Kingsland, 1995; Quinn, 2003). In fisheries science, F. I. Baranov is considered by many to be the “grandfather of fisheries population dynamics” (Quinn, 2003) for his theory of fishing and resultant catch equation (Baranov, 1918), even though his models were initially criticized and not seen or accepted by the western world until decades later (Beverton and Anderson, 2002; Sharov, 2020). Russell (1931) built on Baranov’s theory for his energy balance equation of fish population growth, while Hjort *et al.* (1933) developed a “theory of fishing” based on analysis of aging data which demonstrated that the optimal rate of fishing occurred at intermediate exploitation rates (Holt, 2014). Thompson and Bell (1934) subsequently calculated the yield that resulted from different combinations of natural and fishing mortality. These contributions were followed by von Bertalanffy’s (1938) growth equation, Graham’s (1939) introduction of maximum sustainable yield (MSY), and Ricker’s (1944, 1945) work on instantaneous mortality rates and statistical methods for use in fisheries models. Finally, a short publication in *Nature* by Henry Hulme (an accomplished British mathematician) with Raymond Beverton and Sidney Holt (Hulme *et al.*, 1947) synthesized much of the previous modelling work into “a single, age-based yield equation as a function of recruitment, growth, natural mortality, and fishing mortality, commonly referred to as the ‘yield-per-recruit equation’” (Anderson, 2011).

These early theories and model developments set the stage for one of the biggest breakthroughs in quantitative ecological modelling, which became the foundation of theoretical fisheries science in the form of Beverton and Holt’s (1957) *On the Dynamics of Exploited Fish Populations* (Smith, 1988, 1994; Anderson, 2002; Quinn, 2003; Angelini and Moloney, 2007). Their book “probably constitutes the single most important contribution to fisheries science yet published” (Hilborn, 1994) and is widely regarded as “the most cited reference in fishery science” (Anderson, 2011). Most of the initial applications of Beverton and Holt’s “fundamentals of the theory of fishing” related to the catch equation, yield-per-recruit analysis, and stock-recruit functions (Holt, 1998, 2008). As recognized by Pauly (1986), the “theories of fishing” and models developed by early fisheries population modellers, which were codified in Beverton and Holt (1957), implicitly assumed a “unit” stock that ignored immigration, emigration, and spatial heterogeneity. However, Beverton and Holt understood that the cause of

fishery fluctuations were unlikely to be resolved without accounting for spatial dynamics, which had driven ecological research around the turn of the century, yet had been largely ignored during the subsequent development of quantitative fisheries methods. Thus, in the latter parts of Beverton and Holt (1957) they provided a succinct, yet thorough derivation of how movement could be accounted for in fisheries population models, as well as, tagging and yield-per-recruit analyses. Although their spatial models received less attention than the fundamental demographic models, they represent an important contribution to the fields of spatial ecology and population modelling.

Beverton and Holt’s movement models

Although Beverton and Holt (1957) developed a quantitative theory of fisheries that helped fisheries science leapfrog mathematical applications in terrestrial ecology (Worthington and Skellam, 1958), their treatment of movement relied heavily on the derivation of the random diffusion of animals developed by Skellam (1951). Skellam (1951) modified the logistic population growth model to include two-dimensional movement by adopting the kinetic theory for the physical diffusion of gases to represent large-scale animal movement and plant dispersal. Skellam’s approach was unique because it incorporated movement processes into population models and linked the actions of individuals with the expansion of a population over both time and space (Toft and Mangel, 1991).

Beverton and Holt (1957) rationalized the simplifying assumption of random diffusion for representing a fish’s general foraging strategy by suggesting that (p. 137):

“... we can imagine a bottom-living fish such as a plaice moving in a certain direction until it encounters a patch of food organisms, and after spending some time more or less stationary while feeding on these continuing the search for food in a direction which is random with respect to that in which it first approached the patch of food organisms. In this case the ‘inter-patch’ movement would be analogous to the ‘mean-free-path’ in the kinetic theory of gases and would be the level at which the random direction component is introduced.”

Therefore, the implied mechanism for continuous mixing of bordering populations was the small-scale movement of individuals (Goethel *et al.*, 2011). However, as Skellam (1951) demonstrated, each movement did not need to be random, and the frequency of movement could be used to determine the spatiotemporal scale at which movement could be considered random.

Beverton and Holt (1957) developed two movement model formulations. The first followed Skellam’s (1951) framework closely and was used for calculating the change in concentration from a given point, which was termed the “dispersion” model and based on the Fickian diffusion equation (Porch, 1995a). The change in density (or concentration, C) of fish within a two-dimensional region (x, y) over time (t) was described by

$$\frac{\partial C}{\partial t} = \frac{D}{4} \left(\frac{\partial^2 C}{\partial x^2} + \frac{\partial^2 C}{\partial y^2} \right) \quad 1$$

$$D = \frac{V^2}{n} = Vd = nd^2,$$

in which D was the dispersion coefficient, V was the velocity of movement, and d was the distance of the mean free path (i.e. the

average distance travelled between interactions that altered direction or other attributes; e.g. for gas particles this implies the distance between successive collisions), and n was the number of random movements per unit time. The dispersion model was applied to a time series of inshore and offshore abundance indices for North Sea Plaice (*Pleuronectes platessa*) assuming unidirectional offshore movement. The model was able to accurately recreate observed relative abundance patterns throughout the time series.

Beverton and Holt (1957) suggested that the mean free path may be more affected by external factors (e.g. predator or prey abundance) than by the concentration of the species being modelled (converse to the strict tenets of the kinetic theory of gas particles). This assumption was later embodied in the ecological theory known as the ideal free distribution, wherein the distribution of a species across space is proportional to the availability of free resources in each habitat patch (Fretwell and Lucas, 1969). Although the theory has been refined over time and adapted to include a variety of factors influencing the distribution of a species (e.g. animal personality; DiNuzzo and Griffen, 2020), the theoretical basis remains widely employed and represents a useful concept (Avgar et al., 2020). In fisheries, for instance, MacCall's (1990) "Basin Theory" models fish movement as a density-dependent process based on the ratio of abundance to carrying capacity across the distribution, which demonstrates how diffusion models can be refined by incorporating directed components (termed advection; discussed later in this section) that are linked to resource availability (e.g. prey abundance). Thus, although not strictly based on Beverton and Holt's (1957) diffusion models, frameworks utilizing the ideal free distribution follow the same underlying assumptions about random diffusion and generally support Beverton and Holt's (1957) interpretation of the mean free path as it relates to animal movement.

Application of the dispersion model required information on the location and time for each density observation, which was often not supported by traditional fisheries data (e.g. historical catch data). As a practical solution, Beverton and Holt (1957) developed a spatially discrete approximation to the dispersion model, which described the change in the abundance of fish (N) within spatial regions due to the instantaneous rate of diffusion (τ ; termed the transport coefficient) across a given region's boundary:

$$\frac{dN}{dt} = -\tau N. \quad 2$$

The transport coefficient represented a spatially discrete expression of the spatially continuous dispersion coefficient. Although the spatial discretization retained the basic tenets of random diffusion, it was better suited for the spatial resolution of traditional fisheries data (i.e. spatially stratified management units). Following from 2, the total change in abundance within two adjacent regions (subscripts 1 and 2) could then be described as a function of fishing mortality (F), natural mortality (M), and diffusion across the shared border:

$$\begin{aligned} \frac{dN_1}{dt} &= -(F_1 + M_1 + \tau_{1 \rightarrow 2})N_1 + \tau_{2 \rightarrow 1}N_2 \\ \frac{dN_2}{dt} &= -(F_2 + M_2 + \tau_{2 \rightarrow 1})N_2 + \tau_{1 \rightarrow 2}N_1. \end{aligned} \quad 3$$

However, solving this system of equations required complex and time-consuming numerical simulation, the feasibility of which

was limited due to the lack of digital computers (Goethel et al., 2011; Porch, 2018).

The finite difference approximation of the transport coefficient model with respect to time was developed and applied by researchers in the 1980s and 1990s using both tagging (e.g. Ishii, 1979; Sibert, 1984; Hilborn, 1990) and full population models (e.g. Quinn et al., 1990, Punt and Butterworth, 1994; Porch, 1995b). The resultant fully discretized version utilized difference equations that could be solved analytically, which became known as the "box-transfer" model. The box-transfer model utilized a transfer coefficient (T), the temporally discretized approximation to the transport coefficient, to represent the fraction of a population in a region that moved during a yearly time step, y :

$$\begin{aligned} N_{1,y+1} &= (1 - T_{1 \rightarrow 2})N_{1,y}e^{-(F_{1,y}+M_{1,y})} + T_{2 \rightarrow 1}N_{2,y}e^{-(F_{2,y}+M_{2,y})} \\ N_{2,y+1} &= (1 - T_{2 \rightarrow 1})N_{2,y}e^{-(F_{2,y}+M_{2,y})} + T_{1 \rightarrow 2}N_{1,y}e^{-(F_{1,y}+M_{1,y})}. \end{aligned} \quad 4$$

The approach represents a discrete Markovian movement model, because the probability of movement is the same for all fish in a region in a given year, regardless of their movement histories. The box-transfer model is analogous to the simplification of random diffusion in Newton's Law of Cooling given that both approaches are spatially discretized approximations of continuous theoretical models, which rely on assumptions of uniformity within the region (or object) of study (Beverton and Holt, 1957). For instance, Newton's Law assumes no temperature gradient within the radiating body, and the box-transfer model assumes no gradient in fish density appears throughout a geographic zone (Sibert et al., 1999).

The main underlying assumption of the spatiotemporally continuous Fickian dispersion model, the spatially discrete and temporally continuous transport coefficient model, and the spatiotemporally discrete box-transfer model is the representation of fish movement as random diffusion. However, the assumption allows for small-scale non-random movements that result in a net diffusive movement when viewed from a population-level spatial scale (Sibert et al., 1999). Beverton and Holt (1957) also investigated how a directed migration term could be incorporated, termed advection (Sibert and Fournier, 1994; Porch, 1995a). Their mostly qualitative advection-diffusion model partitioned the transport coefficient into upstream and downstream constituents based on dominant currents. Thus, Beverton and Holt (1957) demonstrated that the random movement assumption does not preclude incorporation of large-scale non-random processes, such as directed migrations (e.g. Jones 1959). However, they warned that careful consideration of these processes was warranted to ensure that model extensions adhered to the underlying assumptions, especially if the primary condition of movement as a random process, which stated that individual movements were independent, was violated (Codling et al., 2008; Smouse et al., 2010). Okubo (1980) demonstrated that the addition of an advection term in 1 represented the limiting form of an uncorrelated but biased (i.e. directional) random walk, whereas a Markovian random walk could be used to approximate the mean free path and purely random diffusion (i.e. as the bias term went to zero). Adding structure into a biased but uncorrelated random walk to account for migration behaviour, attraction to environmental gradients (e.g. temperature or prey fields), or carrying capacity is relatively straightforward (Sibert et al., 1999). Although home range behaviour, large-scale schooling, aggregation, and movement patterns of behavioural contingents (Secor, 1999),

which are common for pelagic fish, would violate the independent movement assumption, these dynamics can be addressed through appropriate alterations to modelling assumptions and the underlying movement process (e.g. use of correlated random walks or mean-reverting processes, see Section 5 Implications for Violation of and Recent Modifications to Beverton and Holt's Movement Model Assumptions; Codling *et al.*, 2008; Smouse *et al.*, 2010; Albertsen, 2019).

Similarly, an important implication of the spatial discretization in the transport and box-transfer models is that τ and T are functions of each region's perimeter (i.e. the size and shape of the geographic unit being modelled) as well as movement. By contrast, D in the dispersion model is only a function of movement (i.e. velocity). Beverton and Holt (1957) urged that the performance of the spatially discrete models would be enhanced if populations or areas were divided into spatial strata or regions that were "as small as is consistent with the accuracy of commercial statistics of catch and effort, since the smaller the size the more faithful will be the representation obtained." Additionally, Beverton and Holt's (1957) diffusion models also assume that fish instantaneously move during a time step, become "well-mixed" once crossing the boundary between regions, and that all fish in a region have the same probability of residence and movement. In reality, fish that are close to the border are more likely to cross the boundary, but at a population level, the relative rates at different locations within a region are likely to average out and sufficiently represent region-wide movement patterns. Despite these limiting assumptions, Beverton and Holt's (1957) diffusion models can often adequately approximate fish movement processes (Hilborn, 1990; Porch, 1995a; Goethel *et al.*, 2011).

Despite the box-transfer model being a gross simplification of the dispersion model, the greater utility of the box-transfer concept can be appreciated in the context of the even simpler "unit stock" concept (Cadrin and Secor, 2009). Most conventional stock assessment models assume no movement across stock boundaries and complete mixing within stock areas. Allowing for connectivity and spatial variation in demographic parameters among regions or simultaneously modelling multiple population units is a meaningful step towards realism and a better understanding of population processes that can be supported with existing information (Berger *et al.*, 2017b; Punt, 2019a, b). Sibert *et al.* (1999) argue that "the challenge for fisheries is not whether the diffusion framework is suitable, but rather to explicitly include population movement and spatial structure in stock assessment models. Diffusion models are one class of models that appear to work." Beverton and Holt (1957) end their section on dispersal by suggesting that care should be taken when applying movement models because of the approximate nature and reliance on spatially explicit data: "... neither knowledge of the mechanisms of dispersion nor accuracy of data and commercial statistics is sufficient to justify the labour involved in a rigorous treatment ...". Additional barriers to applying their models included the lack of complex statistical methods and the associated computing power needed to estimate numerous parameters. However, the basic tenets for incorporating spatial heterogeneity and movement within various types of fisheries models saw both immediate and long-term application.

Revival and adaptation of Beverton and Holt's movement models in fisheries science

The single-species demographic convention of stock assessment grew out of Beverton and Holt's (1957) treatise. Although

assessment scientists recognized that fish move and that "closed" population assumptions were violated by many species, the parsimonious nature of model development, data limitations, and technological constraints precluded complex stock assessment models involving multiple areas and movement. Thus, the aspect of Beverton and Holt's (1957) work on spatial modelling that gained the most immediate traction was the incorporation of movement into tagging analyses. Once estimates of connectivity from tagging data became more widely available, researchers began applying extensions to yield-per-recruit (YPR) models to account for movement of fish and spatial heterogeneity in population parameters. YPR approaches provided a relatively simplistic modelling framework and basic data needs for the provision of management reference points, as compared to full stock assessment frameworks that allowed estimation of abundance and mortality. The complementary advance in computing power led to the "golden age" of quantitative fisheries modelling in the 1980s and 1990s (Quinn, 2003). By the mid-1990s, spatial data collection and statistical modelling had advanced to a point that the application of Beverton and Holt's (1957) movement models could be supported within spatial stock assessments (Berger *et al.*, 2017b). We briefly explore the temporal development of applications of Beverton and Holt's (1957) movement models within fisheries science, starting with tagging models, and concluding with state-of-the-art spatially explicit tag-integrated stock assessments.

Application of Beverton and Holt's models for analysis of tagging data

Analysis of tagging data has evolved, from descriptive mapping and statistics of opportunistic release-recapture data that document movement patterns (Hall, 2014) to more structured release-recapture designs and model-based analysis to estimate movement rates (Amstrup *et al.*, 2006). As Goethel *et al.* (2011) outline, two general methods to analyse tagging information developed out of Beverton and Holt's (1957) movement models: the advection-diffusion-reaction (ADR) models and box-transfer models. The differences in model structure were largely driven by the available data and the goal of the analyses (Goethel *et al.*, 2011). The dispersion model, as altered to account for advection and diffusion, allowed for identification of both random diffusion rates and directional migrations from specific release points. But, the dispersion or ADR approach required the availability of relatively precise release and recapture information. Soon after Beverton and Holt's (1957) publication, Jones (1959) applied the dispersion model in his analysis of tag returns for haddock (*Melanogrammus aeglefinus*) off the Scottish coast using the assumption that there was a "... superimposed directional component of the movement such that the centre of density of the whole fish group actually moves with some velocity ...," which was further explored for yellowfin tuna (*Thunnus albacares*) in the Eastern Pacific by Bayliff and Rothschild (1974).

Following Okubo's (1980) derivation of the advection-diffusion model as a biased random walk, the dispersion model morphed into modern ADR models developed in a series of applications that analysed tagging data to estimate movement rates of Pacific tunas. Deriso *et al.* (1991) analysed data from two dart tagging experiments for eastern Pacific yellowfin tuna by estimating velocity, diffusion, and "direction" (i.e. advection) and deriving discrete transition probabilities among a uniform grid of

spatial strata. Sibert and Fournier (1994) simulation tested advection–diffusion models to evaluate model performance with spatiotemporal patterns in tag recoveries. Sibert *et al.* (1999) developed a general ADR model framework, which utilized finite difference approximations, to estimate movement and mortality of skipjack tuna. Results indicated that the movement model had advantages over a spatially aggregated model for estimating mortality. The generalized ADR model has since been applied widely to analyse conventional and electronic tagging data for many tuna fisheries (e.g. Sibert and Fournier, 2001; Adam and Sibert, 2002). Kleiber and Hampton (1994) analysed data from tagged skipjack tuna with an advection–diffusion–mortality model that included attraction parameters for islands and fish aggregation devices. Such attraction parameters have been widely applied to expand ADR movement models by incorporating habitat attraction covariates, which set the advection component proportional to a habitat preference index. Habitat preference has been based on either abiotic factors (e.g. sea surface temperature) or prey density (Bertignac *et al.*, 1998; Faugeras and Maury, 2007; Lehodey *et al.*, 2008). In general, models that actively account for the causal behaviour leading to movement (i.e. when a heterogeneous home range is optimally utilized for differing processes like foraging, safety, or movement; Getz and Saltz, 2008) are becoming more widespread, especially with the increased collection of electronic tagging data (Patterson *et al.*, 2008), but applications to marine fish species are often limited by data constraints. Extensive spatially resolved data allow fine-scale grids to be implemented in Sibert *et al.*'s (1999) finite difference approximation to ADR models, but data gaps often limit the spatial scale at which estimation models can be applied (Sibert and Fournier, 1994; Goethel *et al.*, 2011). However, the ADR approach has become the basis for many fine-scale, quasi-estimation population simulation models that explore ecosystem functioning along with biotic and abiotic drivers of population dynamics (e.g. SEAPODYM; Lehodey *et al.*, 2008; Senina *et al.*, 2020).

In one of the only applications of the transport coefficient model, Miller and Andersen (2008) modelled movement of Atlantic bluefin tuna (*Thunnus thynnus*). Using a continuous time, discrete space framework allowed modelling movement and mortality processes simultaneously as instantaneous rates. Although modelling movement as a continuous process may reduce bias compared to discrete time models if large-scale movement patterns occur throughout the time step, assuming a continuous movement rate may impose bias if movement occurs during a brief period of time (e.g. if fish are relatively sedentary, but undergo a long-range spawning migration at a well-defined point in time).

Use of the box-transfer movement model has been widely applied where tagging data are used to estimate movement rates between geographic zones by matching observed and predicted tag recaptures by region. The simplified dynamics, including closed form solutions in most instances, and ability to estimate parameters from coarse data have often been cited as rationale for using the box-transfer model (Sibert *et al.*, 1999; Sippel *et al.*, 2015). Box-transfer models are more amenable to modelling the net dynamics of the entire population within a given region, as opposed to the focus on dispersion from a specific release point or location within a species distribution (Goethel *et al.*, 2011; Sippel *et al.*, 2015). Ishii (1979) investigated the movement of tagged yellowfin tuna (*Thunnus albacores*) in coastal Mexico, and Sibert (1984) used a similar approach to model the transfer of tagged skipjack

tuna (*Katsuwonus pelamis*) in the South Pacific. Hilborn (1990) provided a generalized tagging model based on Beverton and Holt's (1957) original work that calculated predicted tag returns for multiple regions using a maximum likelihood formulation to estimate model parameters, such as transfer and harvest rates. The box-transfer approach has been widely utilized and adapted over the last two decades to account for complex movement patterns and alternate tag types (e.g. Kurota *et al.*, 2009; Aires-da-Silva, 2009; Eveson *et al.*, 2012; Hanselman *et al.*, 2015). Additionally, habitat preference and spawning migrations can be incorporated (e.g. Herbst *et al.*, 2016).

Because box-transfer models simplify the movement dynamics, they may suffer from scale dependency issues and often do not explicitly account for directed movement. Conversely, the methodology is more readily incorporated into population models, particularly stock assessments, because they allow estimation of population-level net movement parameters at which scale these dynamic pool models often operate (Goethel *et al.*, 2011; Sippel *et al.*, 2015). Thus, estimates of population scale movement from box-transfer tagging models spurred the development of a variety of spatially explicit stock assessment frameworks (Berger *et al.*, 2017b).

Spatial yield-per-recruit and marine protected areas

Based on the derivation of random diffusion, Beverton and Holt (1957) adapted the YPR model to incorporate movement among regions. In particular, they focused on the impact of implementing different-sized closed areas when fish were allowed to move across the boundary. Results indicated that closed areas effectively delayed the age of recruitment to the fishery resulting in a shift towards an older age structure, and slight increases in yield for highly utilized stocks with moderate movement rates. As reviewed in Guénette *et al.* (1998), Gerber *et al.* (2003), and Fogarty and Botsford (2007), the closed area YPR models became the theoretical basis for the wide implementation of marine protected areas (MPAs). Marine reserve models now often incorporate complete life cycle models including stock-recruit relationships, hydrodynamic-driven larval dispersal models, and complex adult movement dynamics (e.g. diffusion, home range or aggregation behaviour, and environmental forcing; Grüss *et al.*, 2011; Cornejo-Donoso *et al.*, 2017; White *et al.*, 2019). However, most of these approaches are simulation models based on life history information, while estimates and functional forms of juvenile and adult movement are often based on expert opinion. Although Punt and Ciu (2000) demonstrate how a spatial YPR model can be applied with direct estimation from observed data, the approach does not attempt to estimate movement directly, instead utilizing a functional form linked to length using the box-transfer movement model. Once reliable estimates of movement rates between stock areas were available from tagging studies, movement modelling was able to advance beyond the comparatively simple equilibrium YPR models and begin exploring direct incorporation of spatial structure and movement in full stock assessment frameworks.

Spatially explicit stock assessment models

The development of spatial stock assessment models can be categorized into three approximate phases: development (1957–2001); exploration (2001–15); and application (2015–Present; Table 1). The development stage was characterized by proof of

Table 1. The three periods of spatial stock assessment model development including influential research during each period.

	Development	Exploration	Application
Time period description	1957–2001 The initial period of spatial modelling focused on development of tools and determination of feasibility. Research during this period provided applied proof-of-concept studies.	2001–15 The second period put emphasis on exploration of model robustness and identifying critical aspects of spatial dynamics that needed to be incorporated. Research during this period primarily utilized simulation studies to determine bias based on the known underlying simulated dynamics.	2015–Present The present period is characterized by generalized stock assessment models that allow for spatial structure. A paradigm shift in stock assessment modelling has emphasized the use of applied spatial assessment models as the basis for fisheries management advice, but simulation testing remains a fundamental aspect of current spatial modelling research.
Influential research	Beverton and Holt (1957) Aldenberg (1975) Quinn <i>et al.</i> (1990) Butterworth and Punt (1994) VPA 2-Box (Porch 1995b; Porch, 2018) Maunder (1998) MULTIFAN-CL (Fournier <i>et al.</i> , 1998; Hampton and Fournier 2001) Punt <i>et al.</i> (2000) Porch <i>et al.</i> (2001)	Maunder (2001) Miller <i>et al.</i> (2008) Drouineau <i>et al.</i> (2010) Cope and Punt (2011) Taylor <i>et al.</i> (2011) Ying <i>et al.</i> (2011) Carruthers <i>et al.</i> (2011, 2015) Hulson <i>et al.</i> (2011, 2013) Su <i>et al.</i> (2012) Guan <i>et al.</i> (2013) Goethel <i>et al.</i> (2015a,b) McGilliard <i>et al.</i> (2015)	Li <i>et al.</i> (2015, 2018) Punt <i>et al.</i> (2015, 2016, 2017, 2018) Fu <i>et al.</i> (2017) Lee <i>et al.</i> (2017) Vincent <i>et al.</i> (2017, 2020) Vigier <i>et al.</i> (2018) Goethel <i>et al.</i> (2019, 2020) Cao <i>et al.</i> (2020) Mormede <i>et al.</i> (2020) Assessment Platforms CASAL and CASAL 2 (Bull <i>et al.</i> , 2012) SS3 (Methot and Wetzel, 2013) SPM (Dunn <i>et al.</i> , 2020)

concept studies demonstrating how spatial models could be implemented based on [Beverton and Holt's \(1957\)](#) relatively simple movement models, highlighting the data inputs required, and culminating in the development of generalized assessment frameworks that could account for spatial structure. Once the feasibility of spatial stock assessments was established, the exploration phase began to highlight the robustness of spatial models to process error and data limitations, often through simulation analysis. In the last 5 years, as the reliability of spatial models has been more thoroughly demonstrated, there has been a proliferation of spatially explicit stock assessments that have now been utilized for the provision of management advice, indicating progression into the application stage of spatial models ([Punt, 2019b](#)). We briefly outline each phase below.

Development Phase (~1957–2001)

[Aldenberg \(1975\)](#) is widely recognized as the first researcher to explore the inclusion of movement into spatial stock assessment applications using [Beverton and Holt's \(1957\)](#) transfer coefficient model. Despite the lack of an analytical solution preventing estimation of parameters, [Aldenberg \(1975\)](#) demonstrated through numerical simulation that migration was likely to result in biased recruitment estimates when productivity differed greatly among regions. Once the discretized box-transfer model (and the associated analytical solution) became widely recognized, a number of modelling frameworks were developed concurrently in the early 1990s. Migratory catch-age analysis ([Quinn *et al.*, 1990](#)) incorporated estimates of movement rates for Pacific halibut (*Hippoglossus stenolepis*) from an external tagging model, which

helped reduce statistical bias in the spatial assessment model. Spatially explicit VPA frameworks were used to investigate the effect of movement between the eastern and western Atlantic bluefin tuna (*Thunnus thynnus*) populations (e.g. [Butterworth and Punt, 1994](#); [NRC, \(National Research Council\), 1994](#)). However, the inability of early spatially explicit assessments to analyse tagging data directly within model frameworks led to a number of limitations including loss of information, inconsistencies between modelling assumptions, difficulty in determining error structure and including uncertainty, and reduced diagnostic ability ([Maunder, 2001](#)).

Early applications to Atlantic bluefin tuna utilized region-specific tag recapture ratios aggregated across years to help directly estimate time-invariant movement among regions (e.g. [Porch, 1995b](#); [Porch *et al.*, 1995](#); [Punt and Butterworth, 1995](#); [Porch and Turner, 1998](#)). However, the aggregated approach to fitting tagging data often masked signals across years and did not always provide improved estimates of regional abundance compared to models that ignored movement ([Porch *et al.*, 1998](#)). In the late 1990s, fully “tag-integrated” models were developed to analyse tagging data directly within the assessment by incorporating a full tag attrition sub-model and fitting the disaggregated, cohort specific tag recaptures ([Maunder, 1998](#); [Goethel *et al.*, 2011](#)). Tagging models (e.g. [Hilborn, 1990](#)) were run as a sub-model within the assessment, which contributed to a combined objective function that simultaneously compared observed and predicted tag recaptures along with typical fisheries data such as catch, age or length composition, and abundance indices. Simultaneous statistical estimation of all parameters in the assessment, such as movement rates and fishing mortality, was then undertaken, and

the parameters were applied to the tagged and untagged populations.

Maunder (1998) developed one of the first statistical catch-at-age (SCAA) based tag-integrated modelling frameworks and applied it to New Zealand snapper (*Pagrus auratus*) with multiple stocks. The model was termed the integrated tagging and catch-at-age analysis (ITCAAN) and was flexible and easily adapted to various species (Maunder, 2001). Punt *et al.* (2000) developed a similar model for school shark (*Galeorhinus galeus*) off Australia by allowing for movement between two populations, under the assumption that no interbreeding occurred (i.e. animals exhibited natal fidelity). Eight regions were modelled assuming a monthly time step with movement rates estimated for each time step using tagging data from 1947 to 1999. The generic software package MULTIFAN-CL (Fournier *et al.*, 1998) was adapted to address the spatial structure and movement dynamics of tuna in the Western Pacific utilizing a length-based, tag-integrated framework. Originally developed for western Pacific yellowfin tuna (*Thunnus albacares*) distributed across seven spatial strata (Hampton and Fournier, 2001), the spatially explicit tag-integrated version of MULTIFAN-CL has since been applied to a wide variety of tunas and billfishes (Punt, 2019a).

The body of research on spatial modelling with Atlantic bluefin tuna resulted in the generalized assessment package VPA 2-Box (2018), which has been widely used within the International Commission for the Conservation of Atlantic Tunas (ICCAT) community (and elsewhere) since the late 1990s. A unique addition in VPA 2-Box is the inclusion of both a diffusion and overlap movement model, the latter accounted for natal homing behaviour by assuming fish of multiple populations intermixed throughout the year based on estimated diffusion parameters, but returned to their natal population to spawn. Taylor *et al.* (2011) later developed the multi-stock age-structured tag-integrated stock assessment model for Atlantic bluefin tuna, which used an SCAA framework to model five geographic zones and incorporated multiple tagging datasets and tag types (i.e. conventional tags, archival tags, and satellite tags).

Several generic assessment platforms have since incorporated spatial structure, including Stock Synthesis 3 (SS3; Methot and Wetzel, 2013), CASAL (Bull *et al.*, 2012), and the Spatial Population Model (SPM; Dunn *et al.*, 2020), all of which utilize the box-transfer approach. Each platform incorporates time- and age-varying movement rates. For instance, SS3 incorporates a linear ramp to accommodate age-variation whereas CASAL assumes that age-based movement is linked to maturity. CASAL and its successor CASAL2 (<https://github.com/NIWAFisheriesModelling/CASAL2>) also allow for density-dependent migrations based on the relative abundance among regions, as well as, home fidelity behaviour (i.e. natal homing migrations similar to the overlap model of VPA 2-Box). SPM provides the most flexible spatial structure and movement parametrizations, which includes the ability to utilize preference functions similar to many ADR approaches (Dunn *et al.*, 2020; Mormede *et al.*, 2020).

Exploration phase (~2001–15)

Around the turn of this century, ignorance of spatial population structure and connectivity became widely recognized as important factors contributing to the decline of many important fisheries worldwide (Smedbol and Stephenson, 2001; Hilborn *et al.*, 2003; Berkeley *et al.*, 2004). Improved understanding of spatial

structure in marine populations through multidisciplinary stock identification techniques (Cadrin *et al.*, 2014) was impetus to achieve alignment of biological and management boundaries (Kerr *et al.*, 2017; Cadrin, 2020), while simultaneously pursuing spatial stock assessment approaches that could better account for biocomplexity (Berger *et al.*, 2017b).

Spatial stock assessment modelling in the 2000s and early 2010s was largely characterized by a mixture of exploratory applications and theoretical simulations. The goal was often to demonstrate the feasibility of spatial modelling applications, compare the results to existing non-spatial assessments used for management, and explore potential biases in both modelling approaches through simulation analysis (Cadrin *et al.*, 2019). For instance, Goethel *et al.* (2015a) developed a three-region spatial metapopulation model of yellowtail flounder (*Limanda ferruginea*) off New England and applied it to available fishery, survey, and mark-recapture data. The approach was then utilized to develop a tailored operating model to test the robustness of various parametrizations of spatial and non-spatial assessment models to density-dependent movement, data uncertainty, and tagging assumptions (Goethel *et al.*, 2015b). A similar framework was undertaken for Bering Sea pollock (*Theragra chalcogramma*) in which Miller *et al.* (2008) developed a spatially explicit model, which was then simulation tested to explore the potential benefits of developing a hypothetical mark-recapture program (Hulson *et al.*, 2011) and the robustness to climate-induced movement and recruitment patterns (Hulson *et al.*, 2013). Although neither spatial assessment approach was adopted for management advice, both models helped improve understanding of stock structure and inform spatial management decisions. Despite most developments involving box-transfer movement models, applications of ADR models to skipjack tuna were also expanded to integrate fishery catch and size composition data (Senina *et al.*, 2008) and tagging data (Senina *et al.*, 2020).

To overcome issues related to uncertainty in the robustness of spatial assessment approaches, several spatially explicit simulation and management strategy evaluation (MSE) frameworks (i.e. the use of closed-loop feedback simulations to determine the robustness of assessment-management frameworks for providing sustainable harvest recommendations) were developed for both generalized and tailored applications (Berger *et al.*, 2017b; Punt, 2019a,b). The majority of simulation studies have compared the robustness of spatially explicit assessment approaches to spatially aggregated counterparts, often demonstrating that spatial models are more robust to uncertain population structure, demographic heterogeneity, and connectivity (e.g. Cope and Punt, 2011; Carruthers *et al.*, 2015; McGilliard *et al.*, 2015; Punt *et al.*, 2015). In particular, implementation of marine protected areas is highly problematic for non-spatial assessment models, whereas spatially explicit approaches have been able to adequately address the fishery and population spatial structure that results (Pincin and Wilberg, 2012; McGilliard *et al.*, 2015; Punt *et al.*, 2016). Although MSEs have demonstrated that non-spatial assessment may perform adequately when combined with robust harvest strategies, spatial assessments tend to provide more preferred management outcomes across a wider range of uncertainties (Dichmont *et al.*, 2006; Ying *et al.*, 2011; Benson *et al.*, 2015; Punt *et al.*, 2017).

However, acceptance of spatially explicit assessments as the basis for developing fisheries management advice was impeded by a number of factors including increased model complexity, lack of

spatially resolved data or reduced sample sizes when data was broken down by populations or areas, limited understanding by managers and stakeholders, uncertainty regarding model robustness, and institutional inertia (Berger *et al.*, 2017b; Punt, 2019a,b). For instance, spatial models for European hake (*Merluccius merluccius*; Drouineau *et al.*, 2010; Vigier *et al.*, 2018) and Atlantic bluefin tuna (Taylor *et al.*, 2011; Morse *et al.*, 2020) were introduced over a decade ago (almost three decades in the case of bluefin tuna) but are still not directly used for management decisions. Although data limitations remain a primary impediment in many instances, integrated modelling frameworks are often robust to sparse data (e.g. data are not needed for every area and year combination; Maunder and Punt, 2013), tagging data are not always required (Miller *et al.*, 2008; McGilliard *et al.*, 2015) and tag releases can be performed sporadically (Goethel *et al.*, 2019). Additionally, spatial models of intermediate complexity (e.g. accounting for a spatial structure without movement) can still often perform better than ignoring spatial structure completely (Kerr *et al.*, 2017; Cadrin *et al.*, 2019). The advancement of spatially structured stock assessment models was recognized by a session on spatial complexity at the World Conference on Stock Assessment Methods (ICES, 2013; Cadrin and Dickey-Collas, 2014), where we were coincidentally fortunate to hear Sidney Holt's perspectives on the topic of applying more realistic models for stock assessment (Figure 3).

Application phase (~2015–Present)

Over the last 5 years a number of factors have led to the promotion of spatially explicit assessments for the basis of fisheries management advice including: better understanding of the importance of population structure, improved techniques for stock identification, a variety of applications demonstrating the feasibility of spatial assessment models, and simulation work illustrating the improved robustness of spatially explicit models compared to non-spatial counterparts (Berger *et al.*, 2017a,b; Punt, 2019a,b; Cadrin, 2020). In the most thorough review of the literature on spatial assessment approaches to date, Punt (2019a) noted that prior to 2010 only a handful of spatially explicit

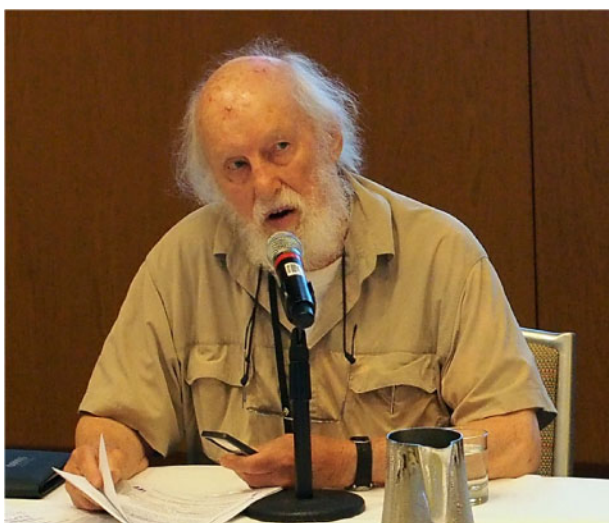


Figure 3. Sidney J. Holt at the 2013 World Conference on Stock Assessment Methods (WCSAM; ICES 2013).

assessment models had been utilized as the basis of management advice, mainly for large pelagic species in the Indian and Pacific oceans. Although it is not surprising that most applications involved wide-ranging and highly mobile species, recent research has clearly demonstrated that spatial structure can be as important for less mobile reef and groundfish populations (Cadrin *et al.*, 2019). However, Punt (2019a) goes on to illustrate that, since 2010, there has been a proliferation of spatial assessments for coastal species, such as snapper, rockfish, coastal pelagics, and invertebrates, which have been used for management advice across the globe (e.g. Australia, New Zealand, South Africa, the United States, and Canada). After more than 60 years, it appears that fisheries assessment and data collection techniques have evolved to adequately address the potential pitfalls caused by spatial structure and connectivity, as outlined by Beverton and Holt (1957).

Implications for violation of and recent modifications to Beverton and Holt's movement model assumptions

Movement model assumptions have been adapted over the last six decades from the simple diffusion models of Beverton and Holt (1957) to account for the complex movement patterns and spatial population structures that are now widely observed in aquatic populations. However, best practices for spatial stock assessment, identified through application and simulation testing, are generally consistent with Beverton and Holt's (1957) movement models and associated assumptions (Goethel *et al.*, 2011; Punt, 2019b). The performance of stock assessments largely depends on accurate representation of spatial extent and structure, in which spatial strata reflect patterns of variation in the fish population and the fishery (Cadrin *et al.*, 2019; Cadrin, 2020). For instance, Berger *et al.* (2021) demonstrated that misalignment of management and population boundaries led to biased area-specific assessments. Accurate stock identification and boundary alignment is a prerequisite to robust assessment performance, but adequately representing spatial population structure, fishery distribution, and connectivity among population units is often also necessary (Berger *et al.*, 2017; Punt, 2019a). Although integrated ADR models have been developed (e.g. Senina *et al.*, 2008, 2020), the box-transfer model, which is directly based on Beverton and Holt's (1957) random diffusion models, still forms the basis of most spatial stock assessment approaches. Porch (1998) provided one of the few explorations of the bias associated with violating the box-transfer random diffusion assumptions in spatial assessments by utilizing an ADR framework to simulate the dynamics of two populations emulating Atlantic bluefin tuna. The box-transfer assessment model (e.g. VPA 2-Box) performed well under high mixing scenarios, but performance was similar to that of models that ignored connectivity, particularly at low movement levels. However, the spatial assessment model was fit to temporally aggregated tagging data, which may have impeded performance. Simulation–estimation experiments that specify box-transfer movement in both the operating and assessment models suggest that spatial models are often robust to the underlying connectivity dynamics, unless they mis-specify the primary pattern of movement (e.g. ontogenetic or time-varying movement; Carruthers *et al.*, 2015; Goethel *et al.*, 2015b, 2020; Lee *et al.*, 2017). Furthermore, the inclusion of tagging data (by release cohort) often improves the performance of spatial

assessments, particularly for estimating complex movement patterns, but care must be taken to adequately model important tag recovery processes (e.g. reporting rate, tag loss, tag mortality, and tag mixing; [Maunder, 2001](#); [Carruthers, 2011](#); [Hulson *et al.*, 2011, 2013](#); [Goethel *et al.*, 2015b, 2019](#); [Vincent *et al.*, 2017, 2020](#)). Similar studies have demonstrated that spatial models appear robust to misspecification of both the number of areas modeled ([Punt *et al.*, 2018](#)) and assumptions regarding the underlying spatial population structure (e.g. misdiagnosing a single population with spatial heterogeneity as a metapopulation and vice versa; [Bosley *et al.*, 2019](#)).

The understanding of connectivity dynamics and spatial population structure of marine species is evolving. Improved knowledge of spatial processes necessitates expansion and adaptation of the underlying assumptions of spatial models to address the variety of potential drivers of connectivity, while also carefully addressing the assumptions associated with movement parametrizations and exploration of their robustness when these assumptions are violated. Furthermore, a better understanding is required of whether box-transfer approaches can adequately reflect net population-level movement resulting from directed movements of individuals using individual-based models (IBM), ADR frameworks, or other approaches that can simulate fine-scale dynamics and the complex movement patterns that result from the behaviour of individuals (e.g. by incorporating the movement ecology paradigm, [Nathan *et al.* 2008](#), into fisheries spatial simulation tools). Similarly, using a continuous-time ADR simulator (e.g. SEAPODYM; [Senina *et al.*, 2020](#)) could further elucidate whether the continuous-time transport coefficient movement model (e.g. [Miller and Anderson, 2008](#)) may better reflect the continuous movement dynamics of marine species compared to discrete, instantaneous box-transfer assumptions.

As noted by [Beverton and Holt \(1957\)](#), accounting for directed movement, whether due to dominant currents, attraction to preferred habitat, or life history migrations (e.g. related to ontogeny or spawning), represents a critical necessary alteration to the random diffusion model for many species. The natal homing assumption (also termed overlap or natal fidelity), wherein there is spatiotemporal overlap of populations, but no interbreeding occurs, has been widely applied to account for return spawning migrations to natal populations (e.g. [Porch *et al.*, 2001](#); [Taylor *et al.* 2011](#); [Guan *et al.*, 2013](#); [Li *et al.*, 2015, 2018](#); [Vincent *et al.*, 2017](#)). Accounting for more fine-scale contingent structure or learned migration behaviour (e.g. entrainment) may also be feasible but has yet to be incorporated into full estimation spatial assessment models ([Secor *et al.*, 2009](#); [Kerr *et al.*, 2010](#); [MacCall *et al.*, 2018](#)) and may require alternate movement processes (e.g. correlated random walks; [Codling *et al.*, 2008](#); [Smouse *et al.*, 2010](#)).

Habitat preference functions (i.e. the intrinsic attraction to a region based on extant environmental properties or distance between regions) or environmental covariates are increasingly being used to help inform time-varying and age-based movement estimates in spatial stock assessments (e.g. [Porch, 2004](#); [Su *et al.*, 2012](#); [Fu *et al.* 2017](#); [Mormede *et al.*, 2020](#)). Functional forms, such as linear ramps or linking movement to maturity, reduce the number of estimated parameters while enabling incorporation of ontogenetic movement (e.g. [Bull *et al.*, 2012](#); [Methot and Wetzel, 2013](#)). Similarly, gravity models, which derive movement parameters from estimates of regional residency, can help reduce the number of parameters being estimated either for time-varying or

age-varying models (e.g. [Carruthers *et al.*, 2011](#); [Taylor *et al.*, 2011](#)), and are easily extended to account for directed or age-based movement patterns (e.g. through addition of viscosity terms or functional forms; [Carruthers *et al.*, 2015](#)). Density-dependent movement assumptions can account for time-varying directed connectivity patterns by relating the probability of movement to the assumed region-specific carrying capacity and relative abundance among areas ([MacCall, 1990](#); [Bull *et al.*, 2012](#); [Goethel *et al.*, 2015b, 2019, 2020](#)). [Goethel *et al.* \(2020\)](#) demonstrate that box-transfer models of intermediate complexity (e.g. estimating ontogenetic and time-varying connectivity using age- and time-blocked movement parameters) can adequately account for complex and unknown movement patterns (e.g. density-dependent, ontogenetic, and climate-induced distributional shifts). However, further simulation analysis is required to determine whether the variety of alternate movement parametrizations can be feasibly applied and if they are more robust compared to simple box-transfer assumptions.

Discussion

It is often easy to take our predecessors' accomplishments for granted and overlook important lessons they learned. Scientific progress is an iterative process, which requires understanding the historical development of knowledge such that new hypotheses can be built, tested, and refined to build upon and improve existing paradigms. As [Schnute and Richards \(2001\)](#) poignantly note:

“From a historical perspective, mathematical fishery models have a natural evolution that begins with the attempt to make sense of biological and catch data collected from fisheries. Pieces of the puzzle have accumulated from a diverse literature on growth, mortality, recruitment, and the effects of fishing. By combining these pieces into a unified whole, the scientist obtains a modern fishery model, and this achievement feels like progress. Because the assumptions have strong historical roots, the modeller can easily ignore their role as rather arbitrary constraints and focus instead on the seemingly worthy goal of integrating the known data into a unified whole...[However] proper use of fishery models comes from a frank recognition of their limitations.”

Utilizing previously developed models without understanding their historical development and associated limitations can be problematic, often leading to models being applied outside the limits of the assumptions for which they were originally developed, and, eventually, inaccurate outputs or model failure.

So, what have we learned from a historical review of [Beverton and Holt's \(1957\)](#) movement models? First and foremost, assumptions matter, especially when developing spatially explicit models ([Hoshino *et al.*, 2014](#); [Berger and Goethel, 2017](#); [Riecke *et al.*, 2019](#)). Many of the underlying assumptions of spatial fisheries models are defined by the tenets outlined in [Beverton and Holt \(1957\)](#), in particular that fish movement can be quantified to emulate the random diffusion of a gas particle. Movement of demersal fishes, such as most flatfishes, generally conform to the random diffusion assumption. However, [Beverton and Holt \(1957\)](#) cautioned that many species do not fit this assumption due to non-random movement patterns, because of behavioural tendencies like schooling or long-distance directed migrations to spawning areas. Alternate assumptions regarding movement have

been developed for these situations, including habitat attraction (e.g. [Porch, 2004](#); [Mormede et al., 2020](#)) and natal homing models (e.g. [Porch et al., 2001](#); [Bull et al., 2012](#)), but careful testing of the feasibility and appropriateness of incorporating alternate hypotheses is required. It is not necessary for spatial models to perfectly reflect the underlying dynamics (e.g. the number of areas, population structure, or movement parametrization) for them to provide adequate, and improved (compared to non-spatial assessments) management advice ([Punt et al., 2018](#); [Goethel et al., 2020](#)).

However, the box-transfer approach should not be blindly applied without first exploring information on stock structure and migration behaviour. Using inaccurate and outdated assumptions can cause a severe underestimation of uncertainty ([Hilborn and Liermann, 1998](#)) and contradicts the attitude of the pioneers of fisheries science whom sought to challenge all theories that were treated as dogmatic. We suspect that Ray Beverton and Sidney Holt would agree that treating any fisheries model as infallible invites misuse or misspecification. When new data become available through technological advances (e.g. Vessel Monitoring Systems, electronic tags, or genetic methods) or breakthroughs in understanding of population processes occur (e.g. evidence of complex behaviour), we are compelled to incorporate these new sources of information and subsequently test model performance and the appropriateness of associated assumptions. However, model refinement requires a thorough understanding of the basic assumptions to better understand how they can be accurately applied and altered. All models are necessarily a gross simplification of the natural processes that are being emulated ([Schnute and Richards, 2001](#)). But, because spatial stock assessments can more realistically reflect population structure, fishery and resource distribution, and connectivity dynamics, there is an increased probability that resultant advice will better enable sustainable fisheries management ([Punt et al., 2017](#); [Cadrin et al., 2019](#); [Berger et al., 2021](#)).

There is also much to learn from historical applications of spatial models that can help avoid reinventing the wheel. For instance, [Aldenberg \(1975\)](#), in one of the first spatially explicit assessment explorations, noted that large productivity differences among regions was likely to bias recruitment estimates in spatial assessment models. However, seldom is [Aldenberg \(1975\)](#) cited for noting this important performance issue with spatially explicit assessment models, which has been subsequently proven correct based on simulation (e.g. [Goethel et al., 2015b](#); [Vincent et al., 2017](#)). Clearly, there is a wealth of insight that can be garnered by modern assessment scientists from deeper exploration of historical spatial models like those developed by [Beverton and Holt \(1957\)](#). [Rothschild \(2015\)](#) supports this assertion, stating that

“A coherent development of knowledge requires an understanding of its provenance. Without such provenance, the student is forced to consider each and every paper independently, constraining a refined criticism and the scientific structure of the ideas that we are attempting to advance . . . How can a field progress if the pillars on which it is built are not read or acknowledged?”

Future directions

[Beverton and Holt \(1957\)](#) could not have foreseen the variety and complexity of many modern stock assessment modelling

approaches that developed from their foundational work. However, their relatively short section on spatial modelling is likely to continue to influence many future facets of fisheries science. For instance, the rapidly increasing application of spatio-temporal models that account for spatial autocorrelation using habitat and species associations (e.g. [Thorson, 2019](#); [Cao et al., 2020](#)) share basic tenets with [Beverton and Holt's \(1957\)](#) continuous time, continuous space dispersion model altered to account for external controls ([Planque et al., 2011](#)).

In the future, we anticipate that the increasing availability of high-resolution spatial data (e.g. tracks of individual animals from satellite and archival tags and precise time and location of fishing from VMS data) will continue the trend of modelling continuous spatial processes (e.g. the dispersion and transport coefficient models), particularly using full spatiotemporal models (e.g. [Cao et al., 2020](#); [Mormede et al., 2020](#)). The increased quantity and spatiotemporal precision of these data will allow finer model resolution, while improving estimation capabilities and, thereby, removing much of the impetus for utilizing box-transfer approaches (i.e. limited, coarse data). We also envision increased cross-platform development of spatiotemporal models where, for instance, modelling approaches become more blended (e.g. integration of spatial autocorrelation approaches used in species distribution models into spatially stratified modelling frameworks).

Additionally, the need to account for spatial processes at each stage of the stock-recruit process (e.g. spawning, egg, larval, settlement, and pre-recruitment phases; [Subbey et al., 2014](#); [Thorson et al., 2015](#)) is being recognized through paradigm shifts in ecological understanding, such as the reproductive resilience hypothesis ([Lowerre-Barbieri et al., 2017](#)). Accounting for spatial dynamics during larval, juvenile, and adult stages is critical to fully understanding how spatial population structure evolves ([Smedbol and Stephenson, 2001](#); [Frisk et al., 2014](#)), which has led to the development of full life cycle models embedded within statistical parameter estimation frameworks (e.g. [Bentley et al., 2004](#); [Archambault et al., 2016](#)). Advances in hydrodynamic modelling and collection of early life history data should further expand the application of spatial full life cycle models that can incorporate variable spatiotemporal resolution (e.g. embedding larval IBMs within spatial stock assessments to better address spatial patterns in stock-recruit dynamics).

Developing spatially structured stock assessments remains challenging because of model complexity, but spatial structure can better represent heterogeneous populations, and estimating movement can help to interpret data more accurately. Some simplifying assumptions, like those suggested by [Beverton and Holt \(1957\)](#), may be needed for spatial stock assessments (e.g. conditioning movement on extant environmental conditions and habitat preference or biological factors, such as maturity or age). However, alternative movement assumptions and integrating all information available appear to be possible solutions to supporting model complexity. For example, time-varying movement can be informed by the integrated analysis of habitat preference along with fishery and tagging data (e.g. [Porch, 2004](#); [Su et al., 2012](#); [Fu et al. 2017](#); [Mormede et al., 2020](#)).

The advancement of stock assessment methods towards integrated modelling has many scientific advantages ([Maunder and Punt, 2013](#)), but these advanced models are more difficult to communicate to fishery managers and stakeholders ([Regular et al., 2020](#)). Thus, improved scientific communication is needed ([Lynch et al., 2018](#)), particularly for complex spatial models that

include connectivity (Berger *et al.*, 2017). Better understanding of spatial models by researchers, including basic theory and assumptions, is expected to facilitate more effective communication with scientists, fishery managers, and fishery stakeholders, which may, in turn, help to confront the institutional inertia that often impedes the application of spatial models (Berger *et al.*, 2017; Punt, 2019a). Better understanding of spatial models is also expected to improve collaboration with fishermen, who have valuable information on movement patterns that can be considered to improve stock assessments (Nies, 1992; Johannes *et al.*, 2000; Murray *et al.*, 2008). Integration of this stakeholder local ecological knowledge through increased participatory modelling and cooperative research initiatives, can help develop appropriate modelling assumptions (e.g. Duplisea, 2018), identify primary components of spatial dynamics that need to be considered, and generate mutual learning of spatial complexities (Goethel *et al.*, 2019). Ultimately, the MSE framework, conducted with full stakeholder input and likely utilizing agent- or individual-based spatial operating models that incorporate complex movement behaviour and the vast array of spatial ecological knowledge, will help identify minimally complex spatial assessment model configurations that can provide robust management advice with the often sporadic or limited data available in many fisheries.

Although the ability to incorporate spatial structure and connectivity is now considered a primary requirement for the next generation of generic stock assessment platforms (Cadrin *et al.*, 2020; Punt *et al.*, 2020), operational application of spatial stock assessment models remains limited, often lagging technological advancements and ecological knowledge (Berger *et al.*, 2017a). In the near future, we believe that rapidly evolving advancements in spatial ecology and spatially explicit data collection will aid in further development and application of operational spatial stock assessments.

Conclusion

In 1947, Michael Graham (Director of the Lowestoft, UK Fisheries Laboratory) tasked Sidney Holt and Ray Beverton with developing a systematic approach to fishery modelling (Beverton and Anderson, 2002; Holt, 2008, 2020). Considering Graham's accomplishments on the topic, he could have taken on the task. However, we suspect that Beverton and Holt (1957) is so forward looking, because they were younger (21 and 24 years, respectively), lacked any preconceived bias, and were not yet entwined in the fishery management treadmill (i.e. Graham provided four uninterrupted years to perform the research; Anderson, 2011; Holt, 2008, 2020). We believe that Beverton and Holt would be proud of the diverse fields that their spatial framework has influenced in recent years and the enduring legacy that the brief section on spatial approaches in Beverton and Holt (1957) has had on both fisheries and terrestrial quantitative modelling. In his treatise on the historical development and current state of fisheries population modelling, Quinn (2003) culminates with the question: "I wonder what things will be like 50 or 100 years from now. Will the names of Baranov, Beverton and Holt, and Ricker still be known?" We suggest, based on their novel and forward-thinking exploration of spatial structure and movement models alone, that the answer in regards to Beverton and Holt will be an emphatic, "yes!".

Data availability

No new data were generated or analysed in support of this research.

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