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Lessons to be learned by comparing integrated fisheries stock assessment models (SAMs) with integrated population models (IPMs)

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ABSTRACT

Integrated fisheries stock assessment models (SAMs) and integrated population models (IPMs) are used in biological and ecological systems to estimate abundance and demographic rates. The approaches are fundamentally very similar, but historically have been considered as separate endeavors, resulting in a loss of shared vision, practice and progress. We review the two approaches to identify similarities and differences, with a view to identifying key lessons that would benefit more generally the overarching topic of population ecology. We present a case study for each of SAM (snapper from the west coast of New Zealand) and IPM (woodchat shrikes from Germany) to highlight differences and similarities. The key differences between SAMs and IPMs appear to be the objectives and parameter estimates required to meet these objectives, the size and spatial scale of the populations, and the differing availability of various types of data. In addition, up to now, typical SAMs have been applied in aquatic habitats, while most IPMs stem from terrestrial habitats. SAMs generally aim to assess the level of sustainable exploitation of fish populations, so absolute abundance or biomass must be estimated, although some estimate only relative trends. Relative abundance is often sufficient to understand population dynamics and inform conservation actions, which is the main objective of IPMs. IPMs are often applied to small populations of conservation concern, where demographic uncertainty can be important, which is more conveniently implemented using Bayesian approaches. IPMs are typically applied at small to moderate spatial scales (1 to 10^4 km^2), with the possibility of collecting detailed longitudinal individual data, whereas SAMs are typically applied to large, economically valuable fish stocks at very large spatial scales (10^4 to 10^6 km^2) with limited possibility of collecting detailed individual data. There is a sense in which a SAM is more data- (or information-) hungry than an IPM because of its goal to estimate absolute biomass or abundance, and data at the individual level to inform demographic rates are more difficult to obtain in the (often marine) systems where most SAMs are applied. SAMs therefore require more 'tuning' or assumptions than IPMs, where the 'data speak for themselves', and consequently techniques such as data weighting and model evaluation are more nuanced for SAMs than for IPMs. SAMs would benefit from being fit to more disaggregated data to quantify spatial and individual variation and allow richer inference on demographic processes. IPMs would benefit from more attempts to estimate absolute abundance, for example by using unconditional models for capture-recapture data.

1. Introduction

Providing management advice using population models fitted to monitoring data is central to applied population ecology. Population models can be used to support conservation goals by estimating the risk of extinction associated with alternative management actions (e.g., Ellner and Fieberg, 2003; Saunders et al., 2018) and the sustainable harvest of commercially and recreationally important species by

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estimating the level of removal that is consistent with optimal management (e.g., Hilborn and Walters, 1992). Initially, population modelling efforts were typically based on fitting models to a single data set. With the development of statistical techniques that integrate multiple sources of data into a single analysis, 'data integration' has become a central theme in applied population ecology. By 'integrated analysis' we mean the explicit, model-based integration of multiple data sets, each of which is informative about some or all parts of a statistical model of the system under study. It is unsurprising that integrated analysis has been developed in many fields as it is intuitive and logical to combine multiple types of data to better inform parameter estimates. Typically, there are practical benefits to data integration: the greater amount of information usually leads to more precise estimates, and combining different types of data may allow the estimation of additional parameters that might not be identifiable with each data set alone (Goodyear, 1977; Fournier and Archibald, 1982; Besbeas et al., 2002; Pacifici et al., 2017; Zipkin and Saunders, 2018; Miller et al., 2019; chapter 10 in Kéry and Royle, 2021; Schaub and Kéry, 2022).

The integrated approach is common to both aquatic (fisheries) and terrestrial (wildlife) modelling, with the result that the same basic modelling approaches are used in both fields. Fisheries typically refer to 'stock assessment models' (SAMs)[1] when an integrated analysis is performed,[2] while wildlife studies refer to 'integrated population models' (IPMs). However, so far there has been very little communication and collaboration between practitioners of these approaches, despite broadly similar ecological problems and the shared goal of a statistical description of some population of interest. Integrated analyses of population size and dynamics have been developed independently for fisheries stock assessment (Fournier and Archibald, 1982) and wildlife research (Besbeas et al., 2002), and reviews of their use in the two fields do not refer to developments outside the authors' field of practice (contrast reviews by Maunder and Punt, 2013 and Punt et al., 2013 for fisheries assessment with Schaub and Abadi, 2011 and Zipkin and Saunders, 2018 for ecology and wildlife assessment). Despite their conceptual similarity, the specific details of how SAMs and IPMs are applied can vary considerably among applications as a consequence of the questions being asked, the data that are available, the characteristics of the population (i.e., small or large population size) and also simply the traditions of the field.

Fisheries modelling has traditionally focused on determining the maximum catch that can be taken from a population over the long-term (i.e., the maximum sustainable yield, MSY) and population size corresponding to MSY, although information on stock status and fishing mortality relative to other management reference points is an additional focus in recent decades. Integrated fisheries stock assessments are based on fitting a population dynamics model to an index of relative abundance, data on removals (landings and discards) and/or the age-composition data of the catch. In contrast, IPMs in wildlife management and ecology have traditionally focused on determining the demographic drivers of population change and on estimating trends in abundance or demographic rates using, for example, capture-recapture data[3] that are combined with population counts, and these types of analyses have naturally been extended to population viability analysis (PVA, Saunders et al., 2018; chapter 10 in Schaub and Kéry, 2022). The usual statistical inference method, often frequentist for SAMs and Bayesian for IPMs, and software, often AD Model Builder (Fournier et al., 2012) or TMB (Kristensen et al., 2016) for SAMs, and WinBUGS (Lunn et al., 2000), JAGS (Plummer, 2003) or NIMBLE (de Valpine et al., 2020) for IPMs, also differ. Only a small handful of marine studies have explicitly (e.g., Maunder, 2004; Jacobson et al., 2020) attempted to bridge the gap between population modeling focused on exploited (in the case of SAMs) and unexploited populations (in the case of IPMs), usually because of the incidental effects of fishing on the latter (Hoyle and Maunder, 2004; Véran and Lebreton, 2008; Gamelon et al., 2021). In the terrestrial realm, analyses of harvested wildlife populations (e.g., wild boar, Gamelon et al., 2021; grey wolves, Horne et al., 2019) have similar goals (sustainable harvest) and data (harvest rates, age- and sex-composition of the harvest) to fisheries assessments as well as data that are common to wildlife analyses (capture-recapture data). Analyses of some fish populations focus on extinction risk or human impacts other than fishing (Deriso et al., 2008) using the same data needed for stock assessments. However, the type of analysis and software used, as well as the vocabulary, differ depending on whether the researcher has a fisheries or a wildlife background. We believe that the choice of the most appropriate analysis method should not depend on idiosyncrasies of the field of research, but rather on the objectives of the analysis, the characteristics of the study design and of the population, and on the data available.

Non-integrated stock assessment models that are based on a single data set (e.g., Adams and Jones, 2022) and integrated models that do not include an explicit demographic population model (e.g., Smith et al., 2022) are not the focus of this study. We here compare the two types of integrated analyses, SAMs and IPMs, to identify similarities and differences, including the structure of the models (Section 2), the typical data sets used for parameter estimation (Section 3), and the key steps involved in constructing SAMs and IPMs (Section 4). We illustrate the two approaches using simple examples (Section 5) and outline the next steps towards a unified approach to address natural resource management problems using comprehensive population models (Section 6). In addition, a common vocabulary and notation or at least explicit translations between terms used for the same concept in different fields is required to share experiences and increase the rate of progress in the application and development of both SAMs and IPMs. We therefore list some of the key quantities, data types and terms and their meanings in the two fields in Table 1.

2. Model structure and implementation

SAMs and IPMs can be viewed as demographic population models linked to multiple observational sub-models to simultaneously estimate parameters and analyze the population itself (Fournier and Archibald, 1982; Schaub and Kéry, 2022). Many SAMs and IPMs use a state-space formulation,[4] where a demographic population model is coupled with several sub-models for individual data sets. However, SAMs and IPMs are not identical. Schaub and Kéry (2022) note that a typical IPM uses data directly at the process level (e.g., fecundity data from counts of young in the nest) and also at the population level (e.g., total population counts or indices of abundance), and these two levels are usually linked using an age-/stage-structured (matrix) population model (Caswell, 2001). An IPM is therefore a joint analysis with a joint likelihood for multiple data sets that are informative about individual demographic processes (survival, productivity, immigration, emigration) and about population size (absolute or relative; structured or unstructured) and that share some parameters (Fig. 1). Data that are informative about some demographic rates are used to obtain the demographic information in data that are aggregated across individuals, such as count data. In contrast, SAMs typically use data aggregated over individuals, with abundance trend and age-composition data providing information on

[1] Data for aquatic animals such as marine mammals and seabirds are often analyzed using methods that incorporate features of IPMs and SAMs (e.g., Robinson et al., 2015).

[2] The term 'stock assessment' is also applied to other approaches that provide advice to support management decision making.

[3] There is a plethora of terms for data in which animals are assigned marks or tags or have natural marks and may be resighted or recaptured if they survive (sight-resight, capture-recapture). We will use the term 'capture-recapture' in the paper, recognizing that animals need not be handled to be marked.

[4] In the sense that they account for process and observation error.

Table 1
Glossary of terms frequently used in this paper and in the literature on integrated stock assessment models (SAM) and integrated population models (IPM). We provide a short definition and related terms.

Term	Our definition	Other related terms
Joint likelihood	The combination of likelihoods of different data sets/types in a single analysis.	-
Capture-recapture data	Data that include individuals that are artificially or naturally marked and that are encountered alive or dead in subsequent time periods.	Mark-recapture data, capture-mark-recapture data, capture-resighting data, multistate capture-recapture data, sight-resight data, tag-recovery data, dead-recovery data, tagging. 'Ring', 'sight', 'tag', and 'mark' are generally used interchangeably.
State-space model	A hierarchical model composed of a process model describing the (typically) temporal development of the state of interest in a Markovian way and a conditional observation model linking the state of interest with observations.	Hidden Markov model (if states are discrete), random effect (the process variability can be modeled as a random effect), latent variable model (in terms of population dynamics), process error, process variability.
Survey bias	The coefficient that represents the relationship between an index of relative abundance or an incomplete population count and the true population size.	Catchability, selectivity (age-specific survey bias), detection probability.
Selectivity	Relative probability of being harvested or sampled by age, size, stage, or sex. It is often parameterized using a logistic or dome-shaped function.	Age-specific catchability, age-specific survey bias.
[Catch] Age/length/size composition data	The proportion of individuals in the catch or sample that are of a given age class, length, or size.	Age/length/size-at-harvest data, age/length/size-frequency.
Forcing function	Data that are not fit in the model, but used to determine the values of a process over time (e.g., a covariate or catch).	
Stock-recruitment relationship	Function that determines the number of "recruits" to a population as a function of some measure of reproductive output.	Stock-productivity relationship, per-capita recruitment, Spawner-recruit curve.
Harvest data	The amount (weight or numbers) that died due to fishing (both landed and discarded fish).	Removal data, catch data.

processes at the population level. Combined with catch data using a joint likelihood, they can provide information on individual processes (e.g., fishing vs. natural mortality), but sometimes several parameters have to be pre-specified (i.e., fixed) to obtain an identifiable model. Some SAMs also include age-length or tagging data for individuals in the joint likelihood, which provide direct information on individual processes such as growth.

Although SAMs are typically applied to fish, especially in marine environments, and IPMs mainly to terrestrial vertebrates, the population models on which they are based have a similar structure. Most SAMs are based on age-structured models[5] often including sex structure and less often spatial structure. Some SAMs are based on size- or stage-structured models, usually for species that are difficult to age such as crustaceans.

[5] Exceptions being biomass dynamics models.

In contrast, IPMs are based either on models that lump all animals into a single variable or on age-/stage-structured models. Most IPMs only model females because of the monogamous mating system of many birds and mammals. However, IPMs that explicitly include both sexes are increasingly being used (Rotelli et al., 2021; Hostetler et al., 2021; Millsap et al., 2023). The use of stage- rather than of age-structured models is more common in IPMs because of the general lack of information on the age composition of wildlife populations. IPMs tend to model survival as a function of age or size/stage given information from capture-recapture data, whereas SAMs separate survival into fishing mortality and natural mortality (which can sometimes be assumed to be a function of age, sex or length). Fishing mortality is, however, usually assumed to be age- and time-specific. When SAMs allow for age-variation in natural mortality, they often do so by pre-specifying the relative probability of mortality by age (Maunder et al., 2023), i.e., rather than estimating these parameters, they are fixed by the analyst.

IPMs are often applied to species with low (10 s-1000 s) population sizes. This means that demographic stochasticity can be important for both survival and reproduction and needs to be included in the model formulation. Consequently, most IPMs are implemented using the Bayesian inference framework because demographic uncertainty is easier to incorporate (see e.g., Besbeas et al., 2005 for an exception). The inclusion of demographic stochasticity is the rule rather than the exception in IPMs even in applications where it is not necessarily needed (Schaub and Kéry, 2022). Where sufficiently long time series of data are available, IPMs can incorporate environmental stochasticity in addition to demographic stochasticity (Schaub et al., 2013; Pace et al., 2017; Pace, 2021). In contrast, SAMs are often implemented using methods that are based on automatic differentiation (e.g., Fournier et al., 2012; Kristensen et al., 2016) to facilitate the estimation of many parameters, most of them being treated as random effects with a variance that is assumed to be known (i.e., using penalized likelihood estimation). Automatic differentiation requires the latent variables to be continuous, and thus precludes easy estimation of count-valued variables such as the discrete number of individuals, which is important to model for small populations. However, SAMs increasingly include environmental stochasticity in processes such as recruitment, survival (natural mortality and/or selectivity) and growth. Some SAMs also allow for variation over time in fishery and survey catchability (Fieberg et al., 2010), which is also the case for IPMs that, for example, are based on capture-recapture data (Schaub and Ullrich, 2021; Nater et al., 2023). Abundance is often large to very large for exploited fish populations, and the recruitment process for fish tends to be dominated by environmental variation, and there is often not a strong relationship between reproductive output and abundance of the first age- or size-/stage-class in the model (Gilbert, 1997; Szuwalski et al., 2015). As a result, uncertainty due to demographic stochasticity in survival and reproduction is generally not included in SAMs or is incorporated using random effects that are used to represent environmental variability.

3. Data types

Table 2 lists typical types of data used in SAM and IPM analyses. In general, both SAMs and IPMs can use any of the data types, but they differ in terms of the data that are considered "essential": catch and an index of abundance (or age-/size-composition data) for SAMs, and data on absolute or relative abundance for IPMs.

SAMs usually, and IPMs always, make use of data on absolute or relative abundance. For SAMs, these data often come in the form of measures of weight, such as biomass estimates from acoustic surveys or fishery catch-per-unit-effort. In contrast, many IPMs are fitted to abundance data in the form of counts or indices of abundance. These can be either estimates of absolute abundance, such as counts of gray whales off the coast of California (Laake et al., 2012), or counts of the number of breeding pairs in a small population (Schaub and Ullrich, 2021), or measures of relative abundance, such as kestrel monitoring at multiple

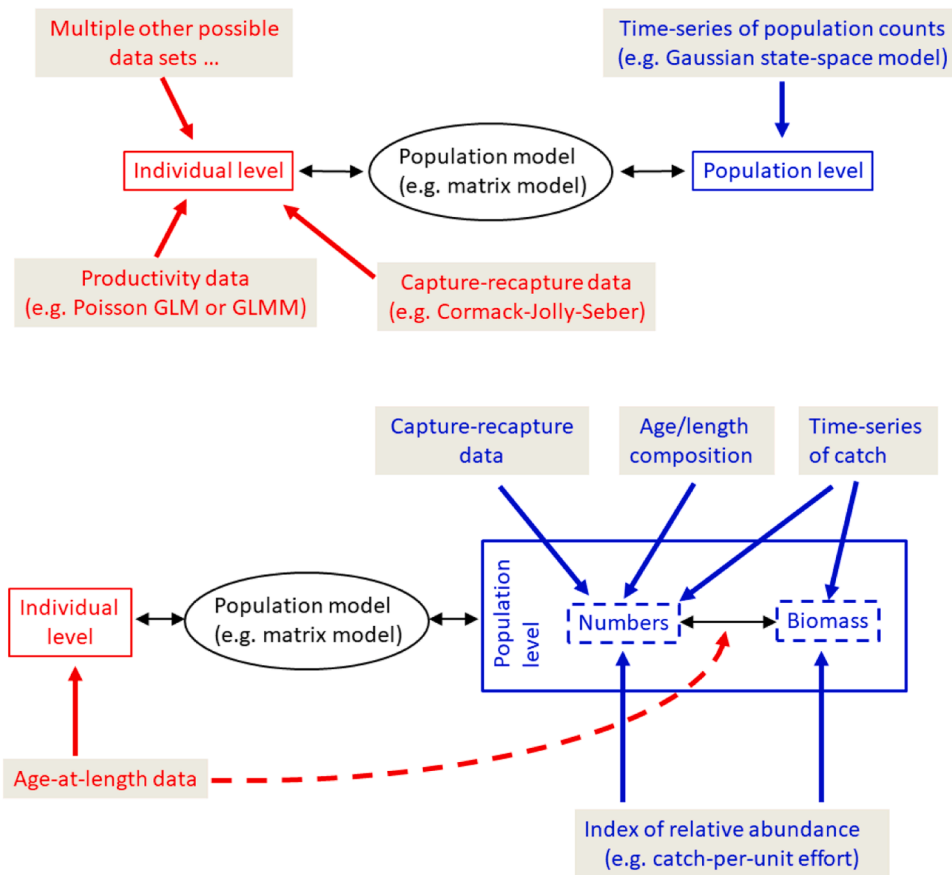

Fig. 1. Graphical representation of an IPM (top, and an integrated SAM (bottom). Data sets (gray shaded) originate from the individual (red box) and the population levels (blue box) and their connection is indicated by arrows. Data sets from both levels are jointly analyzed using a joint likelihood approach, and a population model connects them (indicated by double arrows). For the SAM, there is usually also a link between number of individuals and biomass at the population level, also indicated by a dashed arrow.
(Adapted from Schaub and Kéry, 2022)

Table 2
List of typical data sets used in integrated stock assessment models (SAMs) and in integrated population models (IPMs), application examples and the information the data set typically provides (Table 6.2 in Schaub and Kéry, 2022 provides a more comprehensive list of possible data sets used in IPMs).

Data set	Alternative term	SAM Applications	IPM Applications	Common likelihood functions
Catch / harvest	Removal data	Almost all applications	Black bear: Fieberg et al. (2010); Beluga whales: Jacobson et al. (2020)	Forcing function, normal or log-normal
Absolute abundance / biomass (raw data or estimate)	Population count	Gray whales: Punt and Wade (2012)	Egyptian vulture: Lieury et al. (2015)	Normal, log-normal, Poisson, Negative binomial
Relative abundance / biomass (raw data or estimate)	Population count	Most applications	Lapwing: Brooks et al. (2004); Kestrel: Fay et al. (2019)	Normal or log-normal
Encounters of identifiable individuals	Capture-recapture data, see Table 1.	Skipjack tuna: Hilborn (1990); Yellowfin tuna:Hampton and Fournier (2001)	Horseshoe bat: Schaub et al. (2007); Song thrush: Baillie et al. (2009)	Multinomial, binomial or negative binomial
Age/length/size and stage composition data (from catches / harvests or from observations during monitoring)	Catch age/length/ size-composition data	Fournier and Archibald (1982)	Pintail: Zhao et al. (2019), Black bear: Fieberg et al. (2010)	Multinomial or similar approximation (see Maunder, 2011, for examples)
Telemetry data	-	-	Greater sage grouse: Coates et al. (2018); Black grouse: Rotelli et al. (2021)	Binomial
Length-at-age (conditional age-at-length) data	-	Methot and Wetzel (2013); Lee et al. (2014)	-	Multinomial or similar approximation
Productivity data (e.g., clutch size)	Fecundity data Breeding success data	-	Peregrine falcon: Altwegg et al. (2014); Kittiwake: Acker et al. (2022)	Poisson, Normal or binomial

sites (Fay et al., 2019), or video counts of spawning aggregations (Waterhouse et al., 2020). It is common for estimates of relative abundance (e.g., annual biomass divided by biomass in a reference year) to be more accurate than estimates of absolute biomass (Thorson et al., 2021). However, SAMs usually attempt to estimate absolute abundance using information from both the relative abundance index and the sex- and/or age-composition data using the population model, its parameter estimates and assumptions, and the removal data (see Maunder and Piner,

2015, for details) given the general need to provide catch advice in absolute terms. In contrast, IPMs often do not attempt to estimate absolute abundance, because variation in relative abundance is deemed sufficient to understand population dynamics. This simplifies model formulation and reduces data requirements. However, there is a focus on absolute density for spatially explicit IPMs (Chandler and Clark, 2014) or on absolute population size for IPMs assessing population extinction risk (Saunders et al., 2018; Schaub and Ullrich, 2021).

Data on human-caused removals from the population are rarely used in IPMs (but see e.g., Lee et al., 2015; Jacobson et al., 2020; Gamelon et al., 2021), but are an essential data type in SAMs, where they are included as either landings or discards (e.g., Methot and Wetzel, 2013). Landings data are commonly assumed to be known exactly rather than data to fit to, and even when landings data are modelled, they are usually assumed to be very precise measures of the true landings (Maunder and Punt, 2013). In contrast, discard data are usually estimated from monitoring programs and may be subject to considerable uncertainty (e.g., Zheng et al., 2021). In many SAMs, the estimates of parameters representing the size of the population (i.e., the catchability coefficient associated with abundance indices) are heavily informed by treating the fishery history as a multi-year depletion experiment (Maunder and Piner, 2015). In these cases, abundance indices are expected to decline when harvest is high, with the exact magnitude of this decline informing the estimated size of the population.

Age and stage composition data (i.e., samples of the age or stage composition of the population or of the removals due to harvesting) are more commonly used in SAMs than in IPMs. Traditionally, information on the age composition of removals due to fishing has been summed along cohorts in virtual population analysis (VPA) to estimate absolute abundance by cohort, adjusting for natural mortality (Lassen and Medley, 2001). This approach assumes no error in the catch by age data, which is unrealistic in most cases due to ageing errors, sampling variability, length to age conversion, and missing data. IPMs using age-composition data (often but not exclusively age-at-harvest data) treat them in a similar way as do SAMs based on the integrated analysis paradigm, i.e. as a source of information on recruitment and survival (Gove et al., 2002; Conn et al., 2008; Tavecchia et al., 2009; Broms et al., 2010; chapter 17 in Schaub and Kéry, 2022) or to estimate the production of offspring (Taylor and Udevitz, 2015; Koons et al., 2017).

Length-composition or other size-related data, such as weight, are proxies for age in taxa with indeterminate growth, and are included in most SAMs because these data are easy and cheap to collect from catches or surveys, whereas aging is often time consuming and expensive. In addition, catch is often recorded in weight and management quantities expressed in biomass, and weight-at-age or weight-at-size is needed to calculate these quantities or to convert them into the number of individuals as used in the model. Therefore, modelling growth (length-at-age and/or weight-at-age) is often an important component of SAMs. Some SAMs include both length and age composition data because only a fraction of the catch or survey data is typically aged, while many more fish are measured by length. The age-composition data are sometimes included in the model as age conditioned on length to account for the sampling design which is often based on prespecified length bins or to account for the length-based selectivity of the gear (Lee et al., 2016). IPMs generally do not include length-composition data because management is typically interested in the number of individuals, growth of the usually studied species stops at maturity and the IPM does not differentiate among adults of different sizes. IPMs are more likely to model stage than age, where biological characteristics change with stage. Theoretically, other compositional data related to age or stage (e.g., number of antler points, accumulation of biofauna on shells, or shell condition for crabs) could be modelled in the same way as length-composition data (e.g., Zheng et al., 2021).

Capture-recapture data provide information on a wide range of population parameters and processes, including survival, reproduction, growth, movement and abundance (Williams et al., 2002). SAMs and IPMs use capture-recapture data, but there are notable differences in how they are collected and what information is extracted from them. First, SAMs generally only have information on an initial capture and a subsequent second capture, which is often lethal, because multiple (live) recaptures are very rare in aquatic environments (exceptions are some freshwater fish and marine mammals). In contrast, multiple recaptures are common for terrestrial studies. As a result, the information content of the capture-recapture data available for IPMs is usually much richer than that available for SAMs. Second, SAMs use capture-recapture data primarily to estimate abundance, fishing mortality, or movement in spatially stratified SAMs (Goethel et al., 2021), whereas IPMs also use them to estimate survival (Schaub and Kéry, 2022). Estimating abundance is essential for calculating exploitation rates in SAMs and requires that the number of unmarked individuals evaluated for marks is recorded, the analysis is unconditional and the reporting rate (the probability of a recaptured animal being reported) is correctly specified (Goethel et al., 2023). In some cases, independent estimates of reporting rates can be obtained from experiments on fishing vessels (Vincent and Pilling, 2023) or from reward tags (Pollock et al., 2001; Meyer et al., 2012). In the absence of data on reporting rates the 'recapture conditional' approach to analyzing capture-recapture data (e.g., McGarvey et al., 2010) can be used to estimate movement rates. Tag loss and tagging-related mortality are issues that may need to be addressed when analyzing capture-recapture data. Estimating survival from capture-recapture data, which does not need the number of unmarked individuals to be recorded, requires the joint estimation of recapture probabilities, and parameters related to tag loss and tagging-related mortality need to be modelled appropriately to avoid bias (Lebreton et al., 1992). Sometimes additional information such as a location or state (e.g., breeder or non-breeder) is collected for each encounter. These data allow multistate capture-recapture models to estimate additional parameters such as movement rates or breeding propensity (the probability that a female is reproducing in a year, Lebreton et al., 2009).

Other types of data can also be integrated. In SAMs, these include tag growth-increment in length-structured models (Punt et al., 2013), and environmental data such as temperature, predator abundance, or ocean pH (Miller et al., 2016). Data on reproduction such as clutch or litter size, number of fledglings or pups raised by a female, and encounters of marked dead individuals (ring-recovery data) are often used in IPMs (see Table 6.2. in Schaub and Kéry, 2022).

4. Developing SAMs and IPMs

The steps involved in developing most SAMs and IPMs are very similar:

- Identify the question or set of questions that must be answered or the management decision that must be informed by the analysis and/or the quantities that the model is intended to estimate.
- Select one or a set of population models with different levels of complexity in terms of how the population is structured (e.g., by age, stage or space). The complexity of the model will depend on the goals of the analyses, the knowledge of the species and system, and the data available. This step involves the construction of structured population models that describe the trajectory of population size over time as a function of previous population size and of demographic rates. A life-cycle graph can be helpful to characterize the population model and facilitate its development (Schaub and Kéry, 2022).
- Select how each demographic process (e.g., growth, survival, reproduction) is to be modelled (e.g., age- or stage- specific, as a function of density and/or environmental variables and perhaps subject to demographic and/or environmental stochasticity).
- Identify data sets that could be used for parameter estimation and how the observation process (e.g., harvest selectivity, recapture

probability, survey bias/catchability) is to be modelled. This step may also precede the previous one as the amount and type of the data may affect the way in which the model is formulated.

- Select the likelihood function for each data set (referred to as 'component likelihoods'). In the case of a Bayesian implementation, priors are chosen for the parameters of the model (some of which may be so precise as to 'fix' their values) and in the frequentist framework values are specified for parameters that are not informed by the data (note that likelihood penalties are also commonly used in SAMs that estimate parameters using maximum likelihood[6]). Under an assumption of independence for the data sets, the joint likelihood is defined as the product of the component likelihoods. The joint likelihood requires some degree of sharing of parameters between two or more of its components. A typical linkage is provided by the population model, which contains all the demographic parameters and age-/stage-structured population sizes, and thus provides a sort of 'motherboard' into which all the other data sets can be 'plugged'.
- Fit one or a set of candidate models or configurations (sets of assumptions about model structure and parameter values) using maximum likelihood, Bayesian or related methods.
- Apply diagnostics to eliminate model configurations that are clearly mis-specified and/or fix the mis-specification (e.g., Carvalho et al., 2017, 2021 for SAM; Besbeas and Morgan, 2014; chapter 7 in Schaub and Kéry, 2022 for IPM).
- If multiple models are fitted, use model selection criteria to further reduce the number of models and/or to apply model weighting/averaging methods to construct an ensemble summary to better capture model uncertainty.

5. Examples

In this section we provide two simple, but typical, examples of a SAM and an IPM to illustrate the general characteristics of each.

5.1. A SAM case study: Australasian snapper from the west coast of New Zealand

5.1.1. Background

In the past, the primary tools for stock assessment were usually based on a single data source using VPA or surplus production models. The latter aggregate abundance over age into a single production function and fit to an index of abundance conditioned on catch or on effort (Fox, 1970; Pella and Tomlinson, 1969). Yield-per-recruit (YPR) analyses use estimates or assumptions of age-specific population dynamics processes (natural mortality, growth, and age-specific selectivity to the fishery) to estimate the fishing mortality rates corresponding to optimal yields (Beverton and Holt, 1957). Other approaches were also used such as stock-recruitment analysis (Ricker, 1954; Beverton and Holt, 1957) and catch-curve analysis (Chapman and Robson, 1960).

Integrated analysis was developed in the context of catch age-composition data. It is well-known that catch age-composition data alone do not allow the simultaneous estimation of recruitment and age-specific selectivity of harvest (selectivity-at-age) if both are allowed to vary among years (Pope and Shepherd, 1982). Doubleday (1976) accounted for errors in catch age-composition data by decomposing age-specific fishing mortality into a multiplicative model with an age component that was constant over time and a time component, reducing the number of parameters and analyzed multiple cohorts simultaneously. However, he also found that catch age-composition data alone were not sufficient to provide a reliable estimate of stock biomass. Paloheimo (1980) overcame this problem by assuming that fishing mortality was proportional to fishing effort but ignored any error in the relationship between these variables.

Doubleday (1976) and Paloheimo (1980) laid the foundations for integrated analysis, but it was Fournier and Archibald (1982) who developed the comprehensive statistical framework. They fit an integrated SAM using a joint likelihood framework to data on catch (conditioned on fishing effort) and age-composition, incorporating process error in the effort-fishing mortality and in the stock-recruitment relationship.

We illustrate a typical integrated SAM that is fit to an index of relative abundance and age-composition data, while assuming that catch is known precisely, for a teleost species, the Australasian snapper (*Pagrus auratus*). It is the most valuable commercial and recreational inshore finfish in New Zealand and is distributed around the North Island and the top part of the South Island. It has been exploited since the mid 1800′s and is currently managed under New Zealand's Quota Management System. The species is moderately long lived, but fast growing, reaching ages of 60 years and lengths of one meter, while maturing at 3–4 years of age. We apply the SAM to the snapper stock on the west coast of the North Island of New Zealand.

5.1.2. Population model

A classic traditional integrated SAM fits an age-structured population model to an index of relative abundance and the age-composition of the catch, assuming that the landed catch is correctly recorded, by estimating the average recruitment, the annual deviations in recruitment from the recruitment expected from a stock-recruitment relationship, and the parameters of the relationship between the relative probability of capture and age (i.e., the selectivity curve). Fishing mortality is calculated on the assumptions that the catch in weight and the value of several demographic parameters such as natural mortality are known exactly, or nearly exactly for catch in some implementations. A key objective of a SAM is to estimate the absolute abundance (or biomass) of the population to determine the impact of the removals (harvest) from the population and to separate fishing from natural mortality. The quantities of management interest (e.g., maximum sustainable yield, MSY) are derived and calculated based on the parameter estimates and assumptions about population dynamics, with uncertainty characterized using bootstrapping, asymptotic normal approximations, profile likelihood, or Bayesian methods (Pawitan, 2013; Hobbs and Hooten, 2015).

Here we provide an example that represents some of the key components of most modern SAMs that are fit to multiple data types. The assessment is based on a single sex model that tracks numbers from age 1 year to a plus-group age. It assumes that total mortality is separated into natural mortality (M, assumed to be independent of time and age) and fishing mortality (F_t), with the latter modelled as the product of age-specific selectivity[5] (S_a, assumed to be a logistic function of age) and fully-selected fishing mortality[7]:

$$N_{t+1,a} = \begin{cases} R_{t+1} & \text{if } a = 1 \\ N_{t,a-1}e^{-(M+S_{a-1}F_t)} & \text{if } 1 < a < A \\ N_{t,A-1}e^{-(M+S_{A-1}F_t)} + N_{t,A}e^{-(M+S_AF_t)} & \text{if } a = A \end{cases} \quad (1)$$

where $N_{t,a}$ is the number of fish of age a at the start of year t, R_t is the recruitment (at age 1) during year t, and A is the plus-group age that accumulates all the older fish. Recruitment is often related to reproductive output according to a stock-recruitment, but in this example, recruitment is modelled assuming that it is log-normal, but parameterized with the $\frac{\sigma_R^2}{2}$ term such that $\mathrm{E}(R_t) = \overline{R}$:

[6] This involves (a) treating random effects (such as annual deviations in natural mortality about their expected value) as if they were fixed effects but placing a prior on them, with the variance parameter pre-specified and not estimated, and (b) imposing what amount to priors on fixed effects parameters but treating them as likelihood components.

[7] The fishing mortality rate for the age-class(es) that has the highest selectivity.

$$R_t = \overline{R}e^{\varepsilon_t - \frac{\sigma_R^2}{2}} \tag{2}$$

where $\overline{R}$ is the mean recruitment,[8] ε_t is the recruitment deviation for year t, $\varepsilon_t \sim N(0, \sigma_R^2)$, and σ_R is the amount of temporal variation in recruitment. A penalty (see Equations A.4 and A.5) is added to the objective function to implement the log-normal distributional assumption.

The fully-selected fishing mortality is estimated for each year t. Selectivity, the relative probability of being captured by the fishery is assumed to increase with age and is hence modelled using a logistic equation (parameterized using the age-at-50%-selectivity (a_{50}) and slope of the selectivity at a_{50} in logit-space (a_{slope})):

$$g^{-1}(S_a) = a_{slope}(a - a_{50}) \tag{3}$$

where g(a) is a logistic function.

The total catch in weight is given by:

$$C_t = \sum_{a=1}^{A} w_{t,a} \frac{S_a F_t}{M + S_a F_t} N_{t,a} \left(1 - e^{-(M + S_a F_t)}\right), \tag{4}$$

where $S_a F_t/(M + S_a F_t)$ is the fraction of total mortality attributed to the fishery and $\exp(-(M + S_a F_t))$ is survival, $w_{t,a}$ is the mean weight of an animal of age a during year t. The biomass vulnerable to the fishery at the start of year t, B_t, is a sum over all age classes:

$$B_t = \sum_{a=1}^{A} S_a w_{t,a} N_{t,a} \tag{5}$$

A common feature of many fisheries stock-assessment models is the need to specify the state of the population when the model is initialized. Often, analysts choose to start their population model before large scale fishing began, so that the age structure is a function of natural mortality only. The initial conditions here assume that the population was unfished and, in expectation, at equilibrium with a stable age structure based on natural mortality.

$$N_{1,a} = \begin{cases} R_1 & \text{if } a = 1 \\ \overline{R}e^{-(a-1)M} & \text{if } 1 < a < A \\ \overline{R}\dfrac{e^{-(A-1)M}}{1 - e^{-M}} & \text{if } a = A \end{cases} \tag{6}$$

5.1.3. Parameter estimation, likelihood functions, and penalties

As with most age-structured integrated stock assessments (Fournier and Archibald, 1982; Maunder and Punt, 2013), the objective function (i.e., the negative log-likelihood to be minimized) includes contributions from the data as well as from various penalties (Appendix A). The parameters of the population model (Table 3) are estimated by fitting the model to catch data, an index of vulnerable biomass, and catch age-composition data (data sources that all relate to the population aggregated over individuals). Estimation is carried out by maximizing the penalized log-likelihood. Several of the parameters of the population model are fixed based on auxiliary information (e.g., natural mortality and weight-at-age), because the available data fit in the model are uninformative about them. The remaining parameters are estimated, with a penalty for the annual recruitment deviations based on the log-normal distributional assumption.

5.1.4. Data and results

The historical data are the same as those used by Maunder and Deriso (2003). The stock is modelled from 1931, which is assumed to be an unexploited state, to the start of 1999 where individuals older than 20 are accumulated at 20 + . The model is fitted to catch data for the entire time period (1931–1998), to an index of relative abundance (catch per unit effort for years 1974–1991) and to catch age-composition data (for years 1975, 1976, 1979, 1986, 1987, and 1989–98). Having catches available from 1931 onward allows the model to treat the catch time series as a complete record of removals, improving its information as a 'depletion experiment' to estimate absolute population size. Recruitment deviations are estimated for years that are well represented in the catch age-composition data (1970 to 1995). The model is implemented using TMB (Kristensen et al., 2016); the code, an R script, and data files are included in the supplementary material.

Fig. 2 shows the estimates of biomass, fishing mortality, recruitment, and selectivity. Fig. 3 shows fits to the catch data and the index of abundance. Figs. S1 and S2 show the fits to the catch age-composition data in the form of fits to data for individual years and in the form of bubble plots of standardized residuals.

Table 3
Parameters of the integrated stock assessment model (SAM) for the snapper data with some explanation. Means (MLE) and standard errors (SE) are given for parameters that are estimated. For parameter that were fixed (pre-specified), the values are provided.

Parameter	Maximum likelihood estimate (MLE)	SE
Average recruitment ($\log(\overline{R})$)	7.560	0.026
Natural mortality (M)	Fixed at 0.075 yr^{-1}	-
Fishing mortality (F_t)	Estimated (values not shown)	-
Age at 50% selectivity of the logistic selectivity curve (a_{50})	1.117	0.066
Age at 95% selectivity of the logistic selectivity curve (a_{95})	1.196	0.334
Weight-at-age (w_a)	Fixed	
Recruitment deviates (ε_t)	Estimated for years 1970-1995, which relates to cohorts represented in the age-composition data. Fixed at $\frac{\sigma_R^2}{2}$ for earlier years to ensure recruitment equals $\overline{R}$	-
Standard deviation of the lognormal distribution for recruitment (σ_R)	Fixed at 0.6	-
Standard deviation of the lognormal distribution for catch (σ_C)	Fixed at 0.05 to represent that the catch is known with little error	-
Catchability ($log(Q)$): the coefficient that represents the relationship between an index of relative abundance and the population	-10.597	0.113

5.1.5. Potential model extensions

The model could be converted from a penalized likelihood approach to an explicit state-space approach by making the annual recruitment deviates a random effect and estimating σ_R as a fixed effect (Thorson, 2019). This would integrate over the annual recruitment deviations. A similar approach could be applied to fishing (e.g., treating the logarithms of the annual fishing mortality rates as a random walk, c.f., Berg and Nielsen, 2016) and natural mortality. The number of recruitment deviations could be increased to better reflect uncertainty in historical abundance – similarly, recruitment deviations could be added to the initial conditions to reflect the assumption that the stock was close to, but not exactly at, its unfished level in 1931. A stock-recruitment relationship could be added to the model with the annual deviations around this relationship. The model could have allowed for ageing error, which has been quantified for Australasian snapper (Walsh et al., 2014).

The analysis could be implemented in a Bayesian framework by adding penalties to the objective function that reflect prior distributions, possibly estimating additional parameters that were originally fixed, and using, for example, the tmbstan package (Monnahan and Kristensen, 2018) or reprogramming in JAGS (Plummer, 2003) or NIMBLE (de Valpine et al., 2020).

[8] Equation 2 includes a bias-correction factor so that the expected recruitment equals $\overline{R}$. This bias-correction factor accounts for retransformation bias, and can be calculated in a variety of different ways (Thorson, 2019).

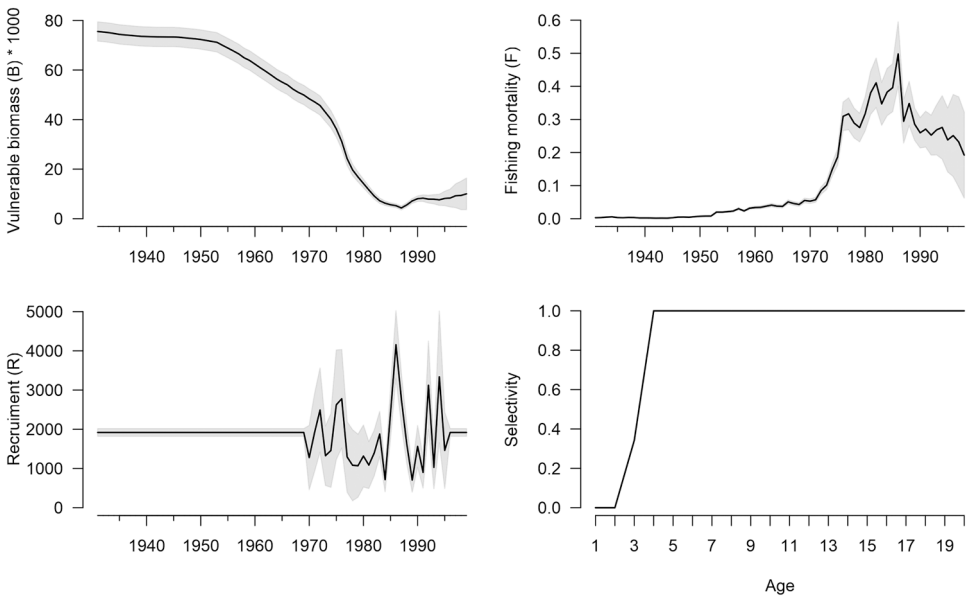

Fig. 2. Estimates of vulnerable biomass (in tons), fishing mortality, and recruitment (in 1000 s of individuals in age class 1) with asymptotic 95% confidence intervals, and selectivity for the New Zealand snapper application.

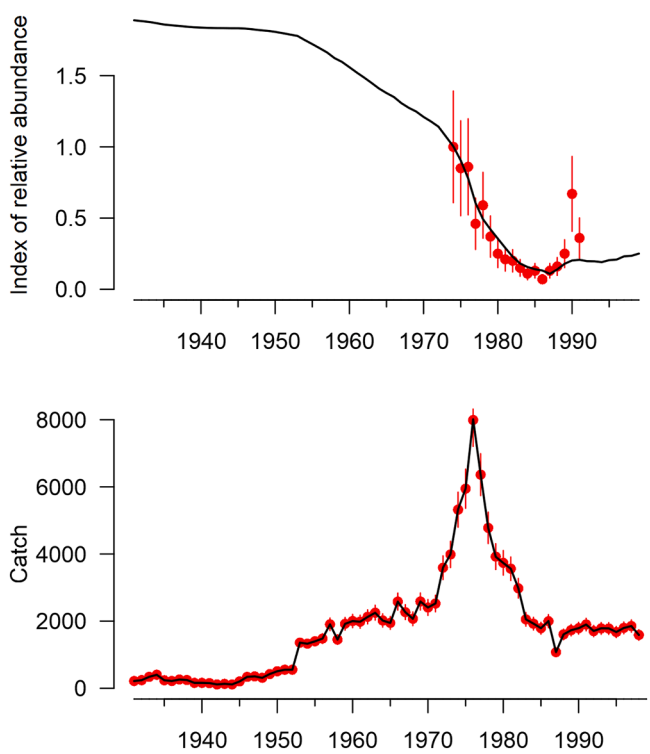

Fig. 3. Fits (black lines) to the index of relative abundance and the catch (in tons) with 95% confidence intervals on the observations for the New Zealand snapper application (red).

5.2. An IPM case study: woodchat shrikes

5.2.1. Background

Prior to the development of IPMs (Besbeas et al., 2002), wildlife population ecologists focused either on estimating demographic rates from individual-level data (e.g., Williams et al., 2002) or on studying population dynamics (e.g., assessing the impact of environmental variables on annual population growth, or assessing density dependence) from population count data (e.g., Lande et al., 2003). Where estimates of key demographic rates were available, age/stage structured population models were often constructed to examine how variation in demographic rates affected population dynamics (e.g., Bro et al., 2000; Gaillard et al., 1998). Population count data, when available, were used either for model validation (e.g., Barbraud et al., 1999; Schaub et al., 2004) or to determine whether the observed changes in demographic rates were sufficient to account for the observed change in population size (e.g., Peach et al., 1999; Siriwardena et al., 2001). The latter approach shares elements with IPMs, but the analyses were piecemeal and ignored the sampling variability of the demographic rates.

Here, we illustrate a typical 'terrestrial' IPM that is fit to count, capture-recapture and productivity data in a bird species, the woodchat shrike (*Lanius senator*). This is an insectivorous, migratory passerine bird that breeds in semi-open farmland around the Mediterranean Sea. Its life cycle is typical of many short-lived passerines that start to reproduce at the age of 1 year, when they are considered adults. The study population was surveyed by Bruno Ullrich from 1964 to 1992 in southern Germany in an area of 120 km^2 (Ullrich, 2017), which was defined in the typical somewhat haphazard way based on the presence of suitable shrike habitat and, more importantly, on logistical considerations (Schaub and Ullrich, 2021; chapter 11 in Schaub and Kéry, 2022). IPMs for somewhat more complex models were developed using the same data, with the main objectives of identifying demographic drivers and of assessing possible demographic causes of population extinction (Schaub and Ullrich, 2021; chapter 11 in Schaub and Kéry, 2022).

5.2.2. Population model

We adopt a female-based stage-structured population model with a pre-breeding census, i.e., the population is modelled in the spring just before reproduction, when all individuals are at least 1 year old. Three classes of females can be identified according to their origin:

- Surviving adults in year t (S_t) are females that reproduced in year t-1 in the study area.
- Local recruits in year t (R_t) are females born locally in year t-1 that return to the study area.
- Immigrants in year t (I_t) are females born elsewhere that appear in the study area for the first time in year t.

The number of surviving adults in year t (S_t) is a function of the

number of breeders in year t-1 (N_{t-1}) and the apparent survival probability of adults from year t-1 to t ($\phi_{a,t-1}$), i.e., $S_t \sim \text{Binomial}(\phi_{a,t-1}, N_{t-1})$. The binomial distribution allows for demographic stochasticity, which is an important component of the demography of small populations (Caswell, 2001). Apparent survival is defined as the probability of surviving and returning to the study area. Thus, permanent emigration from the study area is accounted for by apparent survival, even though it cannot be quantified separately from true survival using these data.

The number of local recruits in year t (R_t) is a function of the number of breeders in year t-1, productivity in year t-1 (ρ_{t-1}) and juvenile apparent survival probability from year t-1 to t ($\phi_{j,t-1}$), i.e., $R_t \sim Poisson(N_{t-1}\rho_{t-1}\ \phi_{j,t-1}\ /2)$. Here, productivity is expressed by the average number of fledglings produced by a female, and assuming an even fledgling sex ratio.

Finally, the number of immigrants in year t (I_t) is specified as $I_t \sim \text{Poisson}(\omega_t)$, where ω_t is the expected number of immigrants in year t. The total female population size in year t is the sum of the three types of females, i.e., $N_t = S_t + R_t + I_t$.

This stage-structured population model provides the link between population size and the demographic processes and connects the individual and the population levels (Fig. 1). The model incorporates demographic stochasticity (represented by use of statistical distributions rather than by expectations) and environmental stochasticity (demographic rates vary annually; modelled with temporal random effects). However, to simplify the model and based on previous results suggesting only limited annual variability in some parameters (chapter 11 in Schaub and Kéry, 2022), the apparent survival of both age classes and the expected number of immigrants are assumed to be constant over time, i.e. $\phi_{j,t} = \phi_j$, $\phi_{a,t} = \phi_a$ and $\omega_t = \omega$.

5.2.3. Parameter estimation, likelihood functions, and penalties

Every year, three data types were collected:

- Population counts: the observed number of breeding pairs (or females) within the study area. Suitable breeding sites were visited multiple times during the breeding season, so the observed number of breeding pairs is more of a census than a relative abundance index.
- Productivity data: the number of young fledged for the nests found - nests that failed before fledging were denoted as unsuccessful with zero young. Note that not all nests of the observed breeding pairs were found.
- Capture-recapture data: a sample of nestlings was marked with a leg ring and a sample of unmarked adults was captured and marked with color rings. Adult breeders were checked with a telescope to identify marked individuals. In 10 out of 29 years, no capture-recapture data were collected due to time constraints.

Appendix B contains the full derivation of the likelihood function, which consists of three components: a) a state-space model for the annual population count data, b) a zero-inflated model for the productivity data, and c) a Cormack-Jolly-Seber (CJS) model for the capture-recapture data. Some parameters are shared among component likelihoods ensuring their integrated estimation based on the information from the three data sets. There is no data set that provides direct information about immigration, so it is a latent or 'hidden' demographic parameter. It can only be estimated in the joint model, but not separately from any of the individual data sets alone (Abadi et al., 2010).

The joint likelihood requires the assumption of independence for the different data sets (Schaub and Kéry, 2022; Frost et al., 2023). It can either be analyzed in the frequentist approach by maximization (Besbeas et al., 2002) or priors can be placed on its parameters and Bayesian inference used. We took the latter approach and fit the model using JAGS (Plummer, 2017) from R using jagsUI (Kellner, 2019), using vague priors throughout (see code for priors).

5.2.4. Results

The MCMC chains converged rapidly. Posterior means and 95% credible intervals for the main parameters are given in Table 4. The estimated total population size is in good agreement with the observed population counts (Fig. 4), and the estimated stage-specific population sizes suggest that local recruitment was low and immigration substantial (Fig. 4). Although we assumed most demographic parameters to be constant over time, population size fluctuated strongly, which is a consequence of the demographic stochasticity affecting this small population.

Based on the parameter estimates we could now conduct retrospective analyses to identify the contributions of each demographic process to the observed temporal variation of the population growth rate (Koons et al., 2017; Schaub and Ullrich, 2021), or conduct prospective analyses to project the population into the future, perhaps under different scenarios of changes in the mean of demographic rates due to management or harvest interventions (Saunders et al., 2018; Schaub and Kéry, 2022). Schaub and Ullrich (2021) performed a population viability analysis and found that extinction was unlikely due to the rescue effect of sustained immigration. Unfortunately, the population did in fact go extinct shortly after the end of data collection, suggesting that immigration was no longer compensating for losses for this increasingly isolated small population.

6. Key similarities and differences between SAMs and IPMs

6.1. Purpose

SAMs and IPMs have the common goals to create a model that best represents 'reality', to estimate the parameters of the model, to check that the model fits the data adequately, quantify the uncertainty of the parameters and derived quantities such as realized population size, and to use the model to address the objectives of the modelling exercise. Moreover, all modelling efforts are undertaken to improve our understanding of the population under study, such as how many animals are there, what is their trend in abundance, and what factors are driving changes in reproduction and survival. However, target audiences of SAMs and IPMs differ and hence the types of specific questions they aim to address.

SAMs are usually developed with the aim of informing management decisions, and almost always in the context of exploited populations. They typically attempt to estimate stock status relative to management reference points, and/or catch limits that will achieve maximum long-term yield or profit, or that will allow a depleted population to recover at a desired rate. The majority of stock assessments worldwide are conducted using a small number of SAMs implemented as software packages (Dichmont et al., 2021), which facilitates review and collaboration among modelling groups. However, there are also research SAMs where the focus is on understanding demographic processes (Dichmont et al., 2021).

The main purpose of IPMs is to improve the understanding of the

Table 4
Posterior means and 95% credible intervals (CRI) of parameters in the integrated population model (IPM) for the woodchat shrike. All model parameters are estimated.

Parameter	Posterior mean	95% CRI
Apparent juvenile survival (ϕ_j)	0.057	0.024; 0.110
Apparent adult survival (ϕ_a)	0.388	0.289; 0.500
Nest success probability ($\text{logit}^{-1}(\mu_o)$)	0.766	0.699; 0.830
Number of fledglings per successful nest (κ)	4.287	4.117; 4.451
Number of immigrants (ω)	7.621	5.445; 9.846
Reencounter first year (p_1)	0.154	0.042; 0.358
Reencounter later years (p_a)	0.486	0.299; 0.695
Variability of number of fledglings (σ_f^2)	1.368	1.248; 1.507
Temporal variability of nest success (σ_o^2)	0.677	0.276; 1.131

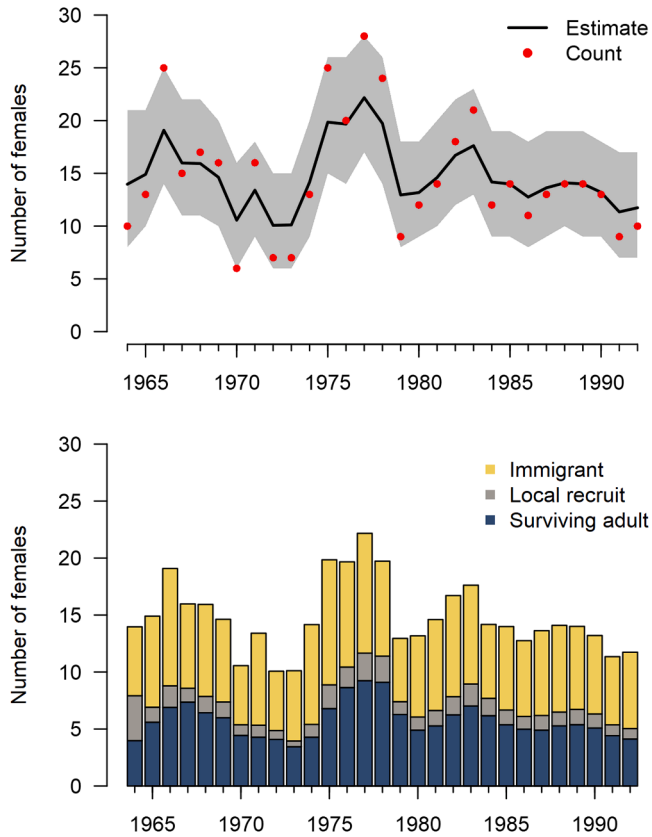

Fig. 4. Estimated number of female woodchat shrikes in spring (corresponding to the number of breeding pairs), along with the counts (top panel), and the decomposition of these females based on their origin into immigrant, local recruit and surviving adult (bottom panel). The shaded area in the top panel shows the limits of the 95% credible interval, the line and column heights show posterior means.

dynamics of the population under study, that is, to estimate annual abundance and demographic rates. Often there is an applied aspect involved. Retrospective and prospective population analyses are performed from the output of an IPM to assess the demographic mechanisms underlying changes in abundance (e.g., Plard et al., 2020) or population viability (e.g., Oppel et al., 2014). The use of IPMs to inform harvest or management has only just begun (e.g., Saunders et al., 2018; Nater et al., 2021; Riecke et al., 2022; Zimmerman et al., 2022; McIntosh et al., 2023). IPMs are also used for fundamental research in population ecology, e.g. for studying mechanisms of density-dependence (Gamelon et al., 2016) or interspecific interactions (Péron and Koons, 2012; Gamelon et al., 2019), or to assess how immigration works (Szostek et al., 2014; Acker et al., 2022).

6.2. Demographic detail and scale

SAMs and IPMs use a population model and linked observation and process sub-models to make use of multiple data types and to inform the values of the parameters of the population model. SAMs and IPMs often differ in the way reproduction is related to the number of reproductive adults, whether demographic stochasticity is included, in the spatial domain of the population under study, and the fitting framework.

Typically, IPMs explicitly account for reproductive and age-0 dynamics along with an assumption about the probability density function for the offspring (e.g., Poisson, log-Normal) whereas SAMs often model abundance implicitly or explicitly from the age or size at which animals are first monitored (e.g., the age at recruitment to the fishery). Both approaches need to specify the extent to which reproductive output is autocorrelated or related to environmental variables. SAMs typically estimate abundance in the youngest/smallest population stage or age class either as random deviations from a mean or as random deviations about an underlying stock-recruitment relationship. Similarly, SAMs model the proportion of an age-/size-class dying due to fishing or natural causes ignoring demographic stochasticity (but not necessarily environmental stochasticity, e.g., Berg and Nielsen, 2016; Miller et al., 2016). In contrast, recently developed IPMs often capture both demographic and environmental stochasticity in survival (see many examples in Schaub and Kéry, 2022). One of the reasons for the difference in approach to modelling recruitment and survival is that most SAMs are applied to very large populations (thousands to millions or even billions of individuals) so that effects of demographic stochasticity can safely be neglected. In contrast, many IPMs are applied to small populations (<100 individuals) where the effects of demographic stochasticity are likely to be important. Another reason is the different biology of the target species. Fish typically produce many eggs (e.g., 100 s – 1000 s), the hatchlings are small, may be pelagic and it is not possible to count them nor to allocate them to a mother. Wildlife species, which are the target of most IPMs, have comparatively small clutches or litters (e.g., 1–10), juveniles are often large enough to be marked, and parental care provides the opportunity to link productivity to a mother.

The outputs of SAMs (such as maximum sustainable yield, catch limits for commercial and recreational fisheries, and trends in spawning stock biomass) are usually expressed in terms of biomass whereas the results of IPMs and SAMs for marine mammals and seabirds are more likely to be expressed in terms of numbers of individuals. This requires many SAMs to include models of how weight changes with age, sex and time, and perhaps also as a function of density and environmental factors (Punt et al., 2001; Punt et al., 2021). SAMs are also often fitted to size-composition data, which requires estimates or assumptions about size-at-age (i.e., growth) and its distribution.

The stock assessment community has developed assessment methods that can directly account for the effects of multispecies predation given data on diets and on trends in abundance and age-/size-composition (e.g., Jurado-Molina et al., 2005; Holsman et al., 2016). These assessment methods are increasingly being applied in North America and Europe but have yet to be directly incorporated into management decision making. To date, multispecies predation models have not been applied to wildlife management problems.

The spatial scale of IPMs tends to be well defined and rather small, whereas SAMs focus on large populations whose boundaries are often not well defined or include the entire species. In addition, SAMs oriented towards commercial fishing may have spatial domains defined on the basis of political rather than biological considerations (Cadrin et al., 2023). SAMs typically assume a closed population with no immigration or emigration, whereas IPMs often assume an open population for which estimates of survival (apparent survival) include emigration implicitly and immigration is modelled explicitly (see e.g., Section 5.2). SAMs are often applied to data over multiple decades (see e.g., Section 5.1), whereas this is rarely the case for IPMs given their need for time-series of individual observations.

6.3. Parameters estimated and estimation frameworks

Most SAMs and IPMs include fixed effects (e.g., unfished biomass/recruitment for SAMs, average survival rate for IPMs) and random effects. The random effects are typically used to represent temporal variation in population processes (e.g., deviations of recruitment from a stock-recruitment relationship for SAMs; temporal deviation of survival from a long-term mean for IPMs), but not always (e.g., semi-parametric representations of age-specific selectivity; Xu et al., 2019). In addition, IPMs include demographic uncertainty by assuming probability distributions for processes with realizations treated as random effects.

SAMs and IPMs are fitted using a variety of methods such as

maximum likelihood and Bayesian inference. IPMs are typically implemented in the Bayesian inference framework (although see Besbeas et al., 2002; Besbeas and Morgan, 2014; Tavecchia et al., 2009; Besbeas and Morgan, 2017 for exceptions) due to its convenience in implementing demographic uncertainty. SAMs are typically implemented with maximum likelihood, or using 'penalized maximum likelihood' [PML], where the random effects are treated as fixed effects subject to a penalty based on the distribution assumed for the random effects, with the associated variance parameter pre-specified. PML has been used primarily due to the lack of efficient software implementations for approximating the integrals over the random effects in what are highly non-linear models, resulting in longer run times and convergence problems.[9] However, some applications (e.g., Maunder and Deriso, 2003), including more recent developments in stock assessment (Berg and Nielsen, 2016; Miller et al., 2016), involve the implementation of SAMs as state-space models, where the likelihood is marginalized over the random effects (process variation) using Laplace approximation, Bayesian integration, or other approaches.

Bayesian approaches (Punt and Hilborn, 1997) are less common for SAMs, again due to computational demands especially due to large sample sizes, but also due to concerns related to assessment outcomes being driven by overly informative priors. However, Bayesian analysis was popular for early SAMs that were less complex (McAllister et al., 1994; Punt and Hilborn, 1997) and one of the first general integrated models was developed explicitly to allow estimation in the Bayesian framework (Coleraine; Hilborn et al., 2003). Bayesian is the primary assessment framework used in New Zealand CASAL (Bull et al., 2012), where Bayesian inference is the main basis for the provision of management advice.

6.4. Types of data

A majority of the data for SAMs are opportunistic (e.g., commercial catch-per-unit-of-effort (CPUE) and catch length composition) rather than being based on a fishery-independent sampling program (e.g., a scientific survey) and therefore are more subject to bias (e.g., due to preferential sampling). Some data sets are collected specifically to account for selective sampling or reporting errors. Typically, few data are sampled that provide information on demographic processes, and hence there is a need to fix rather than estimate some demographic parameters in most SAMs. In contrast, IPMs typically use multiple data sets that provide direct information on demographic processes, and they are collected in a way that accounts for observation error (e.g., capture-recapture data). Population-level data, such as population counts or indices, are also used, but often no data are collected to adjust for bias in these data due to systematic observation errors. It is generally assumed in IPMs that temporal variation in count or index data largely reflects temporal variation in population size, but if this assumption is incorrect it can lead to biased parameter estimates (Schaub and Kéry, 2022).

6.5. Capture-recapture data

Capture-recapture data are used in both SAMs and IPMs, but their purpose, data collection, and analysis are quite different. In SAMs capture-recapture data are used to estimate either mortality rates or abundance. The number of individuals in the sample, both marked and unmarked, is recorded, and no marked individuals are released after capture (they are generally dead or kept). Estimates of survival are usually biased and imprecise due to practical issues with implementing tagging programs for large spatially dispersed fish stocks (Maunder et al., 2023). However, alternative sampling designs such as close-kin mark-recapture (Bravington et al., 2016) may pave the way for survival to be estimated within SAMs.

Wildlife capture-recapture data allow recaptures to be released again, so that there are capture histories of marked individuals over multiple sampling occasions (typically years). The focus of these richer data in the context of IPMs is to estimate survival and state-transition (in the case of multistate capture-recapture data). They are not typically used to estimate population size and recruitment because their estimation requires additional assumptions about the initial capture that are difficult to test. Multiple recaptures of the same individuals allow for complex modeling of survival and recapture processes. For example, survival can be modelled as a function of individual characteristics such as age, stage (e.g., breeder or non-breeder) or body size. Likewise, the recapture probability can be modelled as a function of individual traits, or depending on whether an individual was captured before to account for trap-shyness or trap-happiness (e.g., Williams et al., 2002).

6.6. Data weighting and diagnostics

By default, parameter estimates from integrated analyses represent a sort of 'weighted average' to which all data sets contribute information, and the amount of information contributed by each data set is usually a function of its sample size (Schaub and Kéry, 2022). In addition, by explicitly weighting the data sets, an analyst can regulate the amount of information that a data set contributes, which is sometimes argued to be desired when a large data set is likely to contain unrepresentative information about a parameter (Francis, 2011). However, down-weighting the data when there is model misspecification does not necessarily improve the estimates and the model misspecification should be identified and corrected (Maunder and Piner, 2017). Data weighting also impacts the precision of the estimated quantities. It is common for SAMs to fix the weights assigned to the data sets. For example, the standard deviations of the logarithms of catch and the index of abundance (Eqn A.1 and A.2) are pre-specified based on auxiliary information, while the input sample size for the multinomial distribution for the catch age-composition data (S_t in Eqn A.3) is based on a subjective understanding of the data. The value of S_t is not set to the number of animals measured for age (which would correspond to unweighted data) because it is well-known that the sampling schemes commonly used in fisheries result in sample sizes that are substantially larger than those corresponding to independent sampling (Stewart and Hamel, 2014).

Subjective weighting of likelihood components and penalties, particularly those related to data collected from fishing operations, is common in SAMs. Often the weighting is coupled with an examination of the sensitivity of the results to alternative weighting schemes. This differs from most IPMs where the distribution for a process or data source is either implicit in the model (e.g., Bernoulli for whether a marked animal is resighted), the value of the parameter determining the variance of a data point is given from sampling theory, or the variance parameter is estimated. Therefore, data weighting is usually not performed in IPMs; in fact data weighting is hardly discussed in IPMs (Schaub and Kéry, 2022). The widespread use of Bayesian methods when fitting IPMs facilitates use of priors for variance parameters, and hence greater stability.

Checking the assumptions of statistical models in general is important to avoid biased estimates of key model outputs which could be problematic for the intended use of the model (Conn et al., 2018). All parameters can potentially be biased in an integrated model if the assumptions of at least one component model are violated (Maunder and Piner, 2017), and the parameters most sensitive to bias are the hidden parameters for which little or no direct information is available (Schaub and Kéry, 2022). It is therefore important to have confidence in an integrated model and to perform some form of model checking.

Although there are some suggestions and recommendations on

[9] Auto-differentiation Model Builder ADMB, Fournier et al. (2012), which was traditionally used for most SAMs, supports inference in both the Bayesian and frequentist frameworks but the Bayesian sampling algorithm is slow except for very simple problems and the implementation of the Laplace approximation is also very slow.

goodness-of-fit testing for IPMs (Besbeas and Morgan, 2014; Schaub and Kéry, 2022), there is no omnibus goodness-of-fit test so far, and Schaub and Kéry (2022) speculate that there will never be one. A major problem is that an integrated model requires assumptions beyond those of non-integrated models (e.g., the demography of the individuals appearing in the different data sets must be the same ('common demography assumption' c.f. Schaub and Kéry, 2022), or the data sets must be independent (unless a dependency is explicitly modelled) and it is not clear how to assess these assumptions. It is therefore not surprising that the majority of empirical IPMs have not performed any formal model checking (Table 7.1 in Schaub and Kéry, 2022). When goodness-of-fit tests have been performed, they have been done for each individual data sets, either in a separate analysis or within the IPM. Due to the Bayesian estimation framework used in most IPMs, posterior predictive checks have often been conducted. Sometimes established frequentist tests have been used such as those for capture-recapture data to estimate survival (e.g., Pradel and Lebreton, 1993; Pradel et al., 1997, 2003). Schaub and Kéry (2022) reviewed model assumptions of IPMs and their assessment and showed that posterior predictive checks generally have low power to detect violations of assumptions, that hidden parameters are often the most sensitive to bias, and that violations of assumptions become more problematic for parameter estimation, the more information a data set provides. They also made some ad hoc recommendations based on simulation studies. For example, goodness-of-fit tests should be performed whenever they exist for component data (e.g., capture-recapture for estimating survival) ideally within the IPM. Comparison of estimates from an IPM with the corresponding parameter estimates from a single data set fit is also recommended. A large difference may indicate problems.

Several tests and ideas have been proposed for assessing the fit of SAMs and are reviewed in Carvalho et al., (2017, 2021). Common approaches include standard diagnostics such as residual analysis, but others have been developed including retrospective analyses (Cadigan and Farrell, 2005; Hurtado-Ferro et al., 2015), hindcasting (Kell et al., 2016), likelihood component profiles (Maunder and Starr, 2001; Wang et al., 2014), model and data simplifications (ASPM; Maunder and Piner, 2015), catch-curve analysis (Carvalho et al., 2017), and simulation methods (Piner et al., 2011); all of which could be adapted to IPMs.

7. Lessons learnt and the way forward

IPMs and SAMs vary along several major axes; the objectives being addressed; whether demographic stochasticity is included to understand extinction risk and because of population sizes; whether the aim is understanding absolute population size to regulate harvest sizes or otherwise; whether the spatial extent of a population is well defined or not; whether we have additional sources of information to estimate detectability; and the types of data available. A SAM is in a sense more data- (or information-) hungry than an IPM because of the need to precisely estimate absolute biomass or abundance, and individual level data that inform demographic rates are more difficult to obtain in systems where SAMs are applied. SAMs therefore require more 'tuning' or assumptions than IPMs, where the 'data speak' more for themselves, and consequently techniques such as data weighting or model assessments are more advanced for SAMs than for IPMs.

There are several lessons to be learnt from IPMs for SAMs, and vice versa; here we highlight a few that we think are of particular interest.

7.1. Suggestions for everyone

- SAMs and IPMs should better evaluate the sampled data and choose the appropriate sampling distributions and values for the variance parameters, where appropriate, eliminate model misspecification, and model temporal process variability adequately. Further research is needed to determine if, and when, it is appropriate to apply model weighting in the presence of uncorrectable model misspecification and unmodeled process variation.
- Some of the differences between the SAMs and IPMs are not due to different objectives or data, but rather to the 'tradition' of the field (aquatic vs terrestrial) in which they are applied. Traditions should be overcome in order to move towards a unified approach. This includes the fitting framework (frequentist vs. Bayesian). There may be good reasons for using one or the other, but the decision should be based on these reasons and not simply on tradition. We also believe that the development of the population model, which is a key part of any SAM and IPM, should follow general biological principles, such as how to structure the population (age, stage, size), which components of stochasticity (demographic, environmental) to include, and whether and how to include density dependence. These decisions should be made transparent and explicit.
- During the writing of this paper, the authors discovered that it was sometimes difficult to communicate and exchange ideas, simply because of different terminology. There are terms such as 'stock-recruitment relationship' or 'fledging success' that are used only in SAMs or only in IPMs. Different terminology is an obstacle to moving towards a unified approach. We do not suggest that standardized terminology is necessary, as precise, context-specific terminology is important for communication in a more specialized field. However, to increase transparency, we suggest that appropriate definitions or explanations of certain terms be developed and made available generally in both fields (Table 1 is an initial attempt to highlight some of the key terms that led to confusion among the authors).
- The usual workflow for applying SAMs and IPMs is to identify a management objective or research question, then identify already collected data that might be useful to address the objectives, and then apply a SAM or IPM. Ideally, however, it should be known what data need to be sampled to best address the objectives before data start being collected. This requires knowledge of sampling designs, but sampling designs are poorly understood for both SAMs and IPMs (but see Johnson et al., 2020). We expect that better inference and more efficient studies if sampling designs for SAM and IPM are better understood.

7.2. Suggestions for analysts using IPMs

- IPMs generally assume that population-level data have little or no systematic bias. IPMs could be improved by including data that are informative about such bias, similar to the case for SAMs (see Hoyle et al., 2024).
- Collection of information on the number of unmarked individuals in addition to the marked individuals can provide estimates of absolute abundance, which may be useful when the population size is small, the probability of extinction is desired, and total census counts are not available. This is a situation encountered by one of the authors (MNM) when evaluating the impact of the fishery on the New Zealand yelloweye penguin *Megadyptes antipodes* population (see Maunder et al., 2009 for the mark-recapture component). Absolute abundance can also be estimated if alternative sampling protocols for the count data are used such as repeated counts, double observer approaches or the collection of distance information, but these are, with few exceptions (Chandler et al., 2018; Ross et al., 2018; Schmidt and Robison, 2020; Ramsey et al., 2021; Milligan and McNew, 2022), rarely implemented in IPM.
- Custom data weighting is not applied in IPMs. IPMs use likelihood functions where the variance parameter is inherent in the assumed distribution so that data sets are weighted 'automatically', but there is the possibility of overdispersion due to the sampling design, model misspecification, and unmodelled process variation. These factors can lead to over weighing of some data sets and underestimation of the total uncertainty. There would be benefit to develop new diagnostics (and ideally 'diagnostic cookbooks', c.f. Carvalho et al.,

2021) for use with IPMs. Also see Fletcher et al. (2019) for an integrated model (but not an IPM) where the optimal weights for the data sets combined where estimated by cross-validation.

- Mortality is typically expressed as a probability in IPMs, whereas it is expressed as a hazard rate in SAMs. As the latter is more general (Ergon et al., 2018), we advocate greater use of hazard rates in IPMs. This would to some degree also reduce differences in terminology between IPMs and SAMs.
- The various goodness-of-fit testing techniques developed for SAMs should be explored for IPMs.

7.3. Suggestions for analysts using SAMs

- SAMs typically rely on strong assumptions about demographic processes, whereas IPMs attempt to estimate these processes. Therefore, SAMs could benefit from attempting to sample data that are directly informative about demographic processes.
- Exploiting the additional information on individual variation from multiple recaptures of the same individual in SAMs, where practical (e.g., whales, seabirds), might allow for better understanding in SAMs.
- SAMs, particularly those that aim to capture spatial structure, should consider allowing for the effects of immigration and emigration (e.g., by allowing natural mortality, *M,* to be stochastic).
- SAMs often pre-specify, i.e., fix many of the parameters that determine the dynamics of the population (e.g., stock-recruitment steepness, growth) whereas this is uncommon for IPMs. This will lead to under-estimation of uncertainty – we advocate that where possible SAM developers treat as many parameters as possible as estimable, for example, by providing priors on these parameters and estimating them.

In summary, this paper emphasizes that integrated SAMs and IPMs have much more in common than is generally assumed. Indeed, when viewed from a broader perspective, they are essentially the same: population models that attempt to estimate abundance and demographic rates from a joint analysis of multiple data sets. Despite the many similarities, these types of models have been developed largely independently in the two fields. As a result, certain aspects are more developed in one type of model than in the other, and vice versa. We hope that this paper will encourage more exchange and collaboration between the fields of fisheries stock assessment, population ecology and wildlife management.

CRediT authorship contribution statement

Schaub Michael: Conceptualization, Formal analysis, Writing – original draft. **Kéry Marc:** Conceptualization, Writing – review & editing. **Maunder Mark N.:** Conceptualization, Formal analysis, Writing – original draft. **Jacobson Eiren K.:** Writing – review & editing. **Thorson James T.:** Conceptualization, Writing – review & editing. **Punt André E.:** Conceptualization, Writing – original draft.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: André Punt is one of the editors-in-chief of Fisheries Research. Mark Maunder is on the editorial advisory board of Fisheries Research.

Data Availability

Data are available in the Appendix C.

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Appendices

Appendix A: Derivation of the [penalized] likelihood function for the integrated stock assessment model (SAM).

The negative logarithm of the objective function, which is a combination of component likelihoods for the catch (L_C), index (L_I), and catch age-composition (L_{Age}) data, and the penalties for the recruitment deviations (P_R and P_{Init}) deviates, is minimized:

$$-LnL = -Ln\left(L_C L_I L_{Age} P_R P_{Init}\right)$$

A.1. Likelihood.

The contribution of the catch data to the negative of the logarithm of the likelihood function is based on the assumption that the catches are subject to log-normal error,

$$L_C : ln\left(C_t^{\text{obs}}\right) \sim N\left(ln(\widehat{C}_t); \sigma_C^2\right) \tag{A.1}$$

where C_t^{obs} is the observed catch-in-weight (weight of the captured individuals) for year t, and $\widehat{C}_t$ is the model-estimate of the catch-in-weight for year t (Eq. 2).

The contribution of the index of relative abundance to the negative of the logarithm of the likelihood function is based on the assumption that the survey index is subject to log-normal error,

$$L_I : ln\left(I_t^{\text{obs}}\right) \sim N\left(ln(q\widehat{B}_t); \sigma_t^2\right) \tag{A.2}$$

where I_t^{obs} is the survey index of abundance for year t, q is the catchability coefficient, $\widehat{B}_t$ is the model-estimate of the vulnerable biomass during year t, and σ_t is the sampling coefficient of variation for the index during year t.

The contribution of the catch age composition data to the negative of the logarithm of the likelihood function is based on assumption that the age composition data are multinomially distributed, i.e. ignoring constants independent of the model parameters:

$$L_{Age} = -\sum_t S_t \sum_a \rho_{t,a} ln\left(\widehat{\rho}_{t,a}\right) \tag{A.3}$$

where $\rho_{t,a}$ is the observed proportion of the catch-in-numbers (number of captured individuals) during year t that was of age a, $\widehat{\rho}_{t,a}$ is the model-estimate of the proportion of the catch-in-numbers during year t that was of age a, and S_t is the effective sample size for the fishery age-composition data in year t, set to 50 based on a subjective understanding of the data.

Penalties.

Penalties (corresponds to informative priors in the context of a Bayesian analysis) based on the assumption that recruitment is log-normally distributed is placed on the recruitment deviations, i.e.:

$$P_R : \varepsilon_t \sim N\left(0; \sigma_R^2\right) \tag{A.4}$$

$$P_{Init} : \varepsilon_a \sim N\left(0; \sigma_R^2\right) \tag{A.5}$$

where ε_t is the random deviation in recruitment about the average recruitment, σ_R is standard deviation of the recruitment deviations, and ε_a is the deviation for age a to determine the initial age-structure.

Appendix B. Derivation of the likelihood function for the integrated population model (IPM).

A state-space model (de Valpine and Hastings, 2002; Buckland et al., 2004; Newman et al., 2014) is adopted for the annual population count data and the observed counts are decomposed into one contribution from the underlying true dynamics of state N_t (the state process) and another from an observation process that describes how an observation in year t is related to the true state in year t. The state process is a first-order Markov process and corresponds exactly to the population model. The state (population size) in the first year cannot be written recursively, so a model is needed for it. In a Bayesian analysis we estimate the population size in the first year and therefore place a prior on it.

The likelihood of the state-space model (L_{ss}) is the product of the three likelihoods for the population size in the first year (L_1), for the state process (L_S), and for the observation process (L_O), i.e.:

$$L_{SS}\left(\boldsymbol{N}, \phi_j, \phi_a, \boldsymbol{\rho}, \omega | C\right) = L_1(\boldsymbol{N}_1) \times L_S\left(\boldsymbol{N}_{2...T}, \phi_j, \phi_a, \boldsymbol{\rho}, \omega\right) \times L_O(\boldsymbol{N}|\boldsymbol{C}) \tag{B.2}$$

where plain and bold symbols denote scalars and vectors or matrices, respectively.

The observation model assumes that the population counts are correct on average and have no systematic bias, e.g., due to imperfect detection or double counting, and therefore adopts a Poisson sampling distribution:

$$C_t \sim \text{Poisson}(N_t) \tag{B.1}$$

The second component likelihood is for the productivity data, i.e., the number of fledglings per surveyed brood i (f_i). The distribution of the number of fledglings contains excess zeros caused by a significant number of failed broods. These data could be modelled using zero-inflated models, but for simplicity we first model the probability of a brood being successful using a Bernoulli distribution, and second model the non-zero number of fledglings of successful broods using a normal distribution. Thus, we specify a zero-inflated model in two steps and there are two component likelihoods for the productivity data. For the Bernoulli likelihood the data are recoded such that $z_i = 1$, if $f_i > 0$ and $z_i = 0$, if $f_i = 0$. Then, $z_i \sim Bernoulli(\upsilon_t)$, where υ_t is the probability that a brood attempted in year t was successful (i.e., the nest success probability). The temporal variation of nest success was modelled with random time effects, $\text{logit}(\upsilon_t) \sim \text{Normal}(\mu_\upsilon, \sigma_\upsilon^2)$, where μ_υ is the mean nest success on the logit scale and σ_υ^2 is the temporal variability of the logit nest success. The component likelihood is $L_{P1}(\upsilon, \sigma | z)$.

For the number of fledglings of a successful brood we restrict the productivity data to those that were successful, i.e., $q_i = f_i$ if $f_i > 0$. We use the normal distribution and obtain $q_i \sim Normal(\kappa, \sigma_q^2)$, where κ is the average number of fledglings of successful broods, and σ_q^2 is the variance of the number of fledglings among successful broods. The component likelihood for the number of fledglings of successful broods is $L_{P2}(\kappa, \sigma_q^2 \big| \boldsymbol{q})$. The annual productivity as used in the population model is $\rho_t = \upsilon_t \kappa$.

A Cormack-Jolly-Seber (CJS) model (Williams et al., 2002) with a multinomial likelihood is assumed for the capture-recapture data, i.e. the capture-recapture are treated as 'release conditioned'. These data are summarized as a matrix with rows for each individual captured and columns for years. Each row in the matrix is an individual capture-history where a 1 denotes a capture/recapture/resighting (more generally an encounter) of an individual at the corresponding time step and a 0 denotes an individual that was not encountered at that time step. These data could be analyzed directly using a state-space representation of the CJS model (Royle, 2008; Schaub and Kéry, 2022), but here we arrange them into the m-array format (Williams et al., 2002; Schaub and Kéry, 2022) and use the multinomial likelihood to increase computational efficiency. The m-array ($\boldsymbol{m}$) is a table summarizing how many individuals were released in each year, and when these individuals were first re-encountered after that release. Given a release in year t, we can express the probability of a reencounter in year j as a recursive function of apparent survival (ϕ) and reencounter probability (p), $\pi_{t,j} = \phi^{j-t}(1-p)^{j-t-1}p$. The m-array table also contains a column for the number of released individuals that were never reencountered. The probability that an individual is never reencountered is calculated as the complement to 1 and the sum of the probabilities of reencountered individuals. The likelihood for the capture-recapture data in the m-array format is:

$$\boldsymbol{m}_t \sim Multinomial(\pi_t, R_t) \tag{B.3}$$

where m_t is the tth row in the m-array, R_t is the total number of individuals released in year t, and π_t is a vector with probabilities expressing when individuals that were released in year t were reencountered as a function of apparent survival and reencounter probabilities. For further details, see Schaub and Kéry chapter 4.5) (2022). The component likelihood of the capture-recapture data is $L_{CR}(\phi_j, \phi_a, \boldsymbol{p}_1, \boldsymbol{p}_a \big| \boldsymbol{m})$, where p_1 and p_a are the reencounter probabilities in the first and later years of age, respectively. We expect them to differ because younger females are more likely to fail (and then move away) than older females and therefore have a lower chance to be re-encountered.

The final step in the IPM is to formulate the joint likelihood, which is the product of the three component likelihoods:

$$L_{IPM}\left(\boldsymbol{N},\phi_j,\phi_a,\omega,\upsilon,\kappa,\boldsymbol{z},\boldsymbol{p}_1,\boldsymbol{p}_a,\sigma_q^2,\sigma_\upsilon^2\middle|\boldsymbol{C},\boldsymbol{z},\boldsymbol{q},\boldsymbol{m}\right)=L_{SS}\left(\boldsymbol{N},\phi_j,\phi_a,\upsilon,\kappa,\omega\middle|\boldsymbol{C}\right)\times L_{P1}\left(\upsilon,\sigma_\upsilon^2\middle|\boldsymbol{z}\right)\times L_{P2}\left(\kappa,\sigma_q^2\middle|\boldsymbol{q}\right)\times L_{CR}\left(\phi_j,\phi_a,\boldsymbol{p}_1,\boldsymbol{p}_a\middle|\boldsymbol{m}\right) \tag{B.4}$$

As $\rho_t=\upsilon_t\kappa$ we have replaced $\boldsymbol{\rho}$ by $\boldsymbol{\upsilon}$ and κ in all component likelihoods.

The productivity data could have been analyzed in a single step using a hurdle model, but writing that likelihood in JAGS is a bit complicated and not very intuitive. One might prefer a discrete-valued distribution for productivity instead of the normal. However, a Poisson is far too dispersed for usual fledging counts. Less dispersed alternatives have been developed (e.g., Ridout and Besbeas, 2004; Lynch et al., 2014; Brooks et al., 2019) but they are more complex and we have found that using a normal instead of some of them seems to have little effect on the main conclusions of an IPM.

Appendix C. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2023.106925.

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