

Are multispecies models an improvement on single-species models for measuring fishing impacts on marine ecosystems?

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We review the application of multispecies models as tools for evaluating impacts of fishing on marine communities. Four types of model are identified: descriptive multispecies, dynamic multispecies, aggregate system, and dynamic system models. The strengths and weaknesses of multispecies models and their ability to evaluate the causal mechanisms underlying shifts in production are examined. This comparison provides a basis for assessing the benefits of each modelling approach as a tool for evaluating impacts of fishing in marine ecosystems. Benefits of multispecies models include: improved estimates of natural mortality and recruitment; better understanding of spawner–recruit relationships and of variability in growth rates; alternative views on biological reference points; and a framework for evaluating ecosystem properties. Populations are regulated by competition (food limitation), predation, and environmental variability. Each factor may influence different life-history stages, locally or regionally. However, most multispecies models address only a subset of these factors, often aggregated over functionally different species or age groups. Models that incorporate the important interactions at specific stages and scales will be necessary if they are to continue to supplement the information provided by single-species models.

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Introduction

The past two decades have seen an explosive growth in the number and type of multispecies models directed at fisheries questions. The ultimate motivation of all fisheries models, whether single- or multispecies, is to understand, and inform decision-makers of, the consequences of possible fishing activities. More recently, concern is being directed to the effects of fishing on the wider ecosystem as well as upon the commercially exploited fish species. Ecosystem effects of fishing have been reviewed by several ICES working groups (ICES, 1988, 1989, 1994,

1997). Two types of effects are of particular relevance here: (1) direct mortality on target species and incidental mortality on other biota; and (2) indirect effects related to changes in the flow of energy through the ecosystem. Single-species models can address the first effect, while multispecies models will be required to address the second effect. Here, we consider whether multispecies models are better than single-species models for predicting the consequences of direct mortality, and whether they provide useful measurements of indirect effects.

Multispecies models pose hypotheses about how ecosystems function as explicit computational algorithms.

The hypotheses, in turn, arise from underlying ecological theories. We first examine classes of hypotheses posed in various models. Then we evaluate the degree to which explicit inclusion of each type of ecological process allows us to see more clearly how fishing affects ecosystem properties. Multispecies models could improve our understanding in at least two ways: (1) through a more realistic treatment of uncertainty and variability in population parameters (e.g. natural mortality) of the target species; or (2) by representing additional non-target species and ecological linkages among species, either of which could be altered through fishing.

Major ecological processes

Mechanisms underlying ecosystem form and function have been subject to debate in the ecological literature (Nicholson, 1933; Andrewartha and Birch, 1954; MacArthur and Levins, 1967). Most ecologists acknowledge three primary processes as the underlying forces governing populations: competition, predation, and environmental disturbance. Natural variation in recruitment, survivorship, and growth of fish stocks are consequences of these three processes. Effects of fishing are then superimposed on this ecological background.

Competition is a fundamental structuring process in many ecological theories. Competition requires that the resource shared is limiting, and hence it is closely tied to the carrying capacity of the system for suites of competitors. In most multispecies fisheries models, competition is applied in a weaker sense, requiring that any change in abundance of one species is compensated in the trophic structure, by reciprocal changes in abundance of species with overlapping diets.

Predation is also a fundamental ecological process. The importance of predation as a regulatory process in marine systems has been well documented (Bailey and Houde, 1989; Bax, 1998). Early multispecies models were built largely to estimate predation mortality inflicted on prey. These models represented community dynamics on the basis of tracking the consequences of perturbations of one (or more) species' abundance through direct predator–prey linkages.

Environmental disturbances have been proposed as a major process structuring ecological systems (Andrewartha and Birch, 1954), both by causing direct mortality and by changing the carrying capacity of the ecosystem. The duration and intensity of such disturbances can have varied effects on ecosystem structure. Large, abrupt environmental changes mean populations become mismatched with their carrying capacities (either well above or far below, depending on the direction of the change; den Boer, 1986; Wiens, 1984). Persistence of changes in environmentally determined

productivity levels for long periods may lead to co-existence of competing species when species store the reproductive energy through longevity (Chesson, 1983).

Competition, predation, and environmental disturbance are not independent. For example, predation may reduce the abundance of competitors below their carrying capacity, reducing the effect of competitive interactions of the species' dynamics (Caswell, 1978). Recent reviews suggest that predation (consumer control) and competition (resource control) are both important, with lower trophic levels resource limited and upper trophic levels consumer limited (Brett and Goldman, 1997). Complicating this picture is Rice's (1995) observation that some systems exhibit food webs with "wasp waists", where a few species at an intermediate trophic level may filter production from all lower levels to predators above them. Environmental events can change the carrying capacity for short or long periods and alter the competitive environment indirectly, or through direct mortality may change predator–prey proportions or the relative dominance of competing species (Skud, 1982).

Distinguishing shifts in ecosystem properties induced by humans from natural variability in the same properties is impeded when the mechanisms causing variability in individual stocks remain uncertain. The three primary regulatory forces – competition, predation, and environmental – and their interactions provide a framework within which we can review multispecies models.

Categorization of multispecies models

We aim to identify the types of impacts of commercial fishing that could be measured by multispecies models. Multispecies fisheries models have been reviewed several times (Kerr and Ryder, 1989; Pope, 1991; Magnússon, 1995; Bax, 1998). Kerr and Ryder (1989) suggested various categories of model. While broadly following their classification, we extend it to include a category for coupled biophysical system models. Descriptive multivariate models represent a first category of models that are mainly empirically based with simple dynamics. This category contains both conceptual and statistical models. Rice (this volume) reviews the variety of statistical models used to provide indices of ecosystem health and status, and discusses their role in evaluating impacts of fishing on ecosystem status. Of the remaining categories, the main distinctions and type examples are shown in Figure 1 and their common uses and assumptions are listed in Table 1. We consider how the core ecological processes are addressed in the three remaining categories. Our review, like the multispecies models themselves, focuses almost completely on first-order effects of fishing, environmental forcing, and species ecological interactions as predators, prey, or competitors.

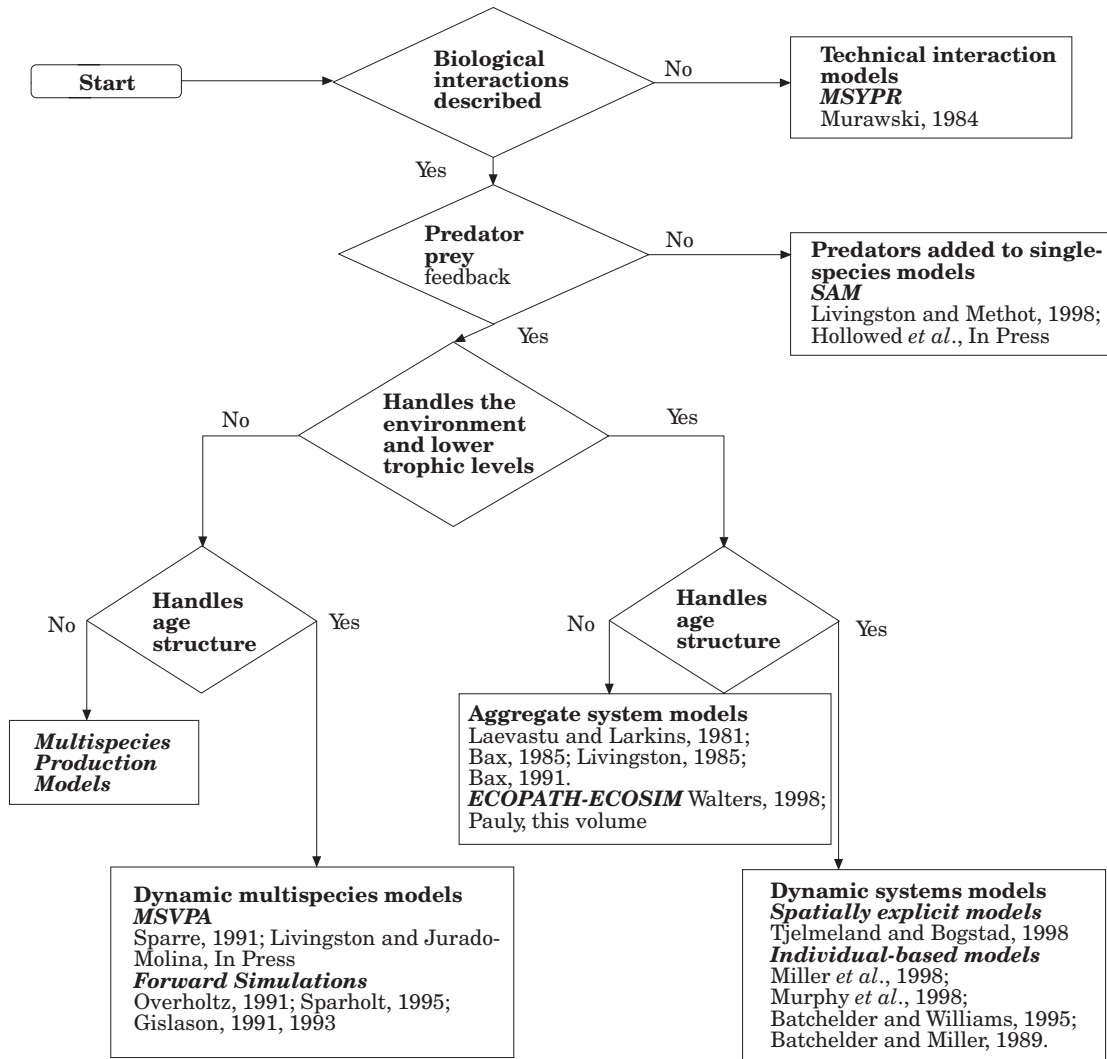


Figure 1. Flow chart summarizing classification of multispecies models. Bold letters indicate model classification and italicized letters indicate subcategories of models; references are provided.

Dynamic multispecies models

Dynamic multispecies models consider functional relationships among individual species in a fished system. They build upon single-species theory to understand the dynamics of multispecies fisheries. The flow chart distinguishes those models that consider technical interactions among species from those that consider predation effects (Fig. 1). These models account for interactions among selected species (often exploited fish species) but do not address the ecosystem as a whole.

Technical interactions involve the simultaneous capture of groups of species. Models of the joint capture of species that do not interact biologically have been developed by Murawski (1984) and Pikitch (1991). Technical interaction models to date have focused on

equilibrium yield per recruit analyses. However, they can be readily developed in the framework of other multispecies model types. For example, biomass dynamic models for aggregate species groups can be specified for jointly harvested species (Brown *et al.*, 1976; Ralston and Polovina, 1982). Models of this type can be appropriate both for interacting and non-interacting species groups.

Dynamic multispecies models consider predator-prey interactions and evaluate interactions between a subset of the species in the ecosystem. They do not model competitive interactions explicitly, but often include constraints such as conservation of total system biomass, or constant input of food from outside the model, which result in changes in abundance of one species indirectly affecting the abundance of species with which

Table 1. Primary use, key assumptions and problems of different multispecies models (DPM: dynamic production models; SS: single-species; MS: multispecies; VPA: virtual population analysis; SAM: statistical assessment model; BBM: bulk biomass model; CBPM: coupled biophysical models; RSA: retrospective stock assessment; SP: stock projection; M: natural mortality; P: predation mortality; M1: M minus P; G: growth rate; S: suitability; R: recruitment; S-S: steady state; ATG: aggregated taxonomic groups; PF: physical forcing).

Model	Primary use	Common assumptions/problems
DPM SS, VPA MSVPA	RSA, exploratory RSA RSA	Constant M and G by ATG. Constant M and G, lacks PF. Constant M1 and S by species/age class, P inversely proportional to amount of prey available. Lacks PF.
MSFOR	SP, exploratory	Constant M1 and S by species/age class, P inversely proportional to amount of prey available. Usually lacks PF, sensitive to assumptions regarding incoming R.
SS, SAM*	RSP, with short (5 year) SP	Capable of estimating M, and G if selectivity and catchability constant. Often lacks PF.
MS, SAM	RSP, with short (5 year) SP	Capable of estimating numerous non-linear functions that could include functional relationships between predator biomass and P, and prey availability and G. Often lacks PF.
Ecopath, BBM, Skebub	Retrospective, exploratory, mass balance	ATG, equilibrium (S-S) assumed. Ecopath: constant M1 and G. BBM and Skebub: G dependent on food availability and temperature.
Ecospace, Dynumes	Ecosystem projections, exploratory	Constant M1 and S by ATG, emigration rates across cells are proportional to movement speed and inversely proportional to cell size. Ecospace does not address seasonal variations in PF and dispersal or migration behaviour of vertebrates.
Ecosim	Ecosystem projections, exploratory	Constant M1 by ATG, sensitive to assumptions regarding incoming R and maximum consumption rates.
CBPM	Retrospective, exploratory, hypothesis-testing	Coupling known without error, mechanisms observed in mesoscale process studies apply to population level, verification difficult.

it shares prey. Environmental conditions are seldom considered. There is no conceptual impediment to adding environmental forcing factors, but when they are coupled to dynamic multispecies models the result is a different class of model (i.e. dynamic system models).

Early dynamic multispecies models that address species interactions (predation mortality and sometimes prey-related growth) stemmed from the ecosystem model of Andersen and Ursin (1977). They developed a simulation model for the North Sea that incorporated predator-prey feedback and the influence of fishery removals. By simplifying the assumptions of food availability, they paved the way for the development of equilibrium multispecies models and dynamic multispecies models with species interactions (Ursin, 1982). The models that resulted include retrospective assessments of species interactions which include (Fig. 1): virtual population analysis (VPA) models allowing for cannibalism (while in a strict sense single-species models, usually considered as honorary multispecies models); multispecies VPA (MSVPA); and statistical assessment models (SAM; single-species with predation). These

models require the same catch-at-age and abundance indices as would be used in a congruent set of single-species models. In addition, they require data on predator ration and feeding preferences, often in the form of synoptic stomach-content data sets.

Strong assumptions are often imposed when simplifying the predator-prey interaction terms in dynamic multispecies models. Commendable effort has been placed on testing the assumptions underlying MSVPA. Rice *et al.* (1991) examined the stability of predator preferences and prey vulnerabilities (expressed as suitabilities) for the North Sea over 4 years and these analyses have since been extended (ICES, 1997). The results indicate that suitabilities were fairly stable over time. The impacts of relaxing assumptions regarding impacts of stock density on growth (Gislason, 1999), reproduction (Sparholt, 1995), and prey switching (Hildén, 1988) have also been examined.

Several dynamic multispecies models have been adapted to provide forward simulations to evaluate potential impacts of fishing (Fig. 1). Studies of the North Sea adopting the combined use of MSVPA and

its forward projection (MSFOR) showed projections to be most sensitive to assumptions about predator recruitment (Pope, 1991).

SAMs invoke a forward fitting process based on maximum-likelihood-fitting algorithms. These models assume an age-structured model with the Baranov catch equation as the underlying population model (Fournier and Archibald, 1982). They allow the analyst flexibility in selecting among multiple options regarding parameter values within the assessment. Using this approach, Livingston and Methot (1998) modified a single-species stock synthesis assessment for Bering Sea pollock to accommodate predation mortality. More recently, SAMs have been modified to consider uncertainty stemming from process and measurement errors. Hollowed *et al.* (in press) used this approach to explore the impact of assumptions regarding predator satiation, and natural mortality other than predation mortality on abundance trends and uncertainty in ending biomass (survivors).

Aggregate system models

Aggregate system models (Fig. 1) are primarily used to examine the energy flow and the mass balance of whole ecosystems. In addition to data aggregation, most models invoke equilibrium (steady-state) assumptions to allow the user to solve for unknown biomasses. Also, most models assume that food composition is known without error, although this assumption can be relaxed when independent biomass estimates are available (Bax and Eliassen, 1990). Equilibrium assumptions can be relaxed by specifying known changes in biomass of any group. A general method of calculating energy flows under the mass-balance assumption has been derived using the ECOPATH model. Pauly *et al.* (this volume) provides a summary of the marine ecosystems where ECOPATH has been applied.

Dynamic simulations from the steady state have been performed from some of these mass-balance food-web models (Laevastu and Larkins, 1981; Bax and Eliassen, 1990) and in some cases spatial resolution and migration have also been incorporated into the simulation. A similar progression of the ECOPATH model is now developing, allowing for dynamic simulation (ECOSIM) and spatial definition (ECOSPACE; Walters, 1998; see also Pauly *et al.*, this volume).

Aggregate system models are primarily used to describe trophic interactions within a community and to examine the energy flow and the mass balance of whole ecosystems. They rarely provide for environmental forcing, although in ECOSIM trends in either the top or bottom trophic level can be introduced, and their effects followed through time (Walters, 1998). As an exception to this generalization, Laevastu and Larkins (1981) developed an aggregate system model of the Bering Sea

that included environmental influences on growth and migration patterns of marine fish. Modelling results generally represent marine ecosystems as predator-controlled. Correspondingly, simulations of overexploitation of dominant predators on Georges Bank show shifts in community structure to dominance of previously subdominant predators (Collie and DeLong, 1999).

Dynamic system models

Dynamic models of the ecosystem attempt to model bottom-up and/or top-down forcing in a dynamic framework. Compared with dynamic multispecies models, dynamic system models have a higher level of detail at the species level and include more detailed coupling of physical forcing and its effect on biological interactions. They may be used to explore hypotheses regarding the mechanisms underlying the maintenance of ecosystem properties (Levin *et al.*, 1997). Several dynamic system models have developed as extensions to dynamic multispecies models to account for temporal and spatial differences in the interactions of organisms. MULTSPEC and BORMICON represent spatially resolved predator-prey interactions between cod, capelin, herring, and marine mammals in the Barents Sea (Tjelmeland and Bogstad, 1998; Bogstad *et al.*, 1992) and Iceland (Stefánsson and Pálsson, 1997), respectively.

Individual-based models (IBM) have been coupled to physical models to simulate processes influencing secondary production in several marine ecosystems. Similar approaches have been used to couple oceanographic forcing to production of larval or juvenile fish on Georges Bank (Werner *et al.*, 1996) and in Shelikof Strait (Hermann *et al.*, 1996). Data limitations have prevented the development of IBMs of the whole ecosystem. The high level of mechanistic coupling invokes a large computational cost. Model formulations are often verified using data sets obtained from interdisciplinary research programmes focused on hypothesis-testing for a selected group of key target species. Thus, they currently must remain restricted in their scope to higher trophic levels.

Some dynamic system models have been developed that represent physical coupling to the dynamics of prey, and linked consequences on some of their predators. For example, the European Regional Seas Ecosystem Model provides a spatially resolved simulation model of the planktonic food web of the North Sea using linked models of primary production, secondary production, and fish production (Bryant *et al.*, 1995; Baretta *et al.*, 1995).

In terms of representation of the basic ecological processes, dynamic system models tend to have more trophodynamic structure than other classes of

multispecies models. Generally, predator satiation and compensatory abundance relationships among competitors are both built in. The modelling emphasis usually is on the coupling of environmental factors to species abundance and interaction rates. Correspondingly, their main use is in exploring responses of systems to environmental disturbances. Lower trophic-level models are possible because many of the functional biophysical couplings can be estimated based on ocean physics when simple trophodynamic relationships are applied. As animals become larger and more mobile and feeding responses become more complicated, the accuracy of model predictions becomes more difficult to verify.

Comparison of multispecies models with single-species models

Direct effects of fishing

Single-species assessments typically include the following steps:

- Conduct a historical reconstruction of the stock to establish key parameters and relationships and to describe the current stock status (assessment).
- Propose specific actions (e.g. total allowable catch) that will steer the stock towards a desired status (short-term forecasting).
- Make long-term predictions of the likely future status of the stock under various management scenarios to establish desirable states (long-term forecasting).
- Advise on the robustness of management procedures (precautionary approach).

It is questionable whether multispecies models provide better advice than single-species models under these headings. The available information regarding trophic interactions and biophysical couplings is limited in most marine ecosystems, and model verification is difficult. Thus, multispecies models should be considered as works in progress. As our knowledge of the functional relationships governing trophic interactions and the role of environmental disturbance on such relationships improves, multispecies models offer the potential of greater biological reality. The performance of multispecies models relative to single-species models is evaluated below.

Report card on assessment

Many single-species models impose strong assumptions regarding natural mortality rates and seldom account for temporal trends in mortality-at-age. Assuming constant mortality places the annual variance in predation mortality into other sources of variability within the assessment (e.g. measurement error when tuned to fishery-independent data). Temporal trends in mortality resulting from applications of dynamic

multispecies models can be used in single-species models to explore the impact of alternative assumptions regarding natural mortality on perceptions of stock status. However, efforts should be made to minimize the circularity of the interchange between single-species VPA and MSVPA, because the results from the former are often used to establish the initial conditions for some of the adult stocks in the latter.

Dynamic multispecies models have commonly been used to evaluate age-specific or temporal trends in estimates of mortality (Sparholt, 1990). The ICES Multispecies Assessment Working Group found that accounting for inter- and intraspecific predation mortality resulted in much higher mortality rates for younger age classes than previously estimated, and these rates varied from year to year (Pope, 1991). Similar results were noted in models of pollock in the Gulf of Alaska (Hollowed *et al.*, in press) and eastern Bering Sea (Livingston and Methot, 1998; Livingston and Jurado-Molina, in press), and Atlantic cod stocks in the Gulf of St. Lawrence, the Scotian Shelf and the Barents Sea.

In practice, average levels of these new estimates of mortality have often been adopted subsequently in single-species assessments. In assessment terms, these changed perceptions of mortality have different effects on large species and on small species. For larger fish, higher mortality applies mainly to pre-recruit and juvenile fish, while for forage fish it applies to all ages. With regard to evaluating ecosystem effects of fishing, proportional upward scaling of pre-recruit year classes adds little to understanding effects of fishing on the older members of the target species. However, the rescaled values may be important in evaluating the effects of other fisheries that take pre-recruits as by-catch.

Imposing temporal trends and revised estimates of natural mortality stemming from dynamic multispecies models changes the estimates of numbers of recruiting ages. Pope (1991) observed that recruitment estimates from multispecies models were typically highly correlated, but scaled upwards, with earlier single-species results. Comparison of results from dynamic multispecies models from six ecosystems show similar results (Fig. 2). It is tempting to interpret these results as showing that using multispecies models makes little difference to recruitment trends and hence offers little benefit either to spawner–recruitment relationships or to the calibration of survey results. However, it is interesting to note that the eastern Bering Sea pollock stock, which exhibits strong cannibalism and is relatively lightly fished, shows temporal variations between single- and multispecies model recruitment estimates. Whether or not these differences stem from differences in the modelling platform used (SAM versus MSVPA) or in the actual feedback mechanisms must yet be determined.

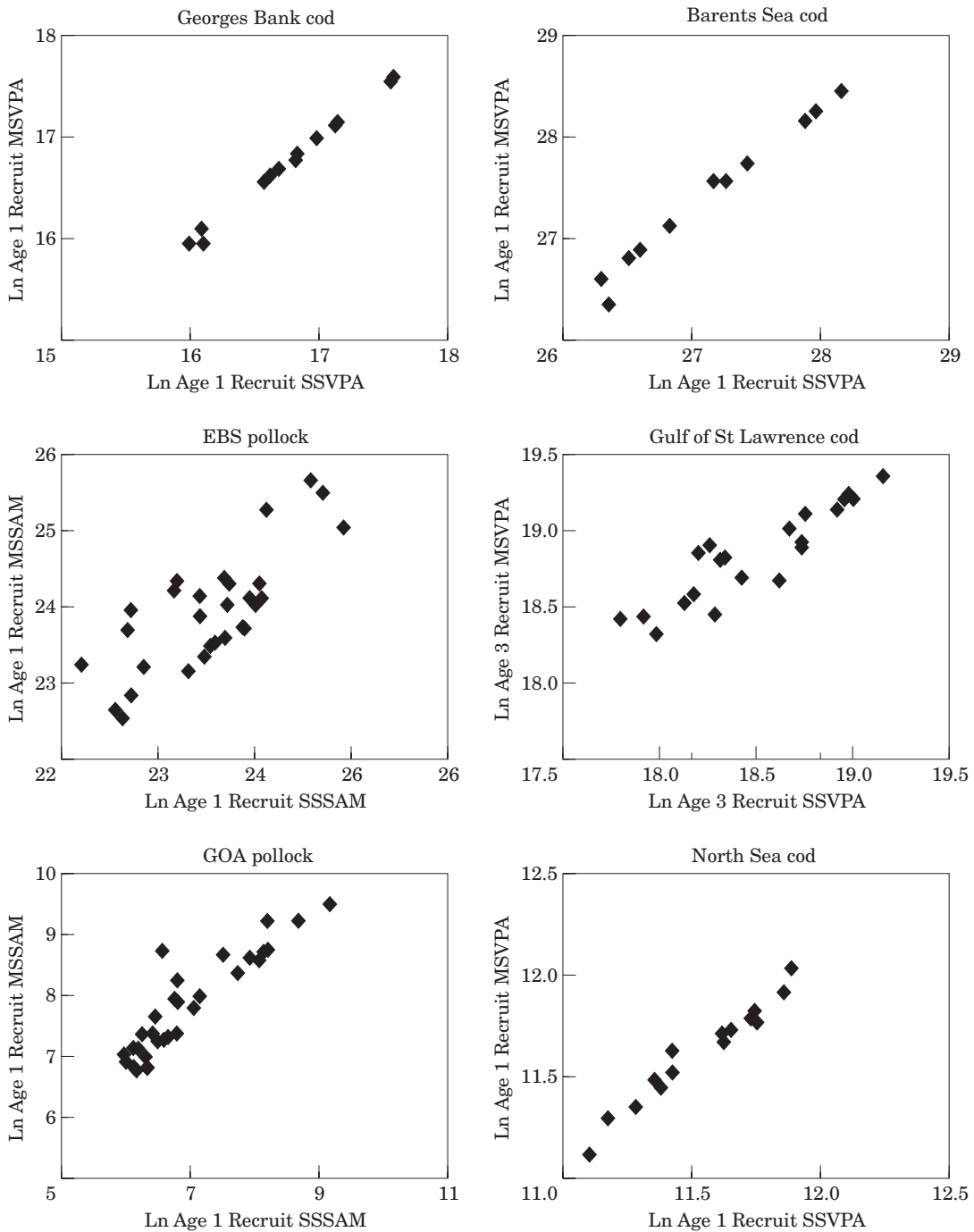


Figure 2. Estimates of recruitment based on single-species and multispecies models from six different ecosystems (EBS: eastern Bering Sea; GOA: Gulf of Alaska).

Accounting for temporal trends in predation mortality has been shown to verify hypotheses regarding the potential role of cannibalism on recruitment success (Sparholt, 1996; Gjosæter, 1998; Livingston and Methot, 1998).

Multispecies models have been used to quantify the relationship between Atlantic cod growth rates and prey availability in Icelandic waters (Stefánsson and Pálsson, 1997), the Barents Sea (Tjelmeland and Bogstad, 1998), and the Baltic Sea (Gislason, 1999). Growth limitation is

apparent in these ecosystems because there are few alternative prey species. Multispecies models can thus help to explain the observed variations in size and age, which in turn affect the calculation of reference levels based on stock biomass, spawning biomass per recruit, and yield per recruit.

Aggregate system models have generally been used to describe trophic interactions within a community. For example, Collie and DeLong (1999) constructed a dynamic production model of the Georges Bank community, which included four aggregated groups of dominant species: flatfish, gadoids, pelagics, and elasmobranchs. The most important interactions were predation of pelagics by gadoids and elasmobranchs and apparent competition between gadoids and elasmobranchs. Overexploitation of the gadoids and flatfish shifted the community structure, allowing the elasmobranchs and, more recently, the pelagics, to increase in abundance. Such models may explain changes that a single-species model would have to regard as random variation. In this example, the multispecies model fit was statistically better than that of the corresponding set of single-species models.

Report card on short-term forecasts

In the case of forage fish, impacts of predation on age-specific natural mortality rates should be considered in short-term forecasts. For example, the spatially resolved MULTSPEC is routinely used to improve predictions of the amount of capelin eaten by cod in the Barents Sea in any one year, and thus help estimate the biomass of capelin left for a directed fishery (Tjelmeland and Bogstad, 1998).

Report card on long-term forecasts

The consequence of fluctuations in natural mortality, in response to changes in stocks of predators, is that altering fishing mortality rates will have indirect effects on prey and predator species. The direction of these effects may be counterintuitive. ICES (1988, 1989) used MSVPA to examine the impact of changes in mesh size and fishing effort in the North Sea. This exercise revealed that changes that result in increased biomass of the smaller predators could have unexpected negative impacts on the species mix in the system. These findings call into question the long-term predictions of single-species models, which frequently predict the highest yield to occur at low exploitation levels or large mesh sizes without considering the implications of larger stocks of predators. Long-term forecasts may also need to account for the effect of prey abundance on predator growth rates.

Aggregate system models have been used to evaluate the overall potential yield from selected regions. These analyses suggested that the overall potential yield from a

multispecies fishery is likely to be less than the sum of the individual potential yields (May *et al.*, 1979; Pope, 1975). From an analysis of aggregate fish population biomass in the North-west Atlantic using a bulk-biomass surplus production model, Brown *et al.* (1976) also concluded that species interactions resulted in a lower system-wide maximum sustainable yield than would be inferred from the sum of individual species' maximum yields. This is the result expected from a tightly coupled system that is at least partly limited by resources, because harvesting resource (prey) species would reduce the capacity of consumer (predator) species to generate harvestable biomass. Similar conclusions were drawn from the use of ECOPATH (Pauly *et al.*, 1998).

Long-term predictions from single-species and multi-species models remain uncertain because of the potential influence of environmental variation on recruitment (Fig. 2), because in both cases they are sensitive to assumptions regarding recruitment variability. Gislason (1993) reported that some MSFOR predictions were not robust to recruitment variability, which constrained their direct application for management decisions. However, it was possible, based on likely predation interactions and resulting changes in abundance for a set of different recruitment models, to determine whether a particular model prediction was robust to changes in recruitment of other species.

Predictions by aggregate models also should be considered uncertain. In particular, the dependence of the results on the level of taxonomic and age-group aggregation has been well documented (Pimm and Rice, 1987; Polis, 1994; Goldwasser and Roughgarden, 1997). Furthermore, as in any modelling exercise, model outputs are sensitive to changes in input parameters that are typically uncertain for some ecosystem components (Livingston, 1985; Bax, 1985).

In summary, it may be possible to predict quite accurately long-term changes in trophic level or changes in size frequency in response to fishing (Pope *et al.*, 1988). The difficulty comes when predictions of the impact of fishing on individual species are desired because of the number of biotic and abiotic factors that could mitigate or exaggerate the direct action of fishing, and of the indeterminacy of systems with many indirect linkages (Yodzis, 1988; Polis, 1994).

Report card on management strategies

ICES (1997) evaluated if and how multispecies interactions might affect biological reference points and rebuilding strategies based on single-species models. The analysis showed that stock–recruitment curves and yield curves may be distorted if multispecies effects are disregarded. Specifically, yield-per-recruit and spawner-biomass-per-recruit may be overestimated if predation effects on stock production are not considered. Also,

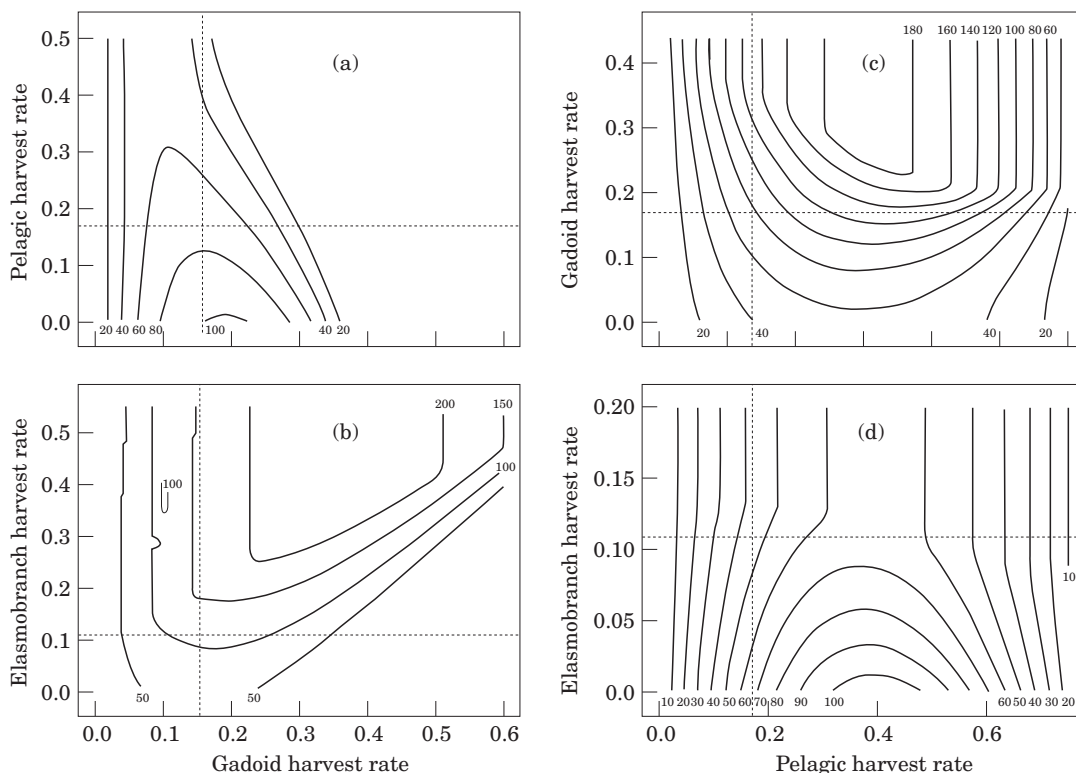


Figure 3. Yield (kt) isopleths based on dynamic multispecies model of the Georges Bank ecosystem (from Collie and DeLong, 1999). Gadoid (left panels) and pelagic (right panels) equilibrium yield obtained for pairs (gadoids, pelagics, and elasmobranchs) of harvest rates (solid contours). Broken lines indicate h_{msy} , the exploitation fraction for maximum sustainable yield from a single-species model.

single-species models tended to underestimate the recovery time in rebuilding programmes. Whether these findings hold true for other ecosystems where fishing mortality is comparatively low, and the role of abiotic factors in controlling recruitment is high, has not been determined, but the results underscore the need for continued research on the short- and long-term implications of species interactions on biological reference points.

Collie and DeLong (1999) and Gislason (1999) applied multispecies simulation models to estimate optimal harvest strategies for the Georges Bank and Baltic Sea ecosystems, respectively. They found that it was impossible to derive a single fixed value for F_{MSY} (Fig. 3). The yield trajectories depended on the harvest strategies imposed on other species in the system and on assumptions regarding the probability of strong year classes. They also noted that maximizing total yield may not be the single best management objective, because it would be achieved by eliminating the large predators.

Report card on depicting the role of environmental disturbance

The larger the role of environmental forcing, the less equilibrium-based models can represent actual system

dynamics. This concern has been recognized by, for example, Caddy (1996) and Shepherd and Cushing (1996), who have argued that stringent stock-recruitment relationships are not present in marine fish populations. Rather, extrinsic factors play such a strong role in recruitment and non-fishing mortality that equilibrium-based models will not capture the system dynamics.

The evidence for environmental forcing is strong in most marine systems (Steele, 1998; Francis *et al.*, 1998). Steele and Henderson (1984) hypothesized that non-linear population processes can be amplified by decadal-scale variability in environmental forcing, resulting in abrupt shifts in fish abundance. Collie and Spencer (1994) and Spencer and Collie (1997) confirmed these results, and demonstrated that fishing mortality and/or decadal variability may cause model systems to change configuration abruptly. Their model was applied to seasonal predation of Pacific herring by Pacific hake off Vancouver Island, British Columbia, where the timing of migration of Pacific hake, and hence predation on herring, may be influenced by changes in oceanographic conditions (Robinson and Ware, 1994).

In the absence of fully validated dynamic system models of marine ecosystems, short-term predictions

could be modified based on evaluations of proxies for environmental processes. [Beamish and McFarlane \(1999\)](#) developed a conceptual model of the Georgia Strait ecosystem based on a long history of research in the region. This model accounts for the influence of decadal-scale climate variability on coho salmon production based on proxies of secondary production, competition for prey, and predatory impacts of Pacific hake. These authors propose that harvest recommendations should be evaluated in the context of observed states of key environmental proxies.

Recent studies show fishing may have direct impacts on benthic invertebrates and the substrates that support them ([Jennings and Kaiser, 1998](#)). The link between fishing, benthic habitat, and fisheries production has been modelled for Australia's north-west shelf ([Sainsbury et al., 1997](#)). This topic is more thoroughly covered by other contributions to this symposium.

Indirect effects of fishing

Report card on depicting biological processes and their coupling

Multispecies modellers must specify the functional relationships between predators and their prey, among groups of competitors, and between physical forcing factors and biological populations. Descriptive models rarely represent these relationships explicitly, although the statistical models' fit to the data usually implicitly assume a specific (often linear) form (Rice, this volume). All other types require choosing some functional form, and the choice often dominates model results. Although it may be incorrect to treat dynamic processes such as natural mortality and growth as constants, misspecification of a process may produce even more erroneous results. Forward fitting models such as SAMs that allow the use of priors for Bayesian analysis provide one possible method for exploring alternative assumptions in a statistical manner ([Iannelli and Fournier, 1998](#)).

Evaluating effects of fishing on ecosystems often has to be pursued by testing hypothetical conceptual models. If hypotheses about ecosystem properties are to be tested, multispecies models are essential, particularly aggregate system models and dynamic system models. These models help identify the sensitivity of model outcomes to assumptions, they provide estimates of gross system mass flows, and they isolate inconsistent population estimates and feeding parameters. However, aggregate system models may fail to diagnose serious errors in model structures and may fail to isolate the components most inaccurately represented because of the many indirect interactions and types of solution algorithms.

Report card on indirect effects of exploitation

Many multispecies models are the product of efforts to expand the factors included in assessment and forecast-

ing to include predator-prey interactions and the effects of physical forcing on stock dynamics ([Rice and Gislason, 1996](#)). As such, they have the advantage of greater biological reality. More generally from an ecosystem perspective, an important element of these models is that they must include the predators having the greatest impact on commercial fish species, usually down to their first year of life. Such predators often have important effects on other components of the marine ecosystem in the same size range (e.g. epibenthos). Hence, estimates of the stomach contents of these predators together with knowledge of their biomass and ration requirements could allow some quantification of predation on these wider components of the ecosystem. Thus, potentially there should be an ability to provide some information on these species by using by-products of multispecies stomach sampling programs. Aggregate models give some ability to predict the effects of fishing beyond the trophic levels included in dynamic multispecies models, though at the expense of considerable generalization.

As with the predictions of multispecies models on target species, we need to question if these can be used to predict indirect effects of fishing. It will be important to develop an idea of what side effects can be specified. On a cautionary note, [Beverton \(1995\)](#) argues that only first-order symmetric interactions, in which a predator and the fishery exploit the same prey species, are predictable. In first-order asymmetrical interactions, in which the predator and a fishery exploit different (interacting) prey species, he argues that even the direction of change is unpredictable. Beyond this level of abstraction, predation interactions become more complicated and the results dependent on the model specifications ([Yodzis, 1988](#)). However, we note that multispecies models may also provide a basis for developing hypotheses, which could be tested through adaptive management such as developed by [Sainsbury et al. \(1997\)](#) for a wider set of ecological hypotheses.

Summary and research directions

Our comparison of single-species and multispecies models indicates that the latter have the distinct advantage of allowing the user to more realistically model natural mortality and growth rates. An exception lies in the use of single-species models for short-term predictions of larger fish species where trends in predation mortality are less evident. Our review also stipulates that long-term predictions of multispecies models should be considered works in progress owing to their sensitivity to parameter estimation and in particular to assumptions about recruitment levels. Likewise, multispecies models may have some part to play in describing the indirect

effects of fishing but again it may be wise to accept general rather than specific predictions.

Our understanding of processes regulating populations has progressed far beyond the equilibrium view contained in many models of marine ecosystems. Several dynamic multispecies models and aggregate system models are based on the principle that population regulation is driven by species interactions and resource limitation. These models incorporate only a subset of the potential factors influencing production. In most systems, temporal trends in predation mortality account for only a minor fraction of the interannual variability in marine production (Fig. 2). Cases where predation mortality did account for a substantial fraction of recruitment variability were located in relatively species-poor, boreal communities, but it is also those communities that have been most thoroughly quantified.

Dynamic system models that address all three regulatory processes are being developed. However, data availability limits their use as prognostic tools for fisheries management advice. In the short term, we may need to rely on the development of predictive models based on conceptual models of ecosystem function that address a limited number of key species. Researchers are exploring the use of this type of modelling construct by considering proxies for ecosystem characteristics when making short-term yield forecasts (Beamish and McFarlane, *in press*; Punt, 1997). The Fisheries Oceanography Coordinated Investigations programme has implemented this approach for a single-species assessment model of Gulf of Alaska pollock by making qualitative recruitment forecasts based on a suite of biophysical proxies for complex processes thought to be important in controlling recruitment (Megrey *et al.*, 1996).

Existing multispecies models have clearly improved our understanding of the dynamics of fish populations, leading to improvements in the single-species models used to predict the impact of fishing on individual target species. But what are the implications of these ideas for modelling the impact of fishing on marine ecosystems? First, it is clear that multispecies interactions need to be placed within the context of the myriad other factors and processes influencing these systems. Second, multispecies interactions occur within a spatial and ontogenetic structure – models that lack this structure are unlikely to have any predictive capacity because of the complexity of the interactions. Third, this complexity means that models with quite different properties may be developed for any one system. Therefore, predictions need to be addressed within a rigorous and testable modelling framework. Finally, the multispecies interactions of most interest in determining impacts of fishing on marine ecosystems are those that cause marked departures from the current condition – models constrained by equilibrium processes are unlikely to capture these departures.

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