

Toward Ecosystem-Based Fisheries Management: Strategies for Multispecies Modeling and Associated Data Requirements

ABSTRACT Considerable effort has been directed in the last decade towards the development of multispecies, ecosystem-based approaches to fisheries management. One aspect of this is the development of models that take into account direct and indirect ecological interactions among species and their environment. We review four multispecies modeling approaches that we feel have great potential for use in fisheries management: multispecies production models, multispecies virtual population analysis, Ecopath with Ecosim, and multispecies bioenergetics models. All four can predict biomass trajectories over time and under various fishing pressures, but with different spatial, temporal, and biological resolution, quantitative/qualitative nature of the results, and insight into system function. We present the data requirements of each model and give examples of field programs that have provided data for model construction and validation. We conclude with a set of issues to consider when designing a coupled field-modeling research program, including the scale of the problem, appropriate sampling platform, and data collection.

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Introduction

Historically, fisheries management has been based on the results of single-species stock assessment models that focus on the interplay between exploitation level and sustainability. These models generally fail to consider the ecology of the species under management (e.g., habitat requirements, response to environmental change), ecological interactions among species (e.g., predation, competition), and technical interactions (e.g., discards, bycatch) (NMFS 1999; Link 2002a,b). However, inclusion of ecological processes into fisheries management plans is now strongly advocated (NMFS 1999; NRC 1999) and in some cases even mandated (NOAA 1996). Multispecies models have been developed to move towards an ecosystem-based approach to fisheries management (Hollowed et al. 2000a; Whipple et al. 2000; Link 2002a,b). Although such models are still designed to yield information about sustainability, they are structured to do so by explicitly incorporating the effects of ecological processes among interacting populations.

The notion that ecological processes have the potential to strongly influence stock abundance is not a new concept to fisheries science. During the 1970s and 1980s, several single-species population models were extended to include multiple species and the ecological interactions among them (Anderson and Ursin 1977; May et al. 1979; Mercer 1982; Kerr and Ryder 1989; Daan and Sissenwine 1991). These models fostered awareness

of the importance and role of ecological processes on yield performances of fish stocks, but were generally viewed as underdeveloped. In recent years, however, this belief has changed significantly, largely due to the sophistication and increased number of multispecies stock assessment models (Hollowed et al. 2000a; Whipple et al. 2000).

From a strictly theoretical perspective, basing fisheries management on multispecies rather than single-species models appears to be more appropriate, since multispecies approaches allow a greater number of the processes that govern population abundance to be modeled explicitly. However, this increased realism requires a greater number of model parameters and additional types of data. Moreover, these data must be generated from fisheries-independent surveys, since it generally is not possible to infer about ecological processes using fisheries-dependent data as required for many single-species models. This fact leads to the question, how should a fisheries-independent survey be designed if the data are to be used to support multispecies modeling?

Link (2002a,b) presented the need to incorporate ecological considerations in fisheries management, advocating an ecosystem-based management approach. The intent here is to continue this discussion by considering various approaches for creating multispecies models and to identify the data requirements of each. Hollowed et al. (2000a) and Whipple et al. (2000) have already provided thorough reviews of various multispecies modeling methods. Therefore, we discuss a subset of these approaches that we consider to have the greatest potential for improving fisheries management. While these models have often been termed "ecosystem-based" (we use this terminology our-

selves for consistency), it is important to note that they generally focus on predator-prey interactions rather than all aspects of an ecosystem. We then present an overview of some existing fisheries-independent surveys that have successfully supported multispecies modeling efforts and introduce our field program in Chesapeake Bay. We hope to offer insight into the design of a research program to support multispecies modeling efforts and produce the best management advice.

Modeling approaches

Multispecies Production (MSP) Models

Single species production (SSP) models are typically used to identify sustainable fishing mortality rates, given growth rate of a population measured as the change in biomass (B) over time. Since the modeled variable is typically biomass, these models are often referred to as biomass-dynamic models (Hilborn and Walters 1992). Due to their simplicity and relatively modest data requirements, SSP models generally serve as a starting point for many fisheries stock assessments. In the absence of immigration and emigration, the general discrete time SSP model takes the form

$$B_{t+1} = B_t + \text{production} - \text{natural mortality} - \text{catch}, \quad (1)$$

where the production term incorporates the addition of biomass from both recruitment (i.e., births) and growth in weight of individuals already present in the population. In the absence of fishing activity, equation (1) indicates that any increases in biomass over time will be dictated by the net difference between production and natural mortality.

To fully develop equation (1), it is necessary to specify a model that describes the change in biomass over time as a function of production and natural mortality. The first widely applied SSP model, formulated by Schaefer (1954) and based on early work by Graham (1935), considered the change in biomass over a given time interval to be governed by the intrinsic rate of growth (r) and the carrying capacity (K):

$$B_{t+1} = B_t + rB_t \left(1 - \frac{B_t}{K}\right) - C_t, \quad (2)$$

where C_t is the catch during time t . Pella and Tomlinson (1969) developed an extension of the Schaefer (1954) model to allow for an asymmetrical relationship between surplus production and stock size. The characteristics of both the Schaefer (1954) and the Pella and Tomlinson (1969) models have been well documented (e.g., see Hilborn and Walters 1992; Quinn and Deriso 1999).

Multispecies production (MSP) models are simple extensions of traditional SSP models. They are constructed by adding terms to equation (2) to characterize ecological interactions with other species—primarily competition and

predation—resulting in a system of linked difference equations (May et al. 1979; Sullivan 1991; Collie and DeLong 1999). Considering the biomass of three interacting species, denoted as B_1 , B_2 , and B_3 , equation (2) can be expressed for species 1 as:

$$B_{1t+1} = B_{1t} + B_{1t} (a - bB_{2t} \pm cB_{3t}) - C_{1t} \quad (3)$$

where the terms r and r/K from above are re-expressed as coefficients a and b , respectively, and c and d are coefficients that characterize the interaction of B_1 with B_2 and B_3 , respectively. Similar equations can be constructed for species 2 and 3.

If B_1 is a prey species and B_2 its predator, then the sign for c will be negative. Conversely, if B_1 is the predator of B_2 , then c will be positive. Finally, if B_3 is a competitor of B_1 , then d will be negative. The magnitude of the coefficients is also meaningful; for example, if B_1 is a predator of both B_2 and B_3 and the coefficient of B_2 is twice the coefficient of B_3 , then B_2 is the preferred food source for B_1 . In the formulation of equation (3), the predation terms (e.g., $-cB_2$) represent a linear relationship between prey availability and predatory consumption (i.e., a Type I functional response—Holling 1959). Alternate expressions have been developed to characterize the more common nonlinear Type II and III feeding responses (Collie and DeLong 1999). Additionally, equation (3) can be re-expressed as a delayed-difference equation to account for time lags between spawning and recruitment (Collie and DeLong 1999).

One advantage of MSP models when compared to other multispecies modeling approaches (e.g., those discussed below) is their relatively low data requirements; only data on catch and biomass are needed. However, it is important to note that this latter requirement is total biomass rather than the typical catch-per-unit-effort (CPUE) relative index of biomass required for SSP models. Total biomass is needed because the competition and predation coefficients in equation (3) are defined on the scale of the total population. Estimates of total biomass can be obtained from fishery-independent survey data and/or traditional stock assessments such as single-species virtual population analysis (SSVPA). As with SSP models, both equilibrium and non-equilibrium methods can be used to derive estimates of the coefficients; however, non-equilibrium methods are generally recommended since the assumption that a stock is at equilibrium is rarely valid. At a minimum, two consecutive years of data are needed, and in most instances it is necessary to use nonlinear estimation techniques to derive parameter estimates (in the absence of multiyear data, coefficients can be estimated using multiple linear regression if equilibrium is assumed—see Sullivan 1991). Once the coefficients are estimated, one can compare their magnitudes to identify the most important interspecific interactions, and the difference equations can be used to

run forward simulations under various scenarios of fishing effort and stock size.

Perhaps the greatest limitation of this approach is that the number of species that can be modeled is relatively low due to the number of coefficients that need to be estimated. Such analyses will be restricted to systems with only a few species such as the Baltic Sea (Sullivan 1991) or in systems where species can be grouped into a small number of trophic guilds (Collie and DeLong 1999). Further, these analyses are restricted to the fish themselves; that is, lower trophic levels and effects of the abiotic environment cannot be included in the model. Nevertheless, the low data requirements combined with a simplistic approach and meaningful coefficients make MSP models a promising method for simulating hypothetical management scenarios while taking into consideration the interactions among exploited fish populations.

Multispecies Virtual Population Analysis (MSVPA)

SSVPA or cohort analysis, as developed by Fry (1949) and Gulland (1965), is a stock assessment technique that uses catch-at-age data to calculate retrospective stock sizes and fishing mortality rates (F) of recruited, age-based cohorts. For a given cohort, the number alive in the previous year is calculated by adding the number caught by the fishery in the current year to the estimated number that died due to natural causes during that same time period. Inherent to this technique are two characteristics worth noting: (1) each cohort is treated separately (i.e., the variables associated with a cohort are calculated independently of those from other cohorts), and (2) an estimate of the natural mortality rate (M) is needed as input for the model. When M is not known, the traditional approach is to derive a rough estimate from life-history parameters (Pauly 1980; Hoenig 1983) or to use an “educated guess.”

The dependence of SSVPA on a reasonable estimate of M has motivated researchers to pay more attention to estimating natural mortality. Although natural mortality occurs from a variety of causes, predation is generally believed to be the dominant source. This belief, combined with preliminary quantitative work on feeding and food consumption of North Sea cod (*Gadus morhua*) (Daan 1973; 1975), served as a foundation for the development of models that accounted for species interactions. Anderson and Ursin (1977) developed an ecosystem model that provided a conceptual framework for modeling predator-prey interactions. Although this complex model could not be adapted to real-world management applications, it ultimately facilitated the extension of SSVPA to multispecies virtual population analysis (MSVPA).

Helgason and Gislason (1979) and Pope (1979) independently combined the theoretical predation relationships of the Anderson and Ursin (1977) model with the SSVPA methodology of Gulland (1965) to develop MSVPA. The primary feature of the method is that the natural mortality rate (M) is split into two components. That is,

$$M = M_1 + M_2, \quad (4)$$

where M_2 is the predation mortality as determined by suitability parameters that reflect the preference of a prey species by a predator, and M_1 is the residual mortality due to all factors not explicitly included in the model (Figure 1). For more information on MSVPA, see Daan and Sissenwine (1991), Magnusson (1995), Gislason (1999), Livingston and Juado-Molina (2000), and Tsou and Collie (2001a,b).

The data requirements for an MSVPA vary according to the role each species assumes in the model and the preferred model output (Figure 2). If species' stock sizes are reconstructed using the MSVPA model, with these species being referred to as “MSVPA-species,” the data requirements include catch-at-age in numbers, fishing mortality

Figure 1. General schematic of a two-species MSVPA with arrows indicating losses due to fishing (F), residual (M_1), and predation (M_2) mortality. Various connections for M_2 are possible and depend on the feeding ecology of the particular predator and prey.

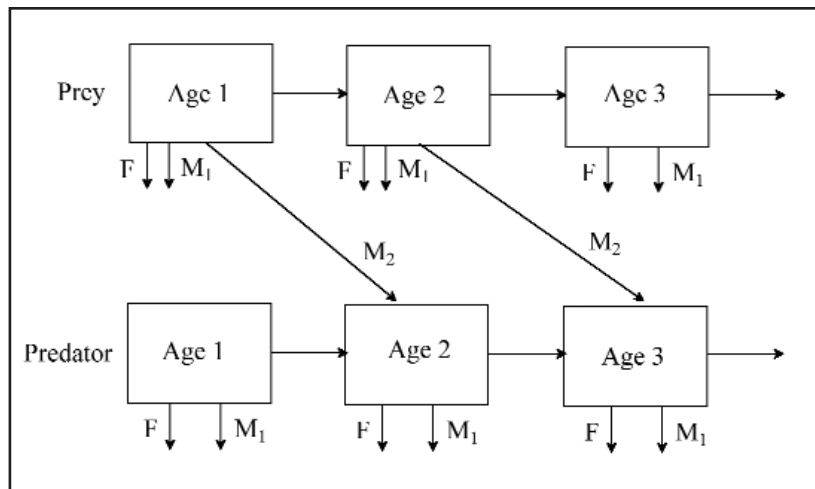
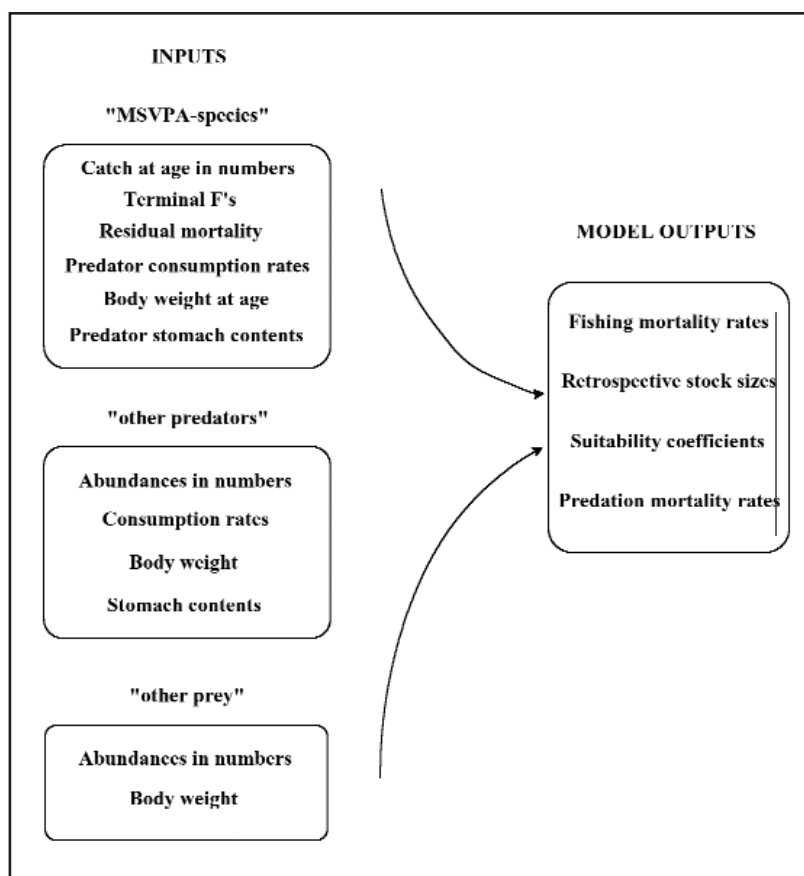


Figure 2. Data inputs and outputs of MSVPA models.



rates in the terminal year and for the oldest age class, residual mortality rates, predator consumption rates, body weights-at-age, and predator stomach contents. Within the MSVPA framework, it is possible to model species as “other predators” or “other prey” in cases where the standard SSVPA results are not desired, but it is known or surmised that these species significantly influence the trophic dynamics of the food web under study. For “other predators,” the data requirements include some estimate of abundances in numbers, body weights, consumption rates, and stomach contents, while for “other prey,” only abundances in numbers and body weights are typically needed.

Ecopath with Ecosim (EwE)

One class of ecosystem models that is widely used to examine trophic dynamics in a fisheries management context is Ecopath with Ecosim (EwE). The development of this modeling technique stems from early work on the ecosystem dynamics of a coral reef in Hawaii (Polovina 1984). Application of the EwE approach begins with the construction of an Ecopath model (Christensen and Pauly 1992; Pauly et al. 2000), which creates a mass-balanced snapshot of the resources and interactions in an ecosystem, represented by trophically-linked biomass pools. The biomass pools generally consist of either a single species or a group of species representing an ecological guild. Biomass pools are created for all major components of the ecosystem, including those at lower trophic levels such as plankton, invertebrates, and detritus.

Mathematically, an Ecopath model is represented by the following expression:

$$B_i(P/B)_i EE_i = BA_i + E_i + Y_i + \sum_{j=1}^n B_j(Q/B)_j DC_{ji}, \quad (5)$$

where B_i and B_j are the biomass of prey i and consumer j , respectively; $(P/B)_i$ is the production-to-biomass ratio, which is equivalent to the total mortality rate in

most instances; EE_i is the ecotrophic efficiency, or the fraction of the production that is consumed within or harvested from the system; BA_i is the biomass accumulation rate; E_i is the net migration rate (emigration-immigration); Y_i is the fisheries catch; $(Q/B)_j$ is the consumption-to-biomass ratio of predators j that eat group i ; and DC_{ji} is the average fraction of species i in the diet of predator j . For more details on Ecopath, see Christensen and Pauly (1992), Walters et al. (1997), and Pauly et al. (2000).

At a minimum, Ecopath requires data on DC_{ji} and Y_i as well as three of the following four input parameters for each organism or functional group in the model: B_i , $(P/B)_i$, $(Q/B)_i$, and EE_i . If three of these are known, Ecopath will estimate the fourth from the mass balance equations. If information on all four parameters is available, Ecopath can be used to estimate either BA_i or E_i . While the parameters listed above represent the minimum data requirements, EwE models contain several additional parameters for which calibration data are highly useful and will serve to increase confidence in model results.

Although Ecopath can be used to describe an ecosystem, it cannot be used to project the effects of different management strategies on the structure and function of an ecosystem. These types of projections are accomplished in Ecosim, a time-dynamic simulation module that re-expresses the static mass-balanced equations inherent to Ecopath as a system of coupled differential equa-

tions (Walters et al. 1997; Walters et al. 2000). This system of equations is used to represent the spatially aggregated dynamics of entire ecosystems, and is combined with delay-difference age/size-structured equations to represent populations that have complex life histories and selective harvesting of older animals. A key element in Ecosim is the expression of the consumption or “flow” rates among linked biomass pools. Consumption of prey i by predator j (Q_{ij}) is modeled as

$$Q_{ij}(B_i, B_j) = \frac{a_{ij} v_{ij} B_i B_j}{(2v_{ij} + a_{ij} B_j)} \quad (6)$$

where a_{ij} is the rate of effective search for prey i by predator j and v_{ij} is modeled as the behavioral exchange rate between vulnerable and invulnerable prey pools. Equation (6) is based on the theory that consumption is limited by “risk management” behaviors of predators and prey at very small time scales. That is, predator-prey interactions are assumed to take place primarily in restricted “foraging arenas” where prey only become vulnerable to predation through their own requirements for resource acquisition (Walters et al. 1997; Walters et al. 2000).

Although Ecosim introduces a number of new parameters, the most sensitive appear to be the vulnerabilities (Christensen et al. 2000). In general, it is not possible to estimate this parameter from field or laboratory data. To mitigate this deficiency, Ecosim includes two independent methods of estimation (see Christensen et al. 2000 for details on these methods) and it is recommended that both be used to estimate the vulnerabilities.

The use of time series data for model calibration is a key element in Ecosim, particularly for determining the appropriate vulnerability exchange rates. Therefore, time series data depicting trends in as many of the following variables and for as long a time period as possible should be viewed as additional data requirements: relative and absolute biomass, fishing effort by gear type, fishing and total mortality rates, and catches.

Individual-based growth and multispecies bioenergetics models (MSBE)

A final approach that we feel has potential for modeling multispecies fisheries but is as yet relatively unexplored is rooted in the development of individual-based growth and bioenergetics models (e.g., Kitchell et al. 1977). These models are based on the energy and/or biomass balance of the study organism:

$$\text{net growth} = \text{consumption} - \text{respiration} - \text{egestion} - \text{excretion} - \text{specific dynamic action} \quad (7)$$

The models are constructed by piecing together mechanistic relationships for each component of the energy or biomass budget to predict the rate of

growth (Figure 3). Rate processes such as consumption and respiration are typically driven allometrically by weight and modified by factors accounting for the effects of water temperature and food concentration (e.g., Type I, II, or III functional responses). This “first principles” approach lends itself well to understanding system function from the individual level, and serves as a tool for identifying gaps in existing knowledge. A population size calculation can be run concurrently using estimates of recruitment and non-predation mortality to predict the number of individuals through time and hence total population biomass. It is here that models for various species can be linked: total population biomass of a prey species drives the feeding response of its predators, and hence consumption of each predator.

Bioenergetics models are parameterized most frequently through the use of laboratory experiments that have produced relationships between key variables (e.g., temperature and consumption). Other data requirements include initial population size, initial individual weight, and the rates of fishing and residual (non-predatory) mortality. These can be estimated from field surveys and single-species stock assessments. The models have been frequently used to compute growth or consumption if one of these rates is known; e.g., the fraction of maximum daily consumption actually achieved is adjusted until predicted growth matches observed growth trajectories (Brandt and Hartman 1993). However, efforts to more fully describe feeding behavior and functional feeding responses make these models useful for predicting both consumption and growth without needing data for one or the other (Brandt and Kirsch 1993; Durbin and Durbin 1998; Luo et al. 2001). These improvements make coupled individual-based models useful for predicting population biomass trajectories in a management context.

The major limitation of individual-based models is the large amount of data required for parameterization. Such datasets are usually the result of detailed laboratory experiments focused on single species. Development of this approach is therefore restricted to species that have been studied in detail. Fortunately, bioenergetics models have been found to be relatively insensitive to parameter estimates for egestion, excretion, and specific dynamic action (Bartell et al. 1986), thus requiring detailed experimental data for only consumption and respiration. The large number of parameters in these models also limits the number of species that can be modeled concurrently.

Individual-based models have been constructed for several fish species, but it appears that these have rarely been coupled to produce a multispecies model. The only example we know of is the European Regional Seas Ecosystem Model (ERSEM), in which fish were modeled from an

energetics approach and incorporated into a larger systems model of the entire North Sea (Bryant et al. 1995). This highlights a key advantage of the individual-based, bioenergetics approach: models for fish can be readily coupled to similar process models of primary production and lower trophic levels to create models of the entire ecosystem. Such systems models can then be used to assess the impacts not only of top-down fisheries management scenarios, but also of bottom-up processes such as nutrient load reductions or climatic regime shifts. At the minimum, MSBE models can be linked to simple empirical models of lower trophic level processes (e.g., primary production) to estimate bottom-up impacts. Such approaches that consider the entire ecosystem are becoming increasingly important, especially in coastal sys-

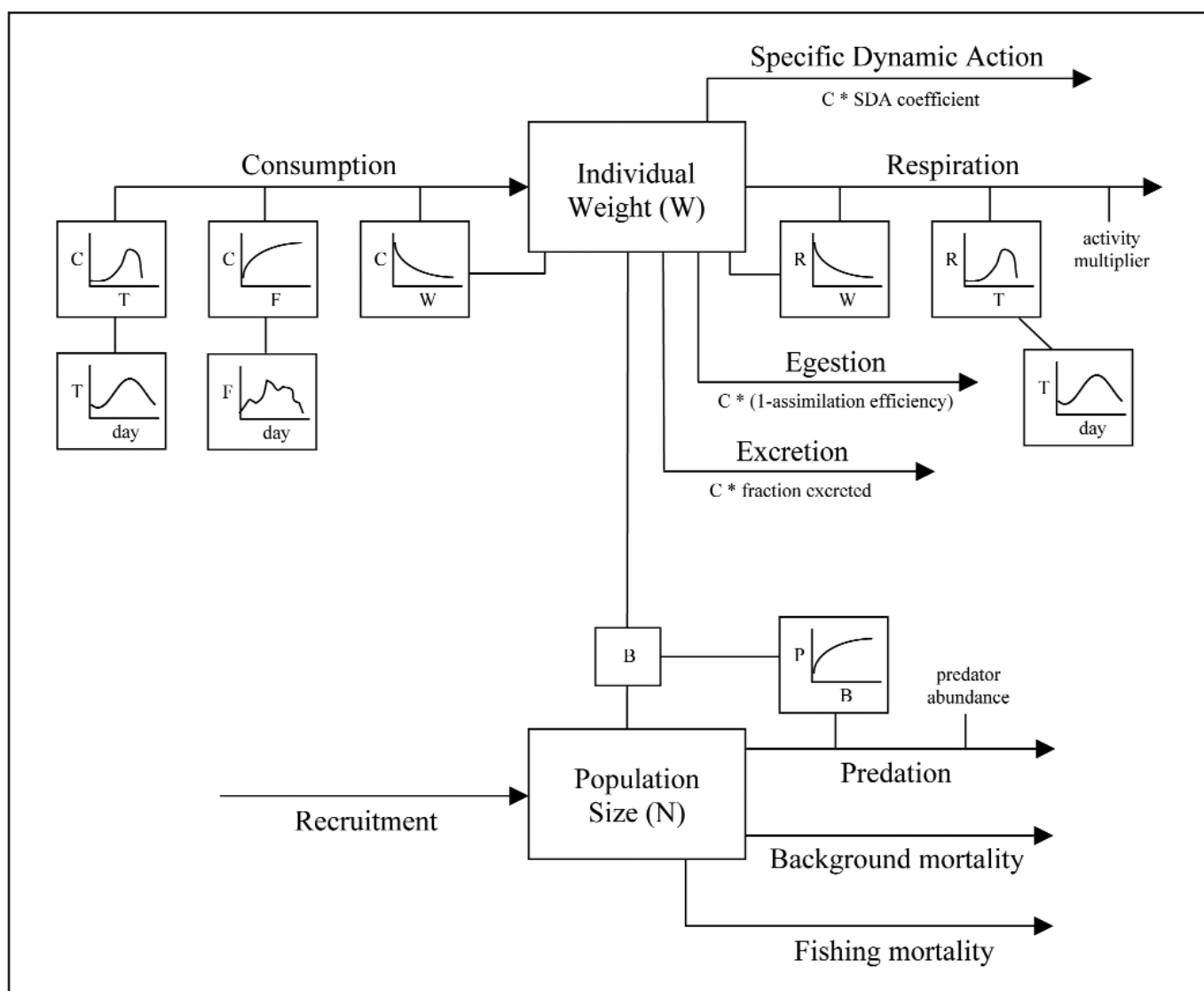
tems where the effects of fishing must be understood in concert with other anthropogenic (e.g., nutrients) and natural (e.g., climate) impacts (Cloern 2001).

Supporting field programs

ICES studies of the North and Baltic Seas

The North and Baltic Seas are the two regions of the world ocean with arguably the greatest wealth of marine science data. This abundance of data is due in large part to the International Council for the Exploration of the Sea (ICES), originally formed in 1902 in response to variability in fish stocks in northern Europe and the need for improved and coordinated measurements of oceanographic parameters, particularly salinity.

Figure 3. Mechanistic diagram of the energy budget for an individual fish and total population size. Graphs demonstrate the type of relationship between input variables, and lines connect all variables involved in the calculation of each input or output. C=consumption, T=temperature, F=food supply, W=weight, R=respiration, SDA=specific dynamic action, P=predation, B=population biomass, day=day of year (1/1–12/31).



Early on, ICES scientists recognized that there was a severe disconnect between the theorists developing multispecies fisheries models and the scientists responsible for data collection. Prior to the 1970s, neither the models nor the data on species interactions were deemed to be particularly useful (Daan and Sissenwine 1991). However, this disconnect was remedied in part by the work of Daan (1973; 1975) on the feeding of cod in the North Sea and of Anderson and Ursin (1977) on the development of a North Sea ecosystem model. This breakthrough combination fostered recognition for the potential utility of multispecies models and ultimately set the stage for the convergence of multispecies modeling activities and data collection.

Since the 1970s, the dedicated work conducted by a variety of ICES researchers has resulted in long-term, “model-driven” databases of population abundance, catch-at-age, weight-at-age, maturity, diet composition, and mortality rates. One notable example of the wealth of data collected in the North Sea is the intensive stomach content sampling program during 1981, the “Year of the Stomach,” in which 55,000 stomachs were sampled to obtain data to support modeling efforts (Daan and Sissenwine 1991; Christensen 1995). To determine if diet compositions used in multispecies modeling were consistent over time, a second intensive sampling of more than 100,000 stomachs was conducted in 1991 (Daan 1997). The attention given to the needs of multispecies models has allowed the various databases collected by ICES to support an enormous number of multispecies modeling activities, most notably the theoretical development of MSVPA and applications of the approach to both the North Sea (Pope and Macer 1991; Daan 1997) and Baltic Sea (Sparholt 1991; Gislason 1999). The data have also been used to construct an Ecopath model of the North Sea (Christensen 1995) and individual-based energetics models embedded in the full ERSEM ecosystem model (Bryant et al. 1995).

Northeast Fisheries Science Center (NEFSC) Food Web Dynamics Program (FWDP)

The origin of the National Marine Fisheries Service (NMFS) and its Northeast Fisheries Science Center (NEFSC) in Woods Hole, Massachusetts can be traced back to a report issued to Congress by Baird (1873). The report called for the creation of a research program designed to investigate five potential causes of declines in fish stocks in southern New England waters. Recognizing the importance of documenting and quantifying predator-prey relationships, two of the five potential causes proposed by Baird involved trophic dynamics.

The research objectives of the Food Web Dynamics Program (FWDP) at the NEFSC are to

(1) assess predation mortality relative to fishing mortality for commercially important species, (2) mechanistically and empirically model species interactions that impact the status of these stocks, (3) relate changes in diet composition to changes in population growth rates, and (4) better understand the northeast U.S. continental shelf ecosystem (Link and Almeida 2000). The data collection program supporting these research objectives is a standardized bottom trawl survey conducted twice a year in the northwest Atlantic from Cape Hatteras, NC to Nova Scotia (approximately 293,000 km²). The trawl survey, which began in 1963, utilizes a stratified random design, where the strata are chosen according to water depth, latitude, and historical fishing patterns. Sampling stations are allotted to each stratum in proportion to its area (approximately one station per 690 km²), with some exceptions to ensure at least two stations are assigned to small strata (Link and Almeida 2000). Since its inception, the survey has provided a wealth of information on the diet composition (since 1973 over 250,000 stomachs have been collected) and trends in abundance and distribution of commercially important fish species (Link and Almeida 2000).

As with the ICES data collection programs, the database generated by the NEFSC bottom trawl survey has supported a large-scale research program. As the aforementioned objectives of the FWDP dictate, the types of research activities conducted are somewhat diverse and range from dietary studies (Garrison and Link 2000a; Link et al. 2002a,b) to inferences about food web structure and function (Link 2002c; Garrison and Link 2000b). With respect to the four modeling approaches described above, data from the trawl survey have been used to develop an MSP model and a series of MSVPA-based analyses of the Georges Bank fish community (Collie and DeLong 1999; Tsou and Collie 2001a,b).

Alaska Fisheries Science Center (AFSC)

The Resource Assessment and Conservation Engineering (RACE) Division of the NMFS Alaska Fisheries Science Center in Seattle, Washington, has conducted surveys to document groundfish distribution and abundance in Alaskan waters since 1971. These surveys have included annual bottom trawls in the eastern Bering Sea since 1979, triennial bottom trawls in the Gulf of Alaska, Aleutian Islands, additional regions of the eastern Bering Sea, and off the west coast of the continental United States since 1977, and additional mid-water trawls since 1977 (Martin 1997; P. Livingston, AFSC, pers. comm.). The Resource Ecology and Fisheries Management (REFM) Division utilizes the data obtained from these surveys for annual stock assessments of 25 species of fish and crabs.

In addition to stock abundance and distribution, AFSC modeling efforts have demonstrated the need for detailed information on diet composition, daily rations, and rates of predation. This need motivated the Resource Ecology and Ecosystem Modeling program within REFM to begin collecting stomach samples of fish caught by the trawl surveys, Alaska Department of Fish and Game trawls, and commercial vessels in 1981 (e.g., Yang and Nelson 1999; P. Livingston, pers. comm.). Approximately 88,500 stomachs were analyzed between 1981 and 1998, with roughly 15,000 last year alone (P. Livingston, pers. comm.). Data are used to assess diet composition and quantify predation by various groundfish species.

The extensive data collected by the AFSC has supported a variety of multispecies modeling efforts by the center's modeling group. Single-species stock assessment models that include predation have been constructed for walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea (Livingston and Methot 1998) and Gulf of Alaska (Hollowed et al. 2000b). Livingston and Jurado-Molina (2000) have constructed an MSVPA model for eight species in the eastern Bering Sea. Full ecosystem models have been constructed in EWE for the eastern Bering Sea (Trites et al. 1999a,b), Gulf of Alaska (S. Gaichas, AFSC, pers. comm.), and northern California Current (Field et al. 2001).

Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP)

The Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP) is a new (initiated in 2002) monitoring survey prosecuted in direct support of multispecies modeling efforts at the Virginia Institute of Marine Science (VIMS) in Gloucester Point, Virginia. In general, ChesMMAP is a large mesh bottom trawl survey designed to sample adult fish in Chesapeake Bay. Due to the dramatic seasonal migration of fishes into and out of the bay, a total of five cruises are conducted each year (March, May, July, September, and November). During each cruise, approximately 80 to 90 stations are sampled in the mainstem of Chesapeake Bay. Sampling stations are chosen according to a stratified random design, where the strata are based on water depth within five 30 latitudinal minute regions, and the number of stations sampled in each stratum of each region is proportional to its area. Once onboard, the catch is

sorted and measured by species or size-class if distinct classes within a particular species are evident. A subsample of each species or size-class is further processed for weight determination, stomach contents, aging, and determination of sex and maturity stage.

ChesMMAP utilizes two types of hydroacoustic gear in an effort to convert relative indices of abundance into estimates of total abundance. The equation necessary for this conversion is:

$$N = \frac{cA}{\left(\frac{a}{e}\right)}, \quad (8)$$

where N is total population size measured in numbers, c is the mean number of fish captured per tow, a is the area swept by one trawl tow, A is the total survey area, and e is the net efficiency (dimensionless). Given that c is observed and A is easily determined, the hydroacoustic equipment is used to derive estimates of a and e. Specifically, net mensuration gear, which is comprised of two wing sensors and a headrope sensor that are attached to the net, collectively provide net opening and height measurements at 10-12 second intervals. This time series of net opening measurements, in combination with GPS data on tow track, are used to calculate area-swept for each tow. The second type of gear is a Biosonics 200KHz 12° split-beam transducer, which is a "look-down" transducer that is towed behind the vessel but in front of the trawl gear. Traditionally, trawl gear and hydroacoustics are used in conjunction for the purpose of verifying the acoustic data with data from the trawl net. However, under this configuration, it is possible to use the acoustic data as a measure of the fish available for capture, and ultimately infer the net efficiency by comparing those data to the actual catches.

As previously stated, the ChesMMAP trawl survey is a new monitoring program. However, its design and implementation was concurrent with the commencement of multispecies modeling activities at VIMS. A portion of the abundance and diet composition data from 2002 have already aided the

Table 1. Qualitative characteristics of four multispecies models.

	MSP	MSVPA	EwE	MSBE
Age / size structure	no	yes	yes	yes
Biomass predictions	yes	yes	yes	yes
Data requirements	low	high	high	high
Mass / energy balance	no	no	yes	yes
Network analysis	no	no	yes	no
Number of species	low	intermediate	high	intermediate
Model output	intermediate	quantitative	qualitative	intermediate
Physiological information	no	no	limited	yes
Predictions with variable F	yes	yes	yes	yes
Spatial resolution	no	no	possible	possible
Taxonomic resolution	species or groups	species	species or groups	species
Temporal resolution	annual	annual	annual	daily

development of multispecies models, most notably a large-scale EwE model of Chesapeake Bay and an MSBE model of a smaller food web involving plankton, Atlantic menhaden (*Brevoortia tyrannus*), bay anchovy (*Anchoa mitchilli*), striped bass (*Morone saxatilis*), bluefish (*Potatomous saltatrix*), and weakfish (*Cynoscion regalis*).

Discussion

The four model types presented all have potential for simulating multispecies fish dynamics in a management context. These models share some similarities but have several important differences (Table 1). All four modeling approaches can predict biomass trajectories over time and under various fishing pressures, but with different resolution, quantitative/qualitative nature of the results, and insight into system function. MSP models, MSVPA, and EwE are generally structured to reflect an annual time step, while MSBE models run on daily or even shorter time intervals. MSVPA techniques produce the most quantitative predictions of age-specific population abundance, while EwE can be used to develop a quantified network of flows within a food web and for qualitative policy exploration. MSP and MSBE models can be viewed as somewhere between EwE and MSVPA in this respect.

The models also vary in their level of parameterization, with MSP models relying solely on statistical fitting procedures to estimate a limited number of coefficients. In contrast, MSVPA, EwE, and MSBE models are highly parameterized, a point reflected in their relatively large data requirements (Table 2). In general, the greater the number of parameters, particularly those for which values are

uncertain, the less confidence one has in model results. To overcome this, we strongly recommend running detailed sensitivity analyses to determine the effect of each parameter on model performance, as well as Monte Carlo simulations, variance propagation analyses, or simulations with stochastically varying parameters to develop a range of likely outcomes rather than a single, deterministic prediction (Kremer 1983).

A final but critical note on modeling approaches is that one needs to validate a model before it can be used to make quantitative and even qualitative management predictions. That is, model results need to be compared to independent time series data (e.g., biomass, abundance) not used in model calibration. The model must reasonably track the data for one to have confidence in its function. Thus, these types of time series data should be considered as a data requirement in addition to those listed in Table 2.

The development of a field program in support of multispecies modeling is not trivial, as is evident from the varying and somewhat complex data requirements (Table 2). Admittedly, three of the four field programs we described (ICES, FWDP, and AFSC) are large in scale and operate in systems where there are long-standing commercial fisheries of great economic value. By describing these programs, we do not wish to imply that multispecies modeling-field programs should be confined only to large-scale regions where there is a large commercial harvest. Rather, these field programs were highlighted because they are firmly established and because their design and data collection is the functional result of knowing a priori the types of data needed to support multispecies modeling activities. In general, we have identified three primary and mutually interacting issues that

Table 2. Data requirements for four types of multispecies models. Note that the requirements shown are for model construction only; under ideal conditions a variety of data (e.g., time series of abundance and/or biomass) would also be available for validation of model output.

	MSP ^a	MSVPA	EwE ^b	MSBE ^c	Source ^d
Landings (in biomass)	X		X		FD data
Fish biomass	X		X		FI data / TSA
Abundance (in numbers) ^e		X		X	FI data / TSA
Catch-at-age (in numbers)		X			FD data
Fishing mortality rate (F) ^f		X		X	TSA
Predator consumption rates		X			literature, gut evacuation models
Predator diet composition		X	X		literature, gut analyses
Residual mortality rate ^g		X		X	literature, best estimate
Weight-at-age		X		X	FI data
Consumption/biomass ratio			X		literature
Ecotrophic efficiency			X		best estimate
Total mortality rate (Z)			X		TSA
Physiological parameters				X	literature, lab experiments
Plankton biomass			X	X	literature, field studies

^a A minimum of two years of data are needed for MSP models.
^b Our list reflects the minimum requirements for EwE; these models contain several additional parameters for which calibration data are highly useful.
^c Abundance and individual weights are required to set the initial conditions only.
^d Abbreviations are: fishery-independent (FI), fishery-dependent (FD), traditional stock assessments (TSA) (e.g., SSVPA).
^e MSVPA models require abundance for "other predators" and "other prey."
^f MSVPA requires this rate for the terminal year and for the oldest age class. MSBE requires a population estimate only if the present case is to be simulated.
^g Residual mortality is natural (non-fishing) mortality due to all sources other than predation.

warrant strong consideration when designing a combined multispecies modeling-field program: scale, sampling platform, and data needs (Figure 4).

In addition to systems comparable in size to the North-Baltic Seas, the northeast U.S. continental shelf, and the Bering Sea-Gulf of Alaska-Aleutian Islands, ecosystem-based approaches to fisheries management and therefore multispecies modeling-field activities are likely to be needed in regions that are smaller in size and not necessarily dominated by commercial fishing activities. The emergence of the ChesMMAAP program supports this idea, given that Chesapeake Bay is an estuary where there are sizeable commercial and recreational fishing activities. It is not unreasonable to think that even smaller systems dominated by recreational fishing could also benefit from multispecies modeling efforts. For example, the trophic cascade work in freshwater lakes (Carpenter and Kitchell 1993; DeMott 2001) has documented that top predators can control the population sizes of lower trophic level fishes, and therefore indirectly influence plankton communities. Provided data were available, multispecies modeling techniques could be used to assess the effects of fishing on community structure and to set catch limits in these systems.

The spatial, temporal, and jurisdictional scale of the system under study needs to be well defined early on so that it directly matches what is feasible in terms of sampling and ultimately data acquisition (Figure 4). Given that ecological interactions can vary substantially over time and space, it is not advisable to build

models of systems encompassing an area larger than what can be comprehensively sampled (and vice-versa, since it makes sense to use all available data). In many cases, we acknowledge that funding (both amounts and sources) will play a large role in determining the scale of a project.

Given a defined scale, decisions need to be made regarding the sampling platform and its ability to provide the necessary data (Figure 4). By highlighting the ICES, FWDP, AFSC, and ChesMMAAP field programs, we did not intend to imply that trawl surveys represent the only sampling platform that can be used to obtain the data requirements for multispecies models. The use of trawl gear in those surveys stems from the fact that the study systems are geographically very large, and that trawling represents the only practical method that can be used to sample on those spatial scales. However, the choice of an active (e.g., trawl, seine, electrofishing) versus a passive (e.g., gillnet, trap, longline) sampling gear is very important. We recommend sampling with an active gear for two primary reasons: (1) data obtained from passive gears generally do not lead to estimates of absolute biomass/abundance, and (2) it is not always possible to obtain accurate measurements of diet composition using passive gears.

With respect to biomass, rough estimates of area-swept/sampled and gear efficiency can be determined for active but not passive gears, which means that estimates of absolute biomass/abundance is possible only with active gears. In terms of diet composition, active gears allow samples to be collected in a short period of

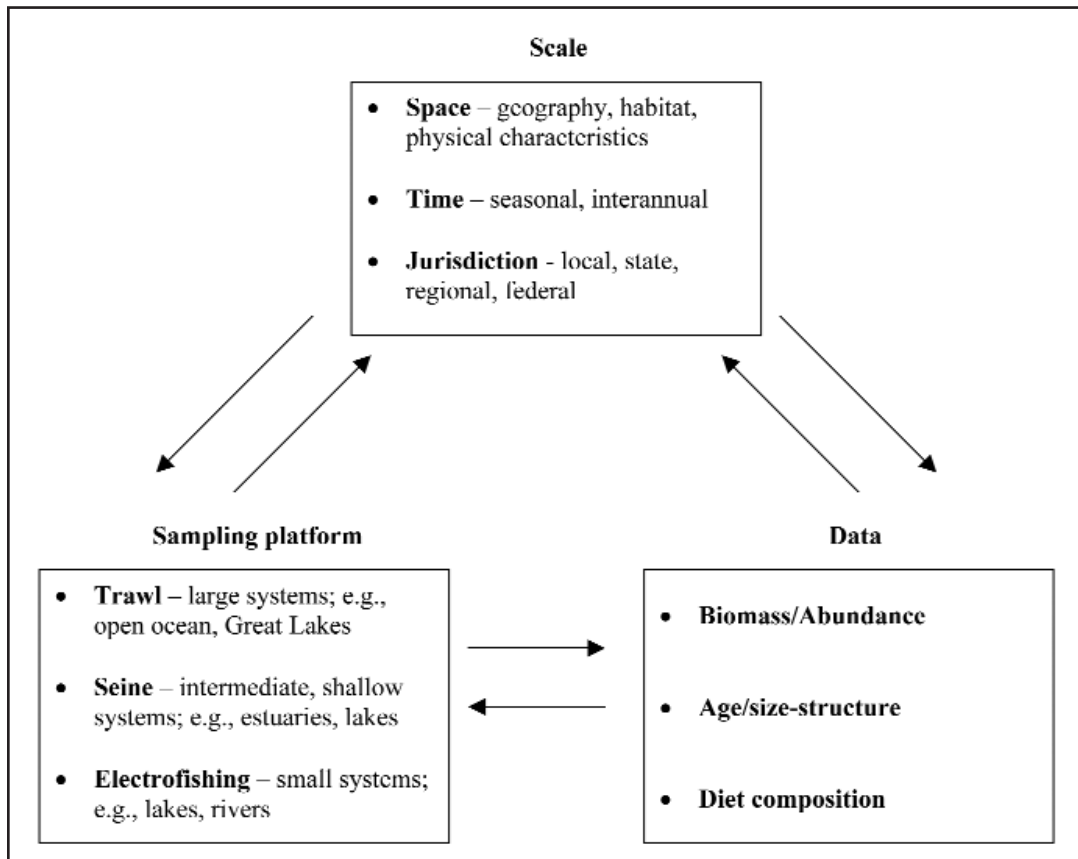



Figure 4. Conceptual diagram depicting the interrelationships between scale, sampling platform, and data collection to be considered when developing a multispecies modeling-field program.

time, which helps to obtain a good representation of stomach content weights at each sampling location (Cortes 1997). Diet composition data and consumption rate estimates derived from passive gears have the potential to suffer from a number of biases. Hayward et al. (1989) found significantly higher median amounts of food in yellow perch (*Perca flavescens*) captured with gillnets when compared to those captured using an otter trawl. They concluded that passive gears tend to only effectively sample active (foraging) fish, which can lead to biased estimates of food consumption. Data obtained from longlines suffers from similar bias, since the gear tends to attract individuals with empty stomachs (Wetherbee et al. 1990). Large fish traps (e.g., pound nets) are also likely to yield biased diet composition data, since feeding within the trap is unavoidable. Note that for all gears (active or passive), selectivity is an issue that needs to be addressed, and efforts should be made to ensure (inasmuch as possible) that all life stages are sampled adequately so that shifts in predator-prey interactions can be documented.

With respect to data to be collected, the primary pieces of information needed from fishery-indepen-

dent surveys in Table 2 are estimates of biomass and abundance, age and size structure, and diet composition (Figure 4). Surveys should thus focus on enumeration, measuring weight and length, aging, and conducting gut content analyses by species and size class. The best system-wide estimates of these parameters will be obtained by sampling as many stations as possible, even if it requires sampling fewer fish at each station or shortening the length of the trawl (Bogstad et al. 1995; Pennington et al. 2002).

In conclusion, a variety of multispecies models have been developed that have the potential to contribute to ecosystem-based fisheries management. The various modeling approaches now need to be put to the test by adapting them to particular study systems and determining both their accuracy and potential for management. The most productive applications will be those that take advantage of a coupled modeling-field program, except in systems where data are already plentiful. The coming years will be most exciting as these models are put to the task of predicting multispecies fisheries dynamics. 

Acknowledgements

We thank two anonymous reviewers and the members of the VIMS Fisheries Ecosystem Modeling and Assessment Project, namely James Gartland, Eric A. Brasseur, Aimee D. Halvorson, and John F. Walter III, for their constructive comments on earlier versions of this manuscript. This work was made possible by funding from the Virginia Environmental Endowment and the Chesapeake Bay Stock Assessment Committee within the NOAA Chesapeake Bay Office. This is VIMS contribution number 2550.



A subsample of a ChesMMA catch depicting a multispecies assemblage in Chesapeake Bay. Species include: clearnose skate, northern kingfish, sheephead, striped bass, summer flounder, Atlantic croaker, and northern puffer.

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