

# ***Food Web Interactions and Modeling***

## **Introduction**

The Chesapeake Bay food web has experienced significant historical alterations due to overfishing, anthropogenic stress, and natural disturbances. Although conventional single-species management approaches do not typically address predator–prey dynamics, these dynamics form the heart of interactions among species affecting abundance and production. Such interactions have dramatic and substantial effects on community structure, ultimately affecting fisheries yields in the Bay, and must be considered when developing or amending ecosystem-based fishery management plans (FMPs).

Fishing mortality—an important fraction of total mortality for most exploited species—represents human predation on fishery resources. Multispecies fisheries management incorporates not only fishing mortality information but also key predator–prey linkages and their contributions to natural mortality. Understanding such food web dynamics allows quantification of the energy and biomass transfers in the food web that dictate sustainable levels of fishery exploitation. Food web relationships are not independent of habitat and water quality issues; they may vary with

changes in the productive capacity of the environment, the abundance of planktonic and benthic prey, and the structure of food webs that support fisheries.

Researchers have a good understanding of some food web relationships in the Chesapeake Bay. Atlantic menhaden *Brevoortia tyrannus*, Atlantic croaker *Micropogonias undulatus*, bay anchovy *Anchoa mitchilli*, blue crab *Callinectes sapidus*, and spot *Leiostomus xanthurus* are integral links between and within benthic and planktonic components of the Bay food web. Heavily exploited, predatory fish consume forage species, such as menhaden and bay anchovy; these predators may also rely on juvenile blue crabs as part of their diet and may ultimately affect the abundance of recruiting crabs.

We must expand our understanding of food web interactions, quantify their effects, develop new food web models, and implement existing models to provide the requisite information that will permit managers to define sustainable catch levels and estimate fishing mortality rates of species in the webs. In this fisheries ecosystem plan (FEP), we have included preliminary diagrammed food webs of managed species, indicating strong and weak

interactions between predator and prey. These webs can guide managers as they explore policy options to develop ecosystem-based regulations—allowing high yields of piscivorous fish, for example, while conserving forage fish resources and important predator–prey relationships. Managers can now use fundamental knowledge of food web structure and relationships in a precautionary manner, but major research is needed to ensure effective multispecies fisheries management in the Bay.

This FEP element addresses the importance and limitations of developing food web models for the Chesapeake, considers the degree of connectivity between particular species (or trophic groups) and their predators and prey, and describes subwebs of the Bay’s economically valuable species. In addition, the element describes and discusses the utility of several recognized multispecies and ecosystem models that managers could adopt for ecosystem-based fisheries management in the Bay.

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*A food web is defined as a “network of consumer-resource interactions among a group of organisms, populations, or aggregate trophic units” (Winemiller and Polis 1996).*

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## **Food Web Dynamics**

### *Importance*

Sustainable use of exploited species will depend, at least in part, upon inclusion of multispecies fisheries management approaches based largely on food web dynamics (Christensen 1996; Daan 1997; Christensen and Pauly 1998; Pauly et al. 1998). Managers have not yet applied a multispecies approach to fisheries management in the Chesapeake, despite its potential utility (Houde et al. 1998) as well as the availability of a food web model for the mesohaline (middle) portion of the Bay (Baird and Ulanowicz 1989), which could provide a framework for additional modeling focused on management needs.

Fishing affects ecosystems by removing biomass from the complex of species that feed upon each other in the web (Pauly et al. 2000). It also shifts the relative abundance of exploited species at different trophic levels. Such changes—from fishing, other anthropogenic stresses (e.g., habitat alteration and pollution), or environmental change—may lead to shifts in the productivity and sustainable yields of species. These shifts, in turn, may affect the value of fisheries, species biodiversity, or the structural integrity of the ecosystem (Winemiller and Polis 1996; Pauly et al. 2000; Jackson et al. 2001; Link 2002a). For instance, researchers have postulated that changes in the abundance of key fishery species, such as the oyster and blue crab, may have altered community structure and pathways of production in the Bay (Jackson et al. 2001; Silliman and

Bertness 2002). Massive fishery-induced reductions in the abundance of eastern oyster *Crassostrea virginica*, a suspension feeder on phytoplankton, have contributed to abnormally high phytoplankton production, eutrophication, and seasonal hypoxia that reduce secondary production and species diversity (Jackson et al. 2001). In coastal salt marshes, declines in blue crab abundance (Lipcius and Stockhausen 2002), due partly to heavy fishing pressure, may have allowed marsh periwinkle *Littoraria irrorata* to become more abundant and overconsume salt marsh grasses—a process which ultimately could lead to the destruction of salt marshes important for blue crab production (Silliman and Bertness 2002).

An ecosystem's carrying capacity, production potential, and total sustainable yield to fisheries cannot simply be calculated as the sums of yields for individual component species (Link 2002a) using traditional, single-species stock assessment techniques. Rather, fisheries production of an ecosystem depends significantly on food web dynamics (Pauly et al. 2000; Link 2002a). To evaluate the impact of a species' fishing mortality upon food web interactions and ecosystem processes, therefore, the ecosystem's chief food web interactions must be defined and quantified (Pauly et al. 2000). Similarly, researchers must consider the effects of other controlling factors, such as habitat quality and environmental conditions (see Habitat Requirements and Externalities elements), within the context of ecosystem-based

management.

Predation is key in determining the abundance and size structure of populations, as well as the organization and functioning of communities in the Chesapeake and other ecosystems (Lipcius and Hines 1986; Hines et al. 1990; Seitz et al. 2001). Predation affects all life stages of marine organisms and constitutes the primary source of natural mortality for fish in well-studied marine ecosystems (Bax 1991, 1998), even for those species with high fishing mortality during their exploitable life stages.

The relative importance of predation and fishing mortality varies among species, but is typically skewed towards predation for younger (and smaller) individuals and towards fishing mortality for older individuals. For instance, predation largely accounts for the mortality of young juvenile blue crabs whereas fishing becomes responsible for 80% of the mortality of older juveniles and adults. Predation may also play a major role in controlling food web dynamics in marine ecosystems, altering the effects of reductions or increases in fishing mortality of species (Andersen and Ursin 1977; Laevastu and Favorite 1988; Bax 1991, 1998; Christensen 1996; Trites et al. 1999; Pauly et al. 2000; Link 2002a).

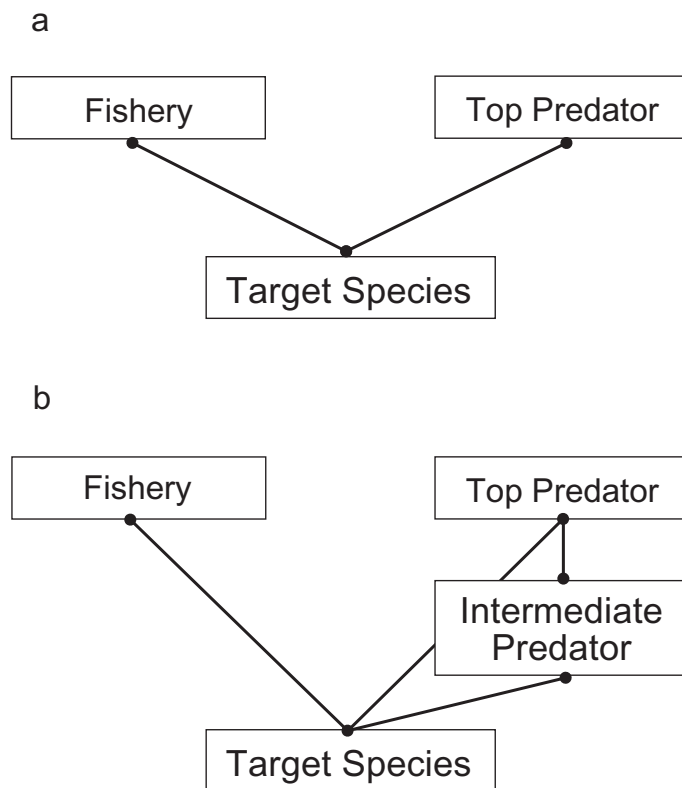
With a heavily fished population at low abundance, predation may limit population recovery despite potentially high recruitment of incoming year classes (Sissenwine 1984; Bax 1991, 1998; Christensen 1996; Link 2002a). In such cases, the predator may have

remained at high population levels or it may be a fished species that has recovered after management-induced reductions in fishing mortality. For example, Lipcius and Stockhausen (2002) hypothesized that predation pressure by Atlantic croaker (at high abundance in Chesapeake Bay for nearly a decade) or by striped bass *Morone saxatilis* (which dramatically resurged during the last decade following rigorous management measures) may be responsible for the lack of recovery of the depressed blue crab population in the Bay. Similarly, restoration of the Bay's native oyster population may be hampered by disease in older juveniles and adults

or by blue crab predation; either of these forces could prevent oyster recovery given that overfishing, habitat degradation, and disease have driven the population to extremely low levels (Rothschild et al. 1994).

For some species, natural mortality through predation—especially on young stages—may prove more significant in controlling population abundance than fishing mortality on recruited stages. Such species may be subject to little or no fishing pressure, but serve as forage species for a spectrum of natural predators (Overholtz et al. 2000). Historically, watermen have fished some forage species (e.g. Atlantic menhaden), which form a major component of the Chesapeake fisheries ecosystem. During the past 50 years, when overfishing has caused declines of top predator species, fisheries have increasingly targeted species at lower trophic levels (Pauly et al. 1998). Significant reductions in the abundance of these species may cause fundamental changes in community structure and the ecosystem (Pauly et al. 1998; Jackson et al. 2001). This process, referred to as “fishing down food webs,” may disrupt natural predator–prey relationships. The effects of such fishing include shifts in trophic-level structure, along with changes in population abundance and age structure of target species. Selective fishing on forage species can precipitate indirect impacts on other species in the food web as predators transfer their emphasis to alternative prey.

In some cases, predation may not play a major role in controlling abundance,



**Figure 1.** Hypothetical simple (a) and moderately complex (b) food webs with top and intermediate predators that are not fished, a target fishery species, and human fishing at a trophic level equivalent to that of the top predator (adapted from Yodzis 2001).

as in shoaling pelagic species (Overholtz et al. 1991, 2000; Jennings and Kaiser 1998), which fluctuate in response to variable ocean conditions. Such variability in controlling mechanisms accentuates the need to define the major food web interactions in an ecosystem before we can understand the relative impacts of natural and fishing mortality upon food web dynamics and ecosystem processes.

### *Limitations*

Despite the growing awareness that fisheries management requires a multispecies approach, considerable debate remains over the reliability of predictions of changes in target species abundance derived from multispecies approaches. Yodzis (2001) provides an illuminating example of the problems associated with predictions of fishery-induced alterations in food webs, examining a situation in which fisheries cull a top predator to increase production of a target species by reducing the natural predation on this species. In this case, fisheries catch a target species consumed by the top predator (Figure 1a). If the cull significantly reduces the population of the top predator, then the abundance and yield of the target fishery species should increase.

This simple view of food web dynamics is based on the assumption that removing a top predator from the system will increase the abundance of prey it would have consumed, which then becomes available to the fishery. If, however, the addition of an intermediate predator complicates the food web (Figure 1b), the potential for

indirect effects confounds the ability to determine either the direction of the system response to the removal of the top predator or its magnitude (Yodzis 2001). In this scenario, the reduced top predator population will eat less of the target species, which

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should result in an increase in its abundance. The top predator will also eat fewer of the intermediate predators, however, which should decrease target species abundance. In this circumstance, the net result of reducing the top predator upon the target fishery species shown in this relatively simple food web remains uncertain. Ultimately, the abundance of the target species might increase, decrease, or be unaffected, depending on the strengths of the various predator-prey links (Punt and Butterworth 1995; Abrams et al. 1996; Yodzis 2001).

Another complication arising from the complexity of food web dynamics is the possibility that ecosystems have alternative stable states (Sheffer et al., 2001; Carpenter 2002). Given that the Chesapeake Bay food web has undergone dramatic, historical alterations due to anthropogenic changes—such as overfishing (Jackson et al. 2001) and eutrophication (Boesch 2000)—and natural disturbances (R. N. Lipcius and R. D.

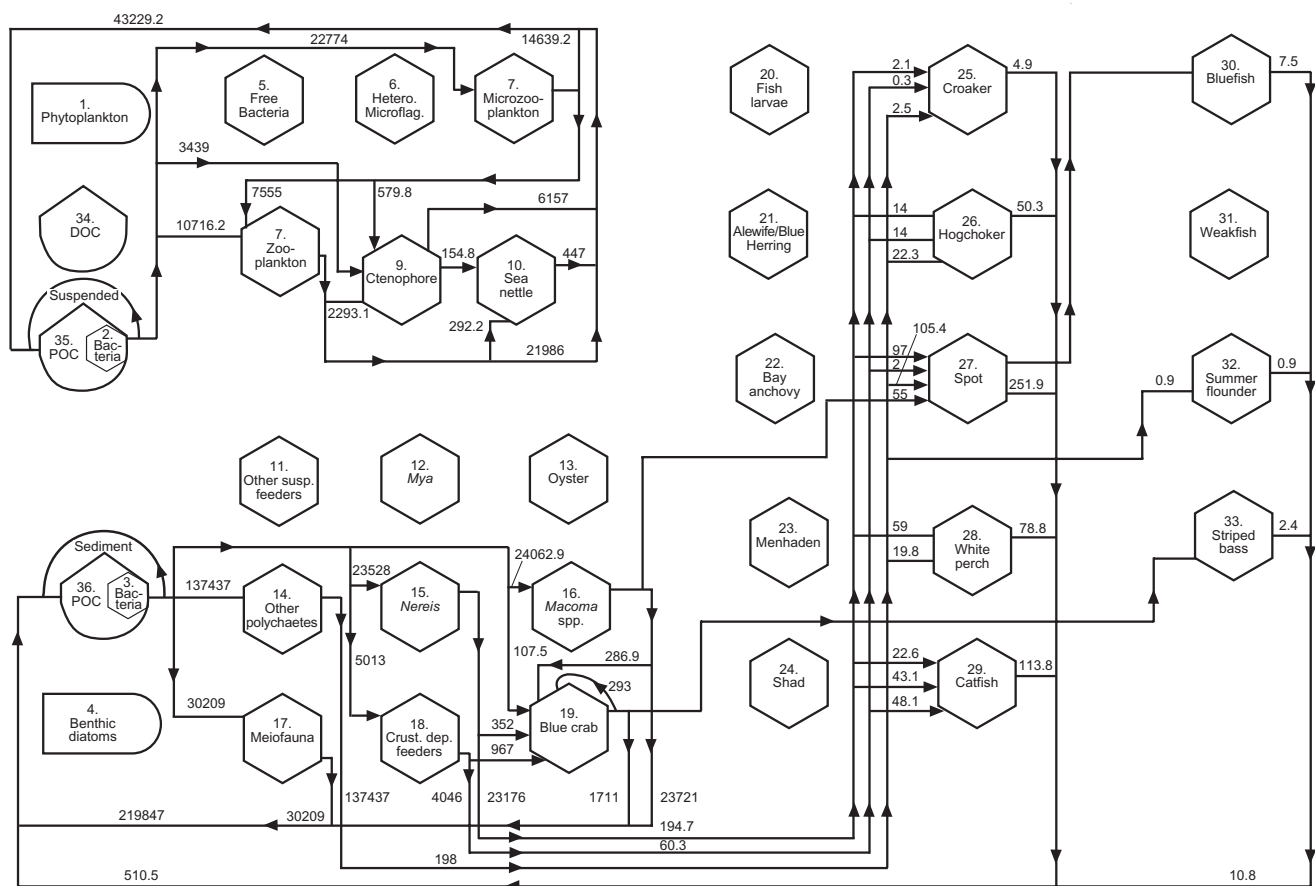
Seitz, unpublished manuscript), restoring the food web to its “pristine” state may prove impossible. Even if managers agree on the preferred food web, its composition, and its biomass structure, such a food web may be unattainable due to the stability of the degraded ecosystem characterized by the distorted food web (Sheffer et al. 2001; Carpenter 2002; Peterson and Lipcius 2003). Stability refers to a situation in which a disturbed or degraded ecosystem is in an “alternative stable state” (Sheffer et al. 2001; Carpenter 2002), which will not easily shift back to the undisturbed state due to feedback mechanisms maintaining the structure of the disturbed stable state. Stability is not limited to pristine systems; it is also a feature of disturbed systems (Sheffer et al. 2001; Carpenter 2002) and contributes to the difficulty in restoring disturbed ecosystems such as Chesapeake Bay.

Management, therefore, should consider the possibility that some desired food web configurations may not be achievable (Peterson and Lipcius 2003), at least in the short term, without massive intervention (Carpenter 2002). For instance, the seaside lagoons of the Eastern Shore harbored extensive seagrass beds that supported a lucrative Bay scallop fishery until the Storm King hurricane of 1933 devastated the ecosystem. The resultant turbid conditions not only precluded restoration of the seagrass beds, but also hindered the reestablishment of

a productive scallop fishery in the seaside lagoons for over 6 decades (R. N. Lipcius and R. D. Seitz, unpublished manuscript).

Three basic approaches exist for the analysis of food webs (Paine 1966; Winemiller and Polis 1996). One is topological, providing a static description of predator and prey links between species or trophic groups. In the following section, we offer a basic topological analysis of the connectivity of species and trophic groups in the Chesapeake Bay food web. A second approach uses quantitative analysis of energy and matter flow through the food web via predation (e.g., Ecopath with Ecosim, Pauly et al. 2000), a modeling approach that researchers have started using in the Bay. The final approach is functional, identifying the species and trophic links that determine community structure. The functional approach typically depends on field experiments that deal with specific links between important consumers (predators) and resources (prey) in the food web (see Silliman and Bertness 2002).

Topological and energy flow analyses are instructive (Pauly et al. 2000; Link 2002b), but not always capable of explaining the dynamics of populations and communities. The dynamic influence of a particular species or trophic group is not necessarily proportional to the energy flow between trophic links (see review of the three analysis types in Winemiller and Polis 1996). For instance, keystone species may initiate trophic cascades (i.e., significant effects of changes in one species upon



**Figure 2.** Food web components of middle (mesohaline) Chesapeake Bay, indicating composite cycling of carbon. This web is generally representative of the major food web components used in previous network (energy flow) analyses of the Chesapeake food web (Baird and Ulanowicz 1989; Monaco and Ulanowicz 1997; Hagy 2002) (adapted from Baird and Ulanowicz 1989).

others in the food web without direct links), forming a key force in structuring marine, aquatic, and terrestrial communities. Yet, their influence often appears disproportionately high relative to their biomass (Power et al. 1996).

Recent research suggests that the blue crab is a keystone species in the Chesapeake. First, the blue crab enhances salt marsh grass production and the associated marsh community by feeding upon marsh periwinkles, which at high densities can reduce salt marsh productivity (Silliman and Bertness 2002). Second, the blue crab

may strongly influence seagrass production and community structure through consumption of seagrass grazers (e.g., amphipods and isopods), which increase seagrass productivity by grazing upon seagrass epiphytes (M. Harris, E. Duffy, and R. N. Lipcius, unpublished manuscript). The influence of these complex mechanisms on community structure in Bay habitats indicate that an experimental, functional approach to food web analysis is needed to identify the major controlling factors of food web dynamics. Unfortunately, the experimental field manipulations typically required to evaluate the

dynamics and functional roles of species in a food web often prove logistically intractable at spatial and temporal scales that capture the full dynamics of an ecosystem. In such cases, topological analyses or modeling may become the only options. A balanced inclusion of the three approaches to food web analysis may best address the food web dynamics of large ecosystems. Moreover, collective uncertainties in food web investigations demand caution in the application of food web analyses to fisheries management.

## **Chesapeake Bay Food Web**

### *General Features*

The Chesapeake Bay food web (Figure 2) contains several features typical of most estuarine food webs:

- 1) Predominance of generalist feeders, both benthic and pelagic, that typically consume prey in proportion to their availability (Baird and Ulanowicz 1989; Monaco and Ulanowicz 1997; Hagy 2002);
- 2) Moderately interconnected trophic pathways between predators and prey (Monaco and Ulanowicz 1997; Dunne et al. 2002);
- 3) Modified food web structure due largely to anthropogenic alterations (Monaco and Ulanowicz 1997; Jackson et al. 2001; Hagy, 2002);
- 4) High fisheries production (Nixon 1982); and
- 5) High phytoplankton primary production, much of which is not consumed and is transformed to

detritus, particularly in the middle Bay (Monaco and Ulanowicz 1997; Hagy 2002).

Although the ratio of primary production in the water column to that in the benthos is 6:1, production in the Bay relies heavily on inputs from detritus and the microbial loop (i.e., organic matter cycles through bacteria to protozoan consumers with subsequent grazing by microzooplankton) to fuel secondary production at higher trophic levels, including most fishery species (Monaco and Ulanowicz 1997). Production of predatory fish in the Bay may depend significantly on benthic deposit feeders, detritus, and the microbial loop, in addition to pelagic primary production (Baird and Ulanowicz 1989; Monaco and Ulanowicz 1997; Hagy 2002), as in many marine ecosystems characterized by high bacterial biomass (Pomeroy 2001). Benthic suspension feeders use phytoplankton production, allochthonous inputs (e.g., external nutrient sources from freshwater inflows), and benthic production (Monaco and Ulanowicz 1997). Consequently, benthic suspension feeders and deposit feeders form critical conduits between the pelagic and benthic components of the food web, since deposit and suspension feeders (such as worms and clams) are eventually consumed by predatory demersal fish and benthic invertebrates. These predators subsequently become prey for larger, pelagic, predatory fish.

The species and trophic groups comprising the Bay's food web have been assigned to specific trophic levels (Table 1) and their importance identi-

Trophic Group	Hagy	Baird & Ulanowicz	Monaco & Ulanowicz
DOC, POC	1.0	1.0	1.0
Phytoplankton	1.0	1.0	1.0
Picoplankton	1.0	1.0	1.0
SAV	1.0	1.0	1.0
Microphytobenthos	1.0	1.0	1.0
Bacteria	2.0	2.0	2.0
Suspension feeders	2.1	2.1	2.2
Eastern oyster	2.1	2.1	2.2
Atlantic menhaden	2.1	2.8	2.7
Meiobenthos	2.3	2.7	-
Rotifers	2.4	2.2	-
Deposit feeders	2.4	3.0	2.8
Microzooplankton	-	2.2	2.6
Mesozooplankton	2.5	2.2	2.2
Ciliates	2.6	2.8	-
Heteroflagellates	3.0	3.0	-
Blue crab	3.1	3.5	3.2
Spot	3.1	4.0	-
Atlantic croaker	3.1	4.0	-
Hogchoker	3.1	3.9	-
American eel	3.1	-	-
Catfish (Bay species)	3.2	4.0	-
White perch	3.4	4.0	-
Bay anchovy	3.5	2.8	2.7
Lobate ctenophore	3.5	3.0	3.2
Alewife/Blueback herring	3.6	3.2	-
Shads	3.6	3.2	-
Striped bass	3.6	3.9	3.8
Weakfish	4.0	3.8	3.8
Bluefish	4.1	4.6	3.8
Sea nettle	4.6	3.4	-
Summer flounder	-	4.0	3.8

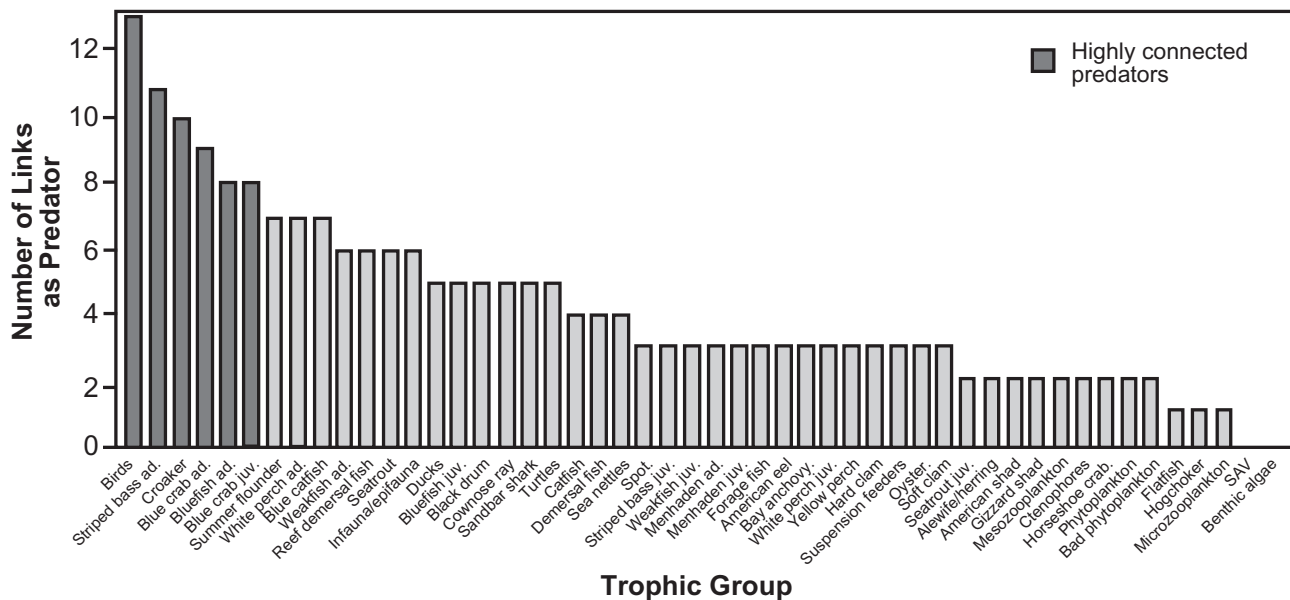
**Table 1.** Trophic levels of Chesapeake Bay food web components after Hagy (2002), Baird and Ulanowicz (1989), and Monaco and Ulanowicz (1997). Numbers refer to the average trophic level of each group, standardized to 1.0 for primary producers and sources of organic carbon (DOC and POC), 2.0 for primary consumers, 3.0 for secondary consumers, and so on.

fied through network analysis of energy flow (Baird and Ulanowicz 1989; Monaco and Ulanowicz 1997; Hagy 2002). Baird and Ulanowicz (1989) and Monaco and Ulanowicz (1997) categorized the principal consumers and trophic groups in terms of energy flow and cycling in the Bay food web. More recently, Hagy (2002) extended the earlier analyses and reached fundamentally similar conclusions. Although the relative importance of a particular species or trophic group as a consumer may differ based on occurrence in the upper, middle, or lower Bay (Hagy 2002), generalities do exist in the Bay's food web. The following conclusions are summarized from the extensive investigations of Baird and Ulanowicz (1989), Monaco and Ulanowicz (1997), and Hagy (2002). Some species may be categorized poorly, however, due to incomplete diet data or an inadequate under-

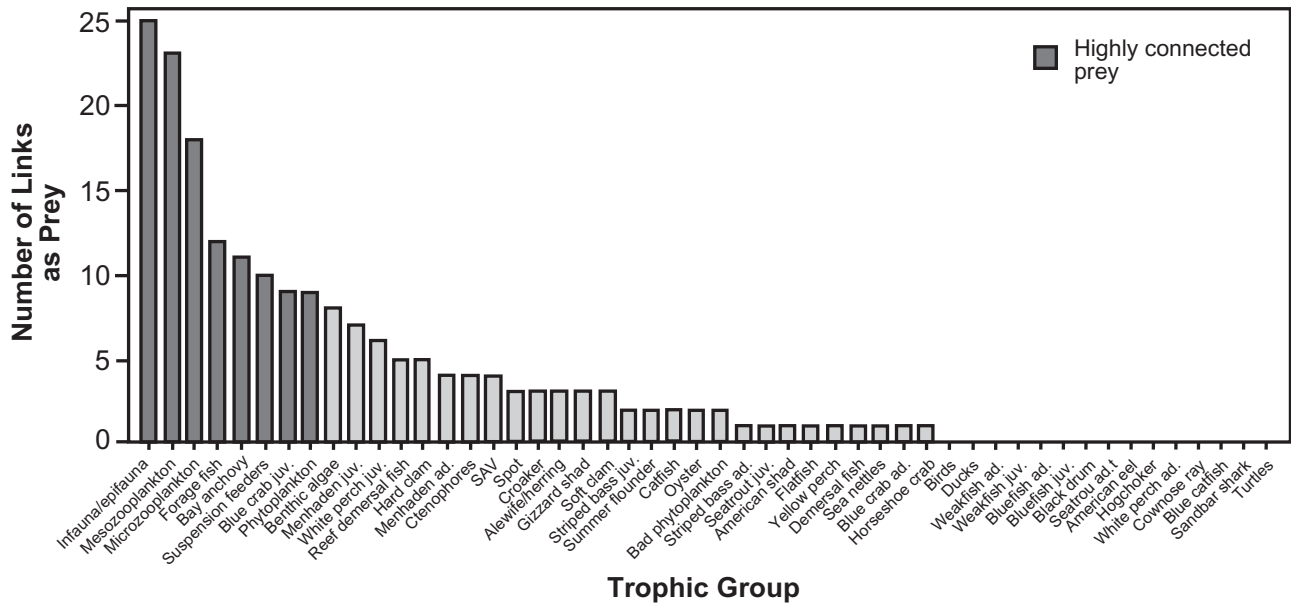
standing of ontogenetic diet shifts. Consequently, the assumed trophic position of individual species should be examined carefully during FMP development or in food web modeling and investigations.

*Food Web Generalities for the Bay.* The following list cites some of the generalities that apply to the Chesapeake Bay food web.

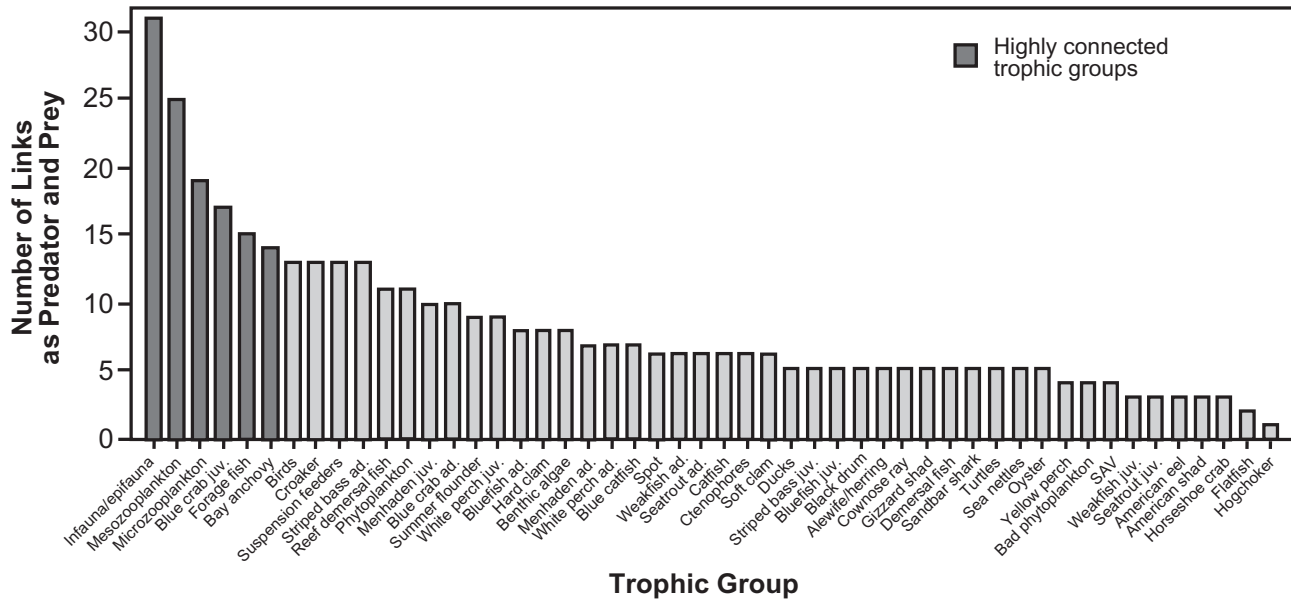
- 1) Of the pelagic consumers, bay anchovy and menhaden transfer the most production from plankton to predatory fish and have the highest secondary fish production.
- 2) The lobate ctenophore (e.g., comb jelly) is a major consumer of mesozooplankton (larger zooplankton such as copepods and cladocerans) and microzooplankton (smaller zooplankton such as nauplii and rotifers) particularly in the middle Bay. This consumption diverts production from forage fish and,



**Figure 3.** Number of links from the species or trophic group listed on the X-axis to prey of that species or trophic group. For example, striped bass adults prey on 11 species or trophic groups; blue crab adults prey on nine species or trophic groups, including blue crab juveniles.



**Figure 4.** Number of links from the species or trophic group listed on the X-axis to predators of that species or trophic group. For example, 23 species or trophic groups prey on mesoplankton and 11 on bay anchovy. Data are derived from the diet matrix (August 2002) of the Chesapeake Bay Ecopath model.



**Figure 5.** Number of links from the species or trophic group listed on the X-axis to predators and prey of that species or trophic group. For example, 25 links occur from mesoplankton to species or trophic groups that are either predators or prey of mesoplankton along with 17 links from blue crab juveniles to either predators or prey. Data are derived from the diet matrix (August 2002) of the Chesapeake Bay Ecopath model.

ultimately, fisheries yield. Ctenophores also prey on bay anchovy eggs and larvae, reducing the potential for fish production. In network analyses, sea nettle (the

medusa *Chrysaora quinquecirrha*) predation on ctenophores appears to compensate for the negative effect of ctenophore predation on bay anchovy. Sea nettles can be

viewed positively in terms of energy flow to fish production within the web, therefore, despite their moderate predation on bay anchovy. Other forage fish species that form important links from the plankton to the benthos and predatory fish include the alosines—alewife *Alosa pseudoharengus*, blueback herring *A. aestivalis*, and American and hickory shads *A. sapidissima* and *A. mediocris*.

- 3) Benthic suspension feeders and deposit feeders, particularly bivalves (e.g., Atlantic rangia *Rangia cuneata*, Baltic macoma *Macoma balthica*, northern quahog *Mercenaria mercenaria*) and various polychaetes (e.g., deep-burrowing *Chaetopterus variopedatus*), consume much of the Bay's detrital, planktonic, and microbial loop output. In the middle Bay, seasonal hypoxia causes low benthic production (Hagy 2002). Network analyses, however, indicate that production remains sufficient to satisfy the demands of demersal (i.e., epibenthic) and benthic (i.e., infaunal) predators. Demersal fish (hogchoker *Trinectes maculatus*, spot, Atlantic croaker) and blue crab are among the chief consumers of the benthos, collectively consuming nearly 90% of benthic production. The most productive of the piscivores include weakfish *Cynoscion regalis*, striped bass, bluefish *Pomatomus saltatrix*, channel catfish *Ictalurus furcatus*, Atlantic croaker, and spot, in no order of importance.

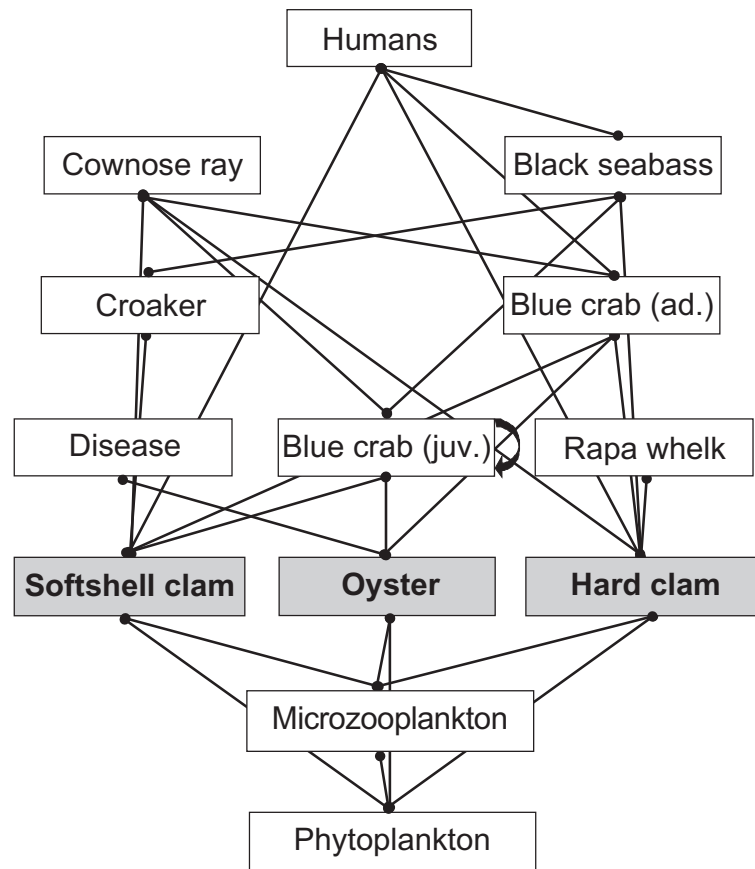
## Connectivity of Predators and Prey

Topological analysis is a useful instrument to determine the structure of particular trophic groups in the food web, illustrating the connectivity between a particular species or trophic group and its predators and prey (Winemiller and Polis 1996). The connectivity (i.e., number of linkages between trophic groups) of the Bay's food web is moderate relative to other terrestrial, aquatic, and marine food webs (Dunne et al. 2002; Link 2002b), suggesting that it is reasonably resilient to modest perturbations such as the loss of a few species (Dunne et al. 2002). Such a loss to the integrity of the food web becomes most pronounced when highly connected species (i.e., species possessing multiple linkages to other predators and prey) are removed from the web (Dunne et al. 2002) and may have severe impacts on food web integrity, carbon cycling, and resilience to environmental perturbations (Dunne et al. 2002). Consequently, scientists and fishery managers must recognize those predators and prey having the highest degree of connectivity with other trophic groups in the food web.

To evaluate the degree of connectivity of the various species and trophic groups of the Bay food web, the NOAA Chesapeake Bay Office (NCBO) EcoPath Working Group used the August 2002 diet matrix of the Chesapeake Bay Ecopath model to define the number of links between species and trophic groups (Figures 3–5). The

most highly connected predators (top 12%; 6 of 50) were piscivorous birds (e.g., American osprey), striped bass adults, Atlantic croaker, blue crab adults, bluefish adults, and blue crab juveniles (Figure 3). Each had links to 8 to 13 species or trophic groups upon which they prey. Of the prey, the most highly connected trophic groups (top 12%; 6 of 50) were those near the base of the food web, including benthic deposit and suspension feeders, invertebrate grazers, mesozooplankton, microzooplankton, littoral forage fish (e.g., silversides), and bay anchovy (Figure 4). Each of these groups had 10 to 25 links to predators. When considering all trophic links, both to predators and prey, the most connected trophic groups (top 12%; 6 of 50) were again those near the base of the food web, specifically infaunal and epifaunal deposit and suspension feeders, invertebrate grazers, mesozooplankton, microzooplankton, blue crab juveniles, littoral forage fish, and bay anchovy (Figure 5). These groups had 14 to 31 links to predators and prey.

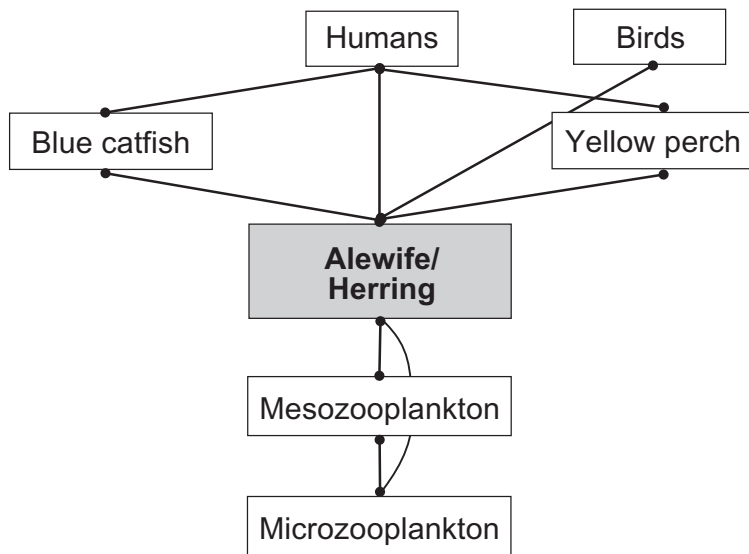
The results bear strong similarity to those of energy flow analyses (Figure 2), indicating that relatively few species and trophic groups drive energy flow and connectivity in the Chesapeake food web. Some species that may be critically important in food webs were not highly connected (e.g., menhaden, ctenophores) due to narrow dietary preferences. The low to moderate connectivity of planktonic consumers, such as menhaden and ctenophores, may result from the



**Figure 6.** Subweb of the hard clam, soft-shell clam, and native oyster.

aggregation of species as trophic groups serving as their prey. If one considers ontogeny and increase in size at progressive life stages of species such as menhaden and lobate ctenophores, then their connectivity may increase. For example, larvae and early juveniles of menhaden primarily consume zooplankton, while ctenophores in the larval stage may have a broader diet than larger individuals. Such patterns may hold for many species, but the connectivity analyses may not fully account for them.

Managers should value all species categorized as important in either the energy flow or the connectivity analy-



**Figure 7.** Subweb of the alewife/herring complex.

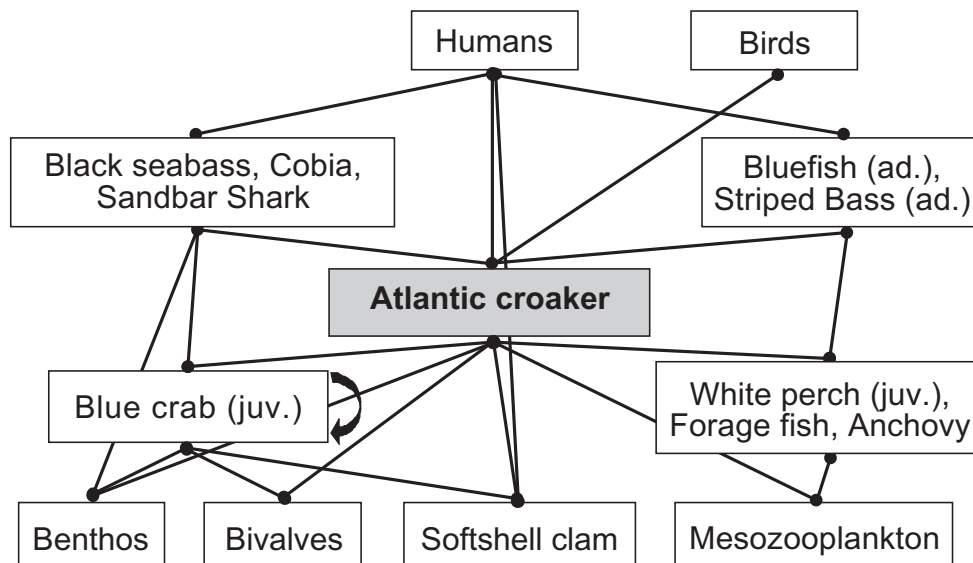
ses. Additionally, the connectivity between certain species might not be clear due to reduced abundance of the species. The most notable example—the native oyster—historically played a dominant role as a consumer of phytoplankton.

The Chesapeake Bay food web has undergone substantial historical

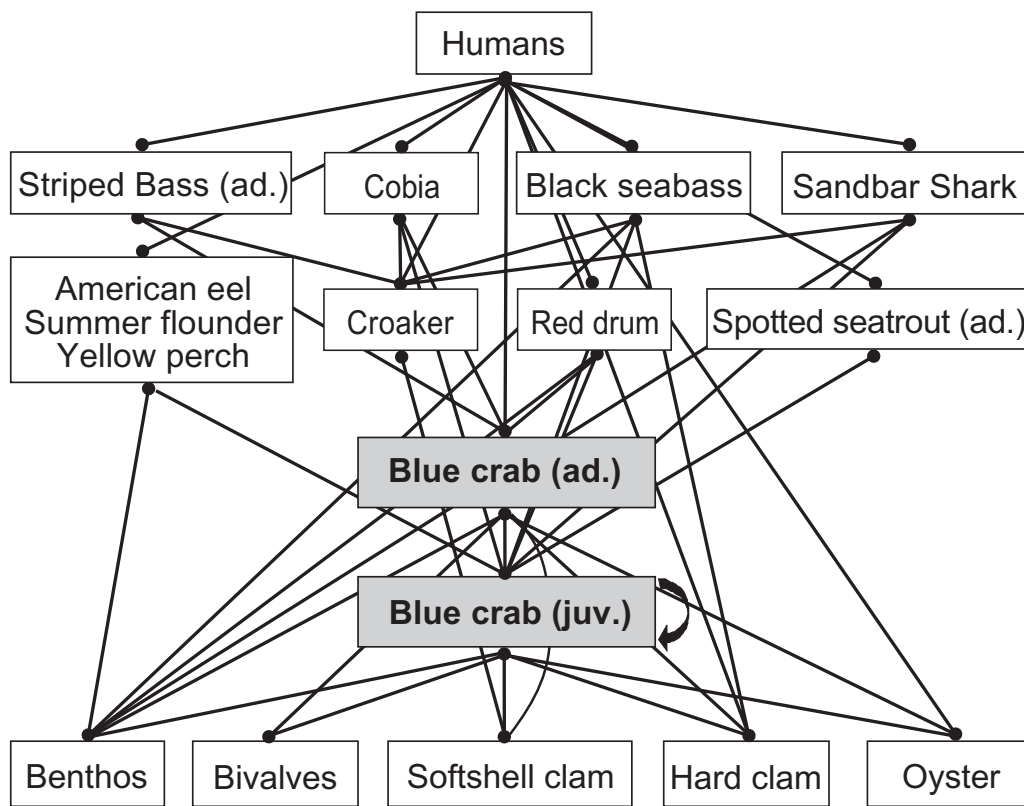
alterations, due in large part to overfishing (Jackson et al. 2001) (see Externalities Element). Most likely, the current major role of detritus in trophic dynamics results from considerable degradation of the Bay food web and the accompanying shift from an ecosystem that functioned largely through benthic algal and seagrass production to one heavily dependent on the microbial loop, phytoplankton production, and detritus (Jackson et al. 2001). Recognizing that the Bay’s food web has endured dramatic change due to anthropogenic stress, we must now accept the possibility that certain components of the food web may not be easily restored.

### Subwebs of Fishery Species

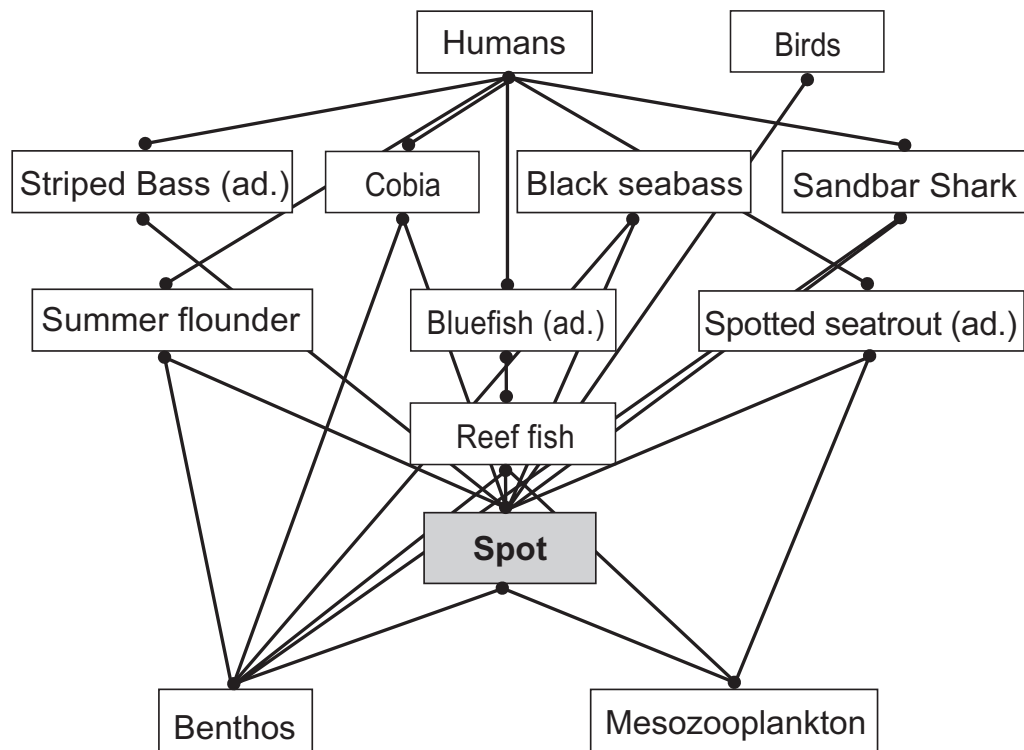
Subwebs of each of the economically valuable species in the Bay can guide the identification of the species’ important predators and prey. The subwebs do not portray the relative importance of links between predators



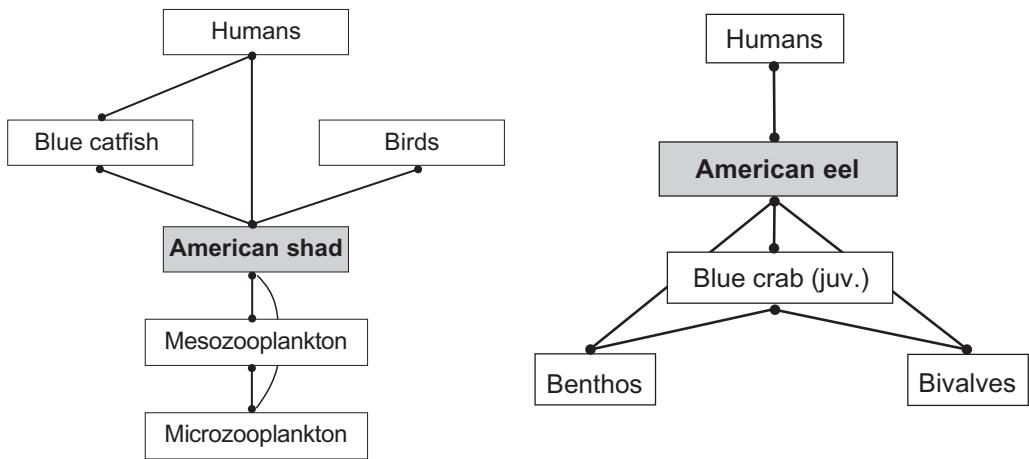
**Figure 8a.** Subweb of the Atlantic croaker.



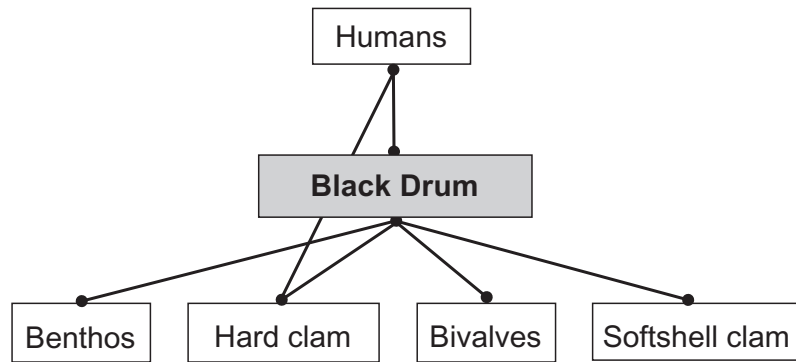
**Figure 8b.** Subweb of the blue crab.



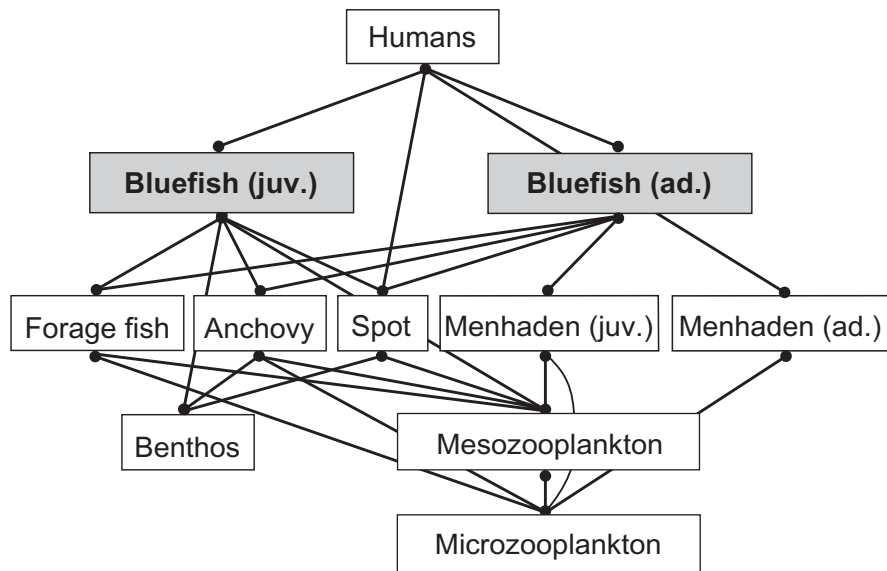
**Figure 8c.** Subweb of the spot.



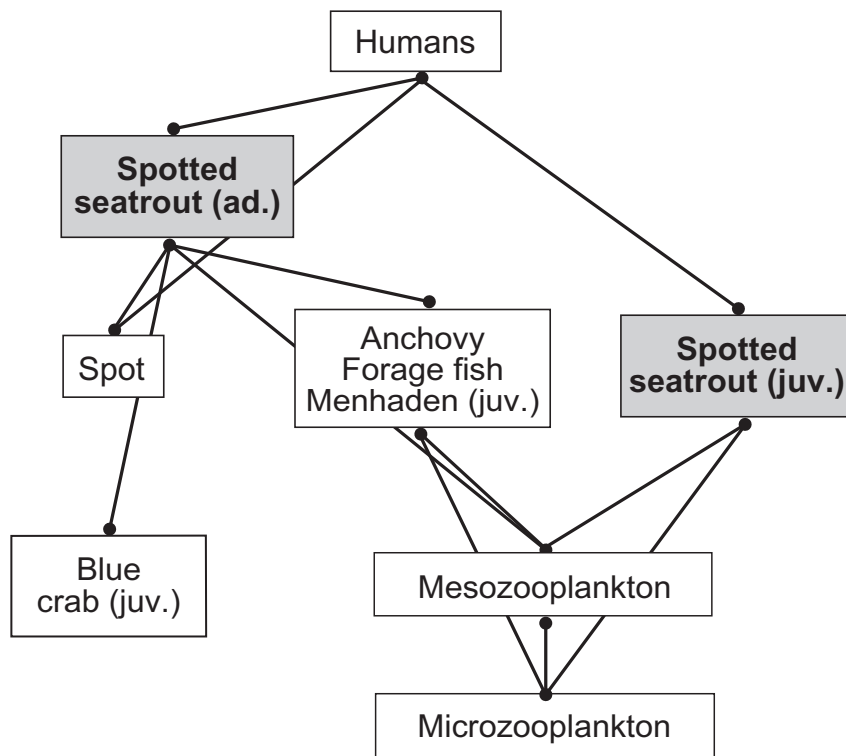
**Figure 9a.** Subweb of the American shad. **Figure 9b.** Subweb of the American eel.



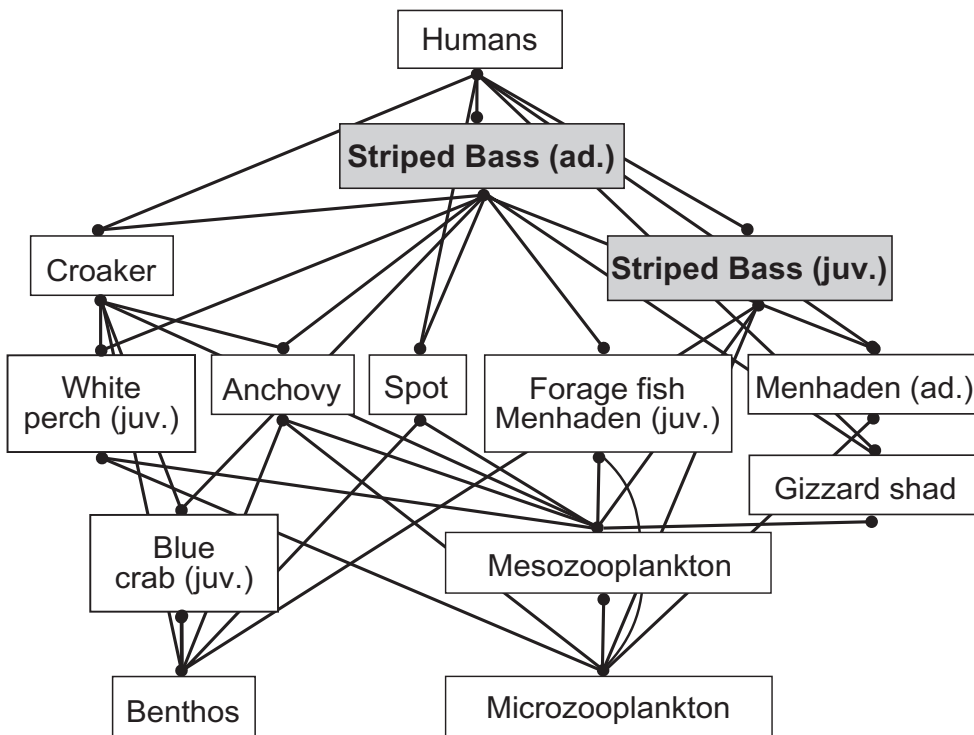
**Figure 9c.** Subweb of the black drum.



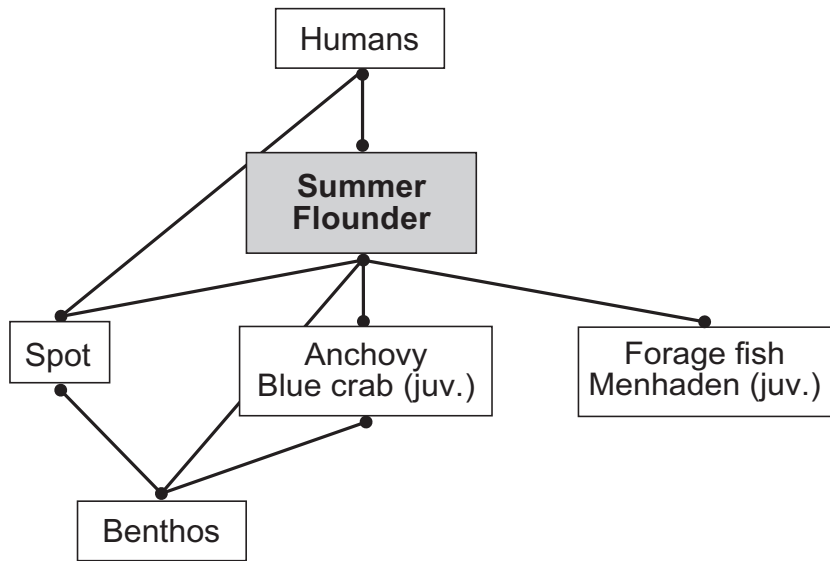
**Figure 9d.** Subweb of the bluefish.



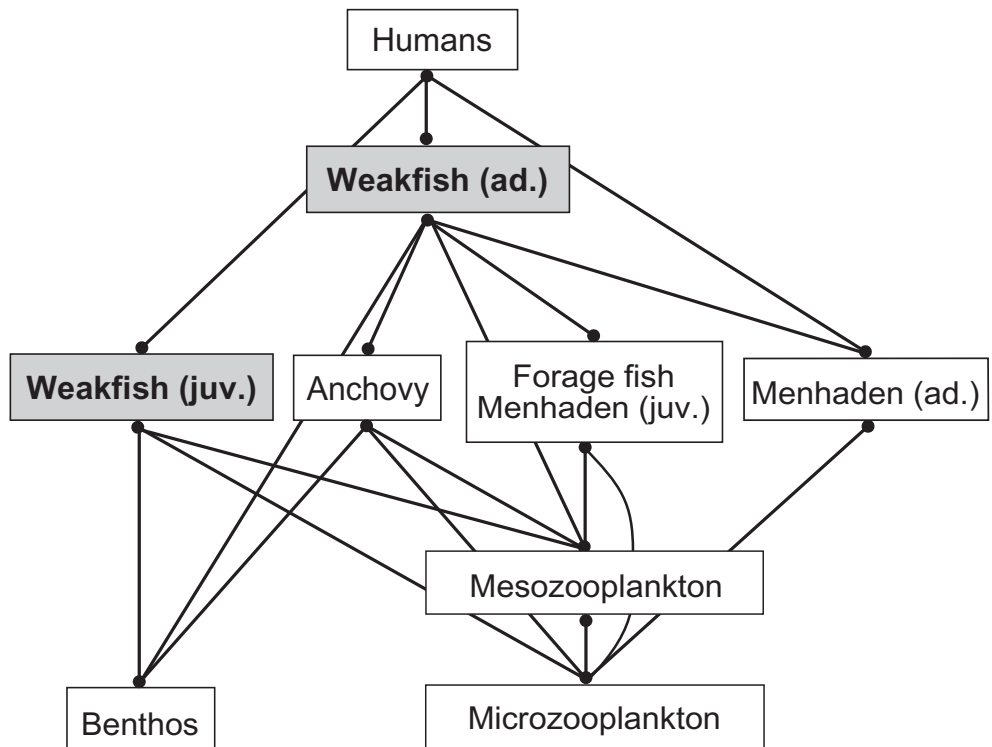
**Figure 9e.** Subweb of the spotted seatrout.



**Figure 9f.** Subweb of the striped bass.



**Figure 9g.** Subweb of the summer flounder.



**Figure 9h.** Subweb of the weakfish.

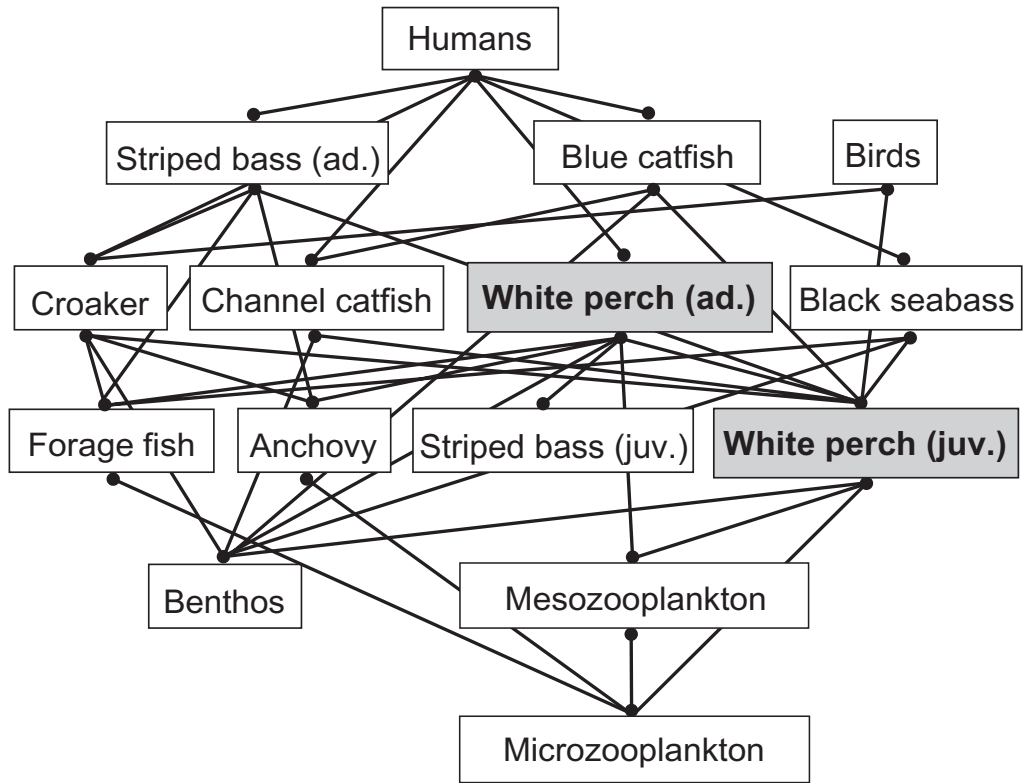


Figure 9i. Subweb of the white perch.

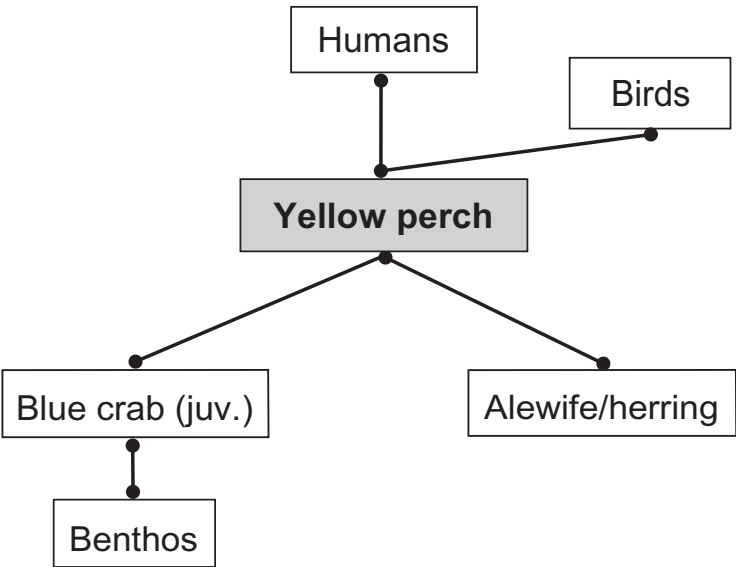
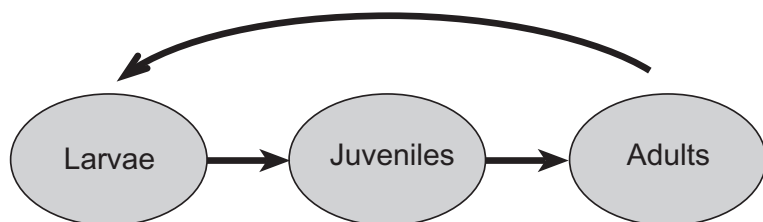


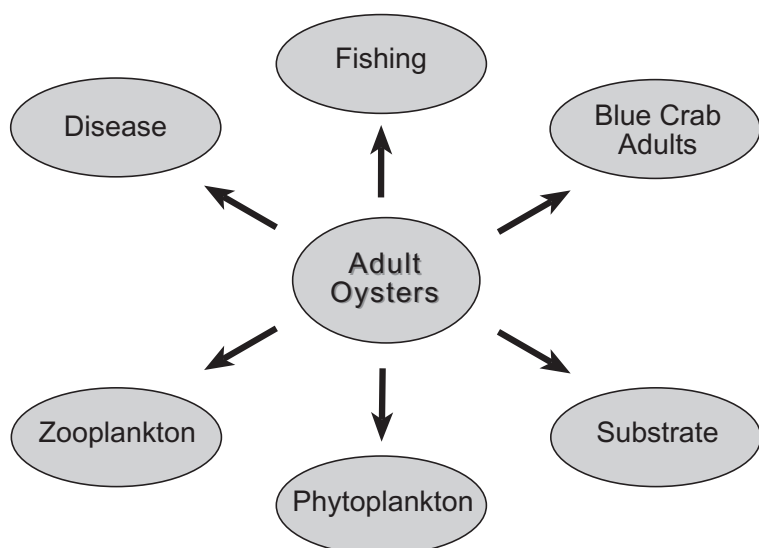
Figure 9j. Subweb of the yellow perch.

## Life Cycle Diagram of the Oyster



**Figure 10.** Simplified life cycle diagram of the Eastern oyster, highlighting its key life stages.

## Predator-prey Interactions and Sources of Mortality



**Figure 11.** Adult stage of the Eastern oyster with major sources of mortality (disease, fishing, blue crab predation), prey (plankton), and habitat needs (substrate).

and prey. Additional factors and processes, external to traditional predator-prey relationships, may prove critical in the dynamics of the species, such as disease in the case of the native Eastern oyster. These factors should be considered in the comprehensive analysis of all sources of mortality affecting a species and in development of ecosystem-based management plans.

The diet matrix of the NOAA Chesapeake Bay Office EcoPath Working Group provided the information to create the subwebs. The first subweb, shown in Figure 6, consists of benthic suspension-feeding bivalves near the base of the food web (Table 1) that support major fisheries, including the northern quahog, softshell (also known as softshell clam) *Mya arenaria*, as well as the eastern oyster.

The next subweb (Figure 7) includes finfish near the base of the food web, specifically the alewife-blueback herring complex. Following is the suite of subwebs that includes most of the intermediate trophic links, and those with a high degree of connectivity, such as Atlantic croaker, blue crab, and spot (Figures 8a, 8b, and 8c). Finally, we detail the food webs of higher-level predators, including most of the top predatory fishes, specifically American shad, American eel *Anguilla rostrata*, black drum *Pogonias cromis*, bluefish, spotted seatrout *Cynoscion nebulosus*, striped bass, summer flounder *Paralichthys dentatus*, weakfish, white perch *Morone americana*, and yellow perch *Perca flavescens* (Figures 9a–9j).

For all subwebs illustrated above, the NCBO EcoPath Working Group is modifying the predator and prey linkages as new information is gathered and incorporated into the current Ecopath model. Updated subwebs may be downloaded at <http://noaa.chesapeakebay.net/fepworkshop/netfep.htm>. Further details on the prey and predators are

available on the web site.

### Incorporation of Food Web Dynamics into FMPs

The following list provides general guidelines for incorporating food web dynamics into FMPs.

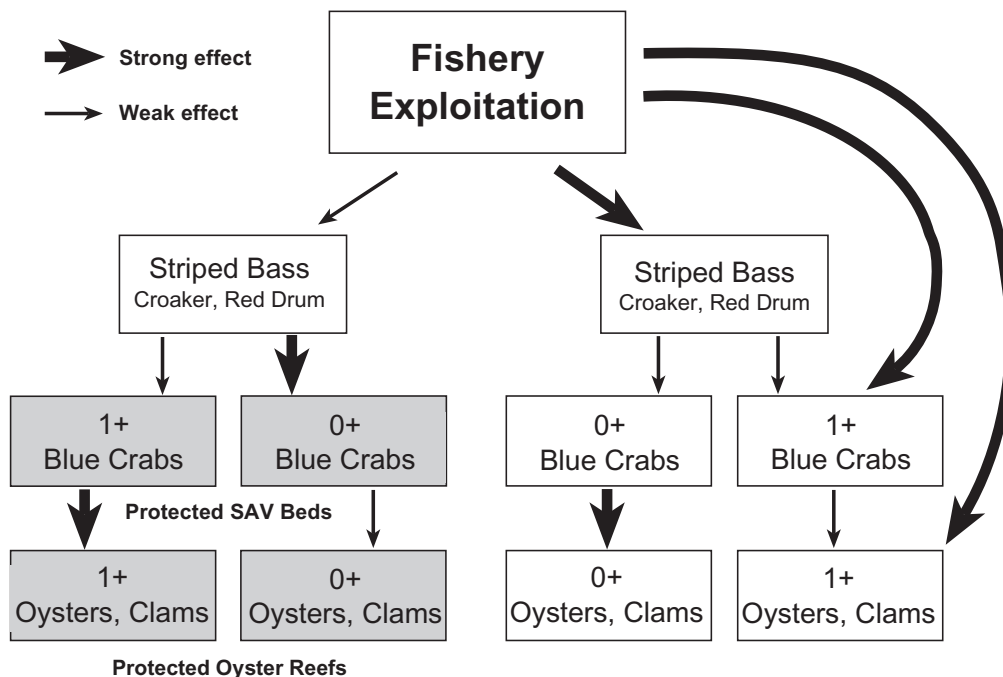
- 1) Develop and define the life cycle diagram of the target species.

The life cycle diagram explicitly recognizes the critical life stages and sources of mortality. For example, Figure 10 diagrams a simple life cycle diagram for the Eastern oyster. Although simplistic, elaboration of such diagrams in terms of habitat requirements and sources of mortality allows one to discern if key processes or sources of mortality have been ignored in

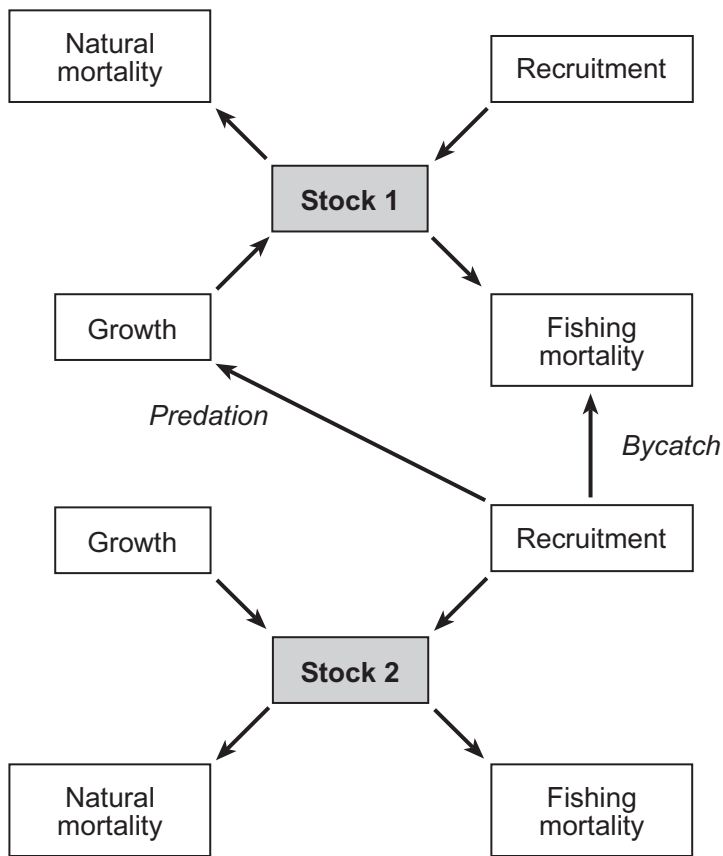
the analysis of the food web and its predator-prey relationships (Caswell 2000).

- 2) Identify the major predator-prey interactions and sources of mortality for each life stage by expansion of the life cycle diagram (Figure 11).
- 3) Identify critical habitat relationships for each life stage.

Expansion of the life cycle and food web diagrams should consider habitat needs (see Habitat Requirements Element), including possible use of protected or closed areas in management and conservation of exploited species. Figure 12 shows an example of stage-specific predator-prey interactions with probable modification in protected areas for



**Figure 12.** Potential food web interactions in no-take protected (shaded) and open-to-fishing (clear) habitats for a benthic component of the Chesapeake Bay food web that emphasize predator-prey relationships of striped bass/blue crab and other demersal fishes. This example, while hypothetical, indicates the kind of process that fisheries managers should follow in developing multispecies fisheries management plans that account for predator-prey interactions in complex ecosystems such as the Chesapeake.



**Figure 13.** A conceptual description of two fish stocks ( $S_1$  and  $S_2$ ) linked through both biological and technical interactions. A predator-prey relationship is shown in which  $S_1$  preys upon the juveniles of  $S_2$ . Increased predation by  $S_1$ , therefore, leads to an increase in its growth rate and a decrease in the rate at which the juveniles of  $S_2$  are captured incidentally by the fishery that targets recruitment rate for  $S_2$ . Thus, an increase in the fishing mortality rate will again lead to a decrease in the recruitment rate for  $S_2$ . Adapted from Miller et al. (1996).

striped bass/blue crab/bivalve linkages.

Although such detailed linkages are difficult to evaluate and fully understand, they do reflect ecological reality; therefore, considering subsets of the food web remains important in developing and implementing ecosystem-based fisheries management.

- 4) Compare and contrast analyses of food web dynamics with food web

modeling.

This exercise entails a thorough and comprehensive comparison of the findings from food web analyses (i.e., topological, energy flow, functional) with those from modeling efforts, as described below.

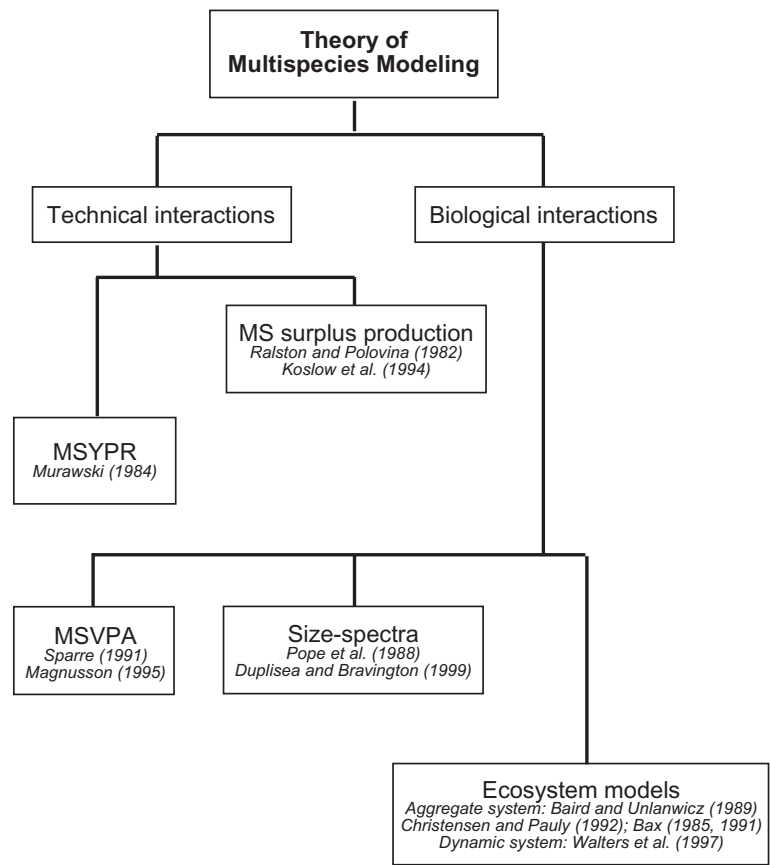
### Multispecies Modeling Approaches

Historically, fisheries management has relied on single-species models that ignored the effects of biological and technical interactions on population abundance (Figure 13). Traditional fisheries models focus on the interplay between exploitation level and sustainability, generally not considering in detail the biology and ecology of the managed species. In recent years, however, researchers have started to overcome this deficiency by considering the feasibility of ecosystem-based approaches to fisheries management. One important element of ecosystem-based management is development and incorporation of multispecies models into management programs. Like single-species models, multispecies models yield information about sustainability but are structured to do so by more accurately reflecting biological and ecological reality.

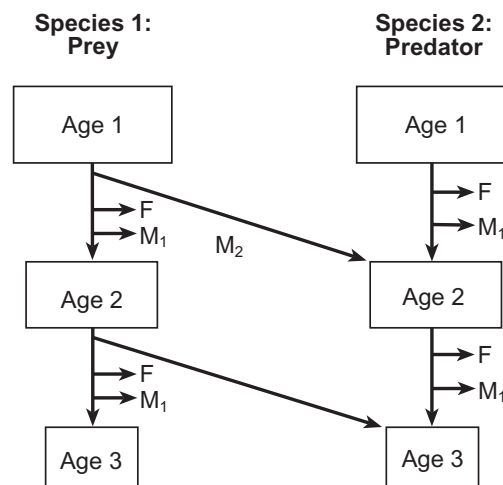
Over the past several years, the number and types of multispecies models that provide insight on fisheries issues have grown significantly (Hollowed et al. 2000). This growth has been fueled by the need to better inform fisheries policymakers and managers; however, recent concerns about fishing effects on the structure of ecosystems has also prompted

research on multispecies modeling and implied predator-prey relationships. From a theoretical perspective, basing fisheries stock assessments on multispecies (rather than single-species) models appears more appropriate, since multispecies approaches allow explicit modeling of more of the processes that govern population abundance. This increased realism, however, requires additional parameters (particularly for models that assess the impact of biological interactions), which in turn creates the need for more types of data. In the absence of these additional data, or if unreliable data are used to meet the requirements of multispecies stock assessments, more uncertainty in management outcomes will undoubtedly arise compared to single-species stock assessment methods. Consequently, multispecies models are not replacements for single-species models, but rather tools that provide additional types of stock assessment insight when used in concert with single-species models (National Research Council 1999).

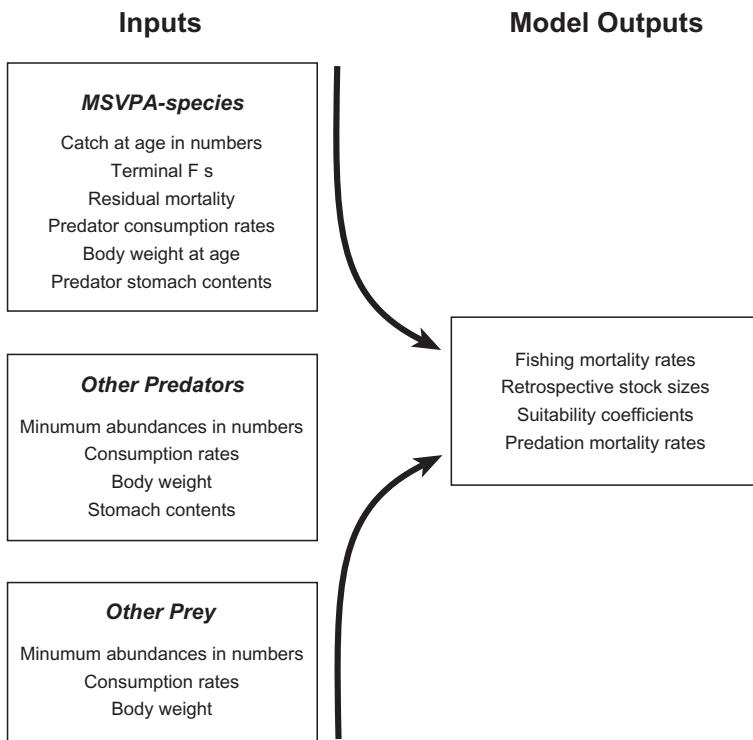
In recent years, interest has grown in multispecies fisheries management in the Chesapeake region, as evidenced by the development of fisheries steering groups, the convening of multispecies technical workshops (Miller et al. 1996; Houde et al. 1998), and the requirement for development and implementation of multispecies fisheries management plans by the *Chesapeake 2000* agreement (CBP 2000). In this section, we describe and evaluate some multispecies models commonly applied to understand the



**Figure 14.** General overview of multispecies fisheries models. Adapted from Hollowed et al. (2000).



**Figure 15.** General schematic of two-species MSVPA with arrows indicating losses due to fishing ( $F$ ), predation ( $M_2$ ), and residual ( $M_1$ ) mortality (Jennings et al. 2001).



**Figure 16.** Types of data needed to perform an MSVPA based on the role each species assumes in the analysis. “MSVPA-species” are those predators and prey for which retrospective stock sizes are reconstructed using the MSVPA model and “other predators” and “other prey” represent species for which VPA-type results are not desired, but the researchers know or surmise that these species significantly influence the trophic dynamics of the food web under study. From Latour et al. 2003.

effects of both biological and technical interactions; these models have potential for development and application in the Bay.

This overview should inform fisheries managers and policymakers about the capabilities of more commonly applied multispecies modeling techniques. For biological interactions, we review multispecies virtual population analysis (MSVPA), size spectrum analysis, and ecosystem models (Ecopath with Ecosim). For technical interactions, we review multispecies yield per recruit (MSYPR) and

multispecies surplus production models (Figure 14).

## Biological Interactions

### *Multispecies Virtual Population Analysis*

Single-species virtual population analysis (VPA), as developed by Fry (1949) and Gulland (1965), is a stock assessment technique that uses commercial-catch-at-age data to calculate retrospective stock sizes and fishing mortality rates ( $F$ ) of recruited, age-based cohorts. This approach often is referred to as cohort analysis. 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 from natural causes during that same time period. Inherent in this technique are two important features: each cohort is treated separately (i.e., the variables associated with a cohort are calculated independently of those from other cohorts); and an estimate of the natural mortality rate ( $M$ ) is required as input for the model. When  $M$  is not known, the traditional approach is to estimate it roughly from life history parameters or to use an educated guess.

The dependence of VPA on a reasonable estimate of  $M$  has motivated researchers to focus on natural mortality estimations. Although natural mortality occurs from various causes, predation is generally believed to be the dominant source of mortality. This belief, along with preliminary quantitative work on feeding and food consumption of

North Sea cod *Gadus morhua* (Daan 1973, 1975), provided the foundation for the development of models that accounted for species interactions. Anderson and Ursin (1977) developed an ecosystem model that gave a conceptual framework for modeling predator-prey interactions. Although this complex model could not adapt to real-world management applications, it ultimately facilitated the extension of VPA to multispecies virtual population analysis (MSVPA).

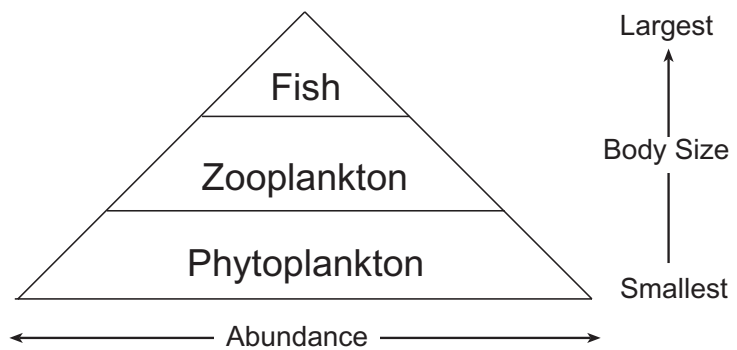
Helgason and Gislason (1979) and Pope (1979) independently combined the theoretical predation relationships of the Anderson and Ursin (1977) model with the VPA methodology of Gulland (1965) to develop MSVPA. The primary feature of the method is the split of the natural mortality rate into two components.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

$$M = M_1 + M_2 \quad (1)$$

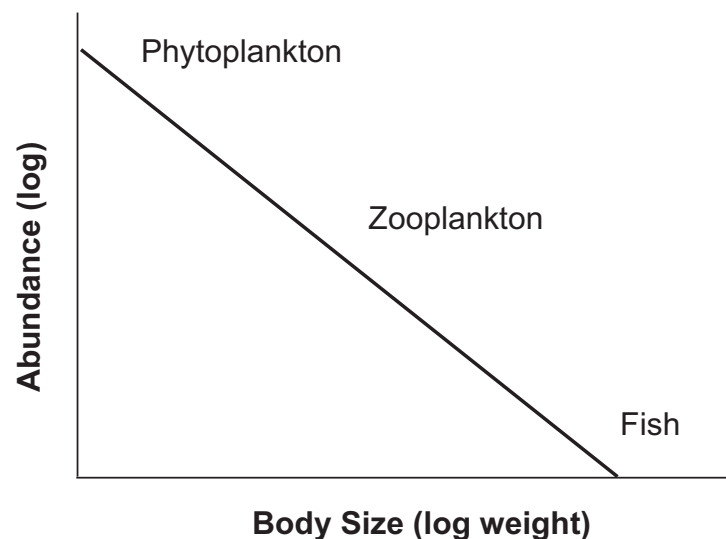
in which  $M_2$  represents the predation mortality between and within the exploited species in the ecosystem—as determined by suitability parameters that reflect predator preference for a particular prey species—and  $M_1$  represents the mortality due to all factors not explicitly included in the model (Figure 15). For a review of the MSVPA approach, see Sparre (1991), Magnusson (1995), and Jennings et al. (2001).

The data requirements for an MSVPA vary according to the role each species assumes in the model and the preferred model output (Figure 16). If species' stock sizes are reconstructed using the MSVPA model, with these species referred to as

“MSVPA-species,” the data requirements include catch-at-age in numbers, fishing mortality 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.



**Figure 17a.** Trophic pyramid relating the abundance of general species groups within an aquatic ecosystem. The width of the pyramid is proportional to abundance; the height is proportional to body size (Jennings et al. 2001). With biomass used as a metric rather than abundance, the pyramid would be greatly compressed with little difference among trophic levels (Sheldon et al. 1972; Kerr and Dickie 2001).



**Figure 17b.** Plot of normalized biomass (i.e., number density) as a function of body size. The slope of the line is a qualitative representation of the structure of an aquatic ecosystem (Jennings et al. 2001). As with Figure 17a, using biomass instead of abundance results in a “flat” slope, although a small negative slope sometimes occurs.

With MSVPA, modeling species as “other predators” or “other prey” is possible in cases for which the standard VPA results are not desired, but the researchers know or surmise that these species significantly influence the trophic dynamics of the food web under study. For “other predators,” data requirements include minimum abundances in numbers, body weights, consumption rates, and stomach contents; for “other prey” only minimum abundances in numbers and body weights are typically required.

#### *MSVPA in Chesapeake Bay*

To date, MSVPA has not been used for stock assessments of fish populations in Chesapeake Bay, although it is recognized as a possible approach (Miller et al. 1996; Houde et al. 1998). An expanded MSVPA model for assessment of the Atlantic menhaden stock in the coastal waters of the eastern United States is currently under development (Garrison and Link 2002) to supplement existing single-species assessments of the Atlantic menhaden stock and to allow fisheries managers to evaluate possible alternatives to the current management scenario. The MSVPA model addresses four major topics through evaluation of

- 1) The nature and magnitude of linkages among menhaden and its key predators;
- 2) The current use of menhaden as a directed fishery, its ecological role as a forage fish, and sustainability of the stock;
- 3) The possible optimal size (or age) composition of Atlantic menhaden

to support its ecological role as a prey species and the goals of the directed fishery; and

- 4) The biological reference points for menhaden recommended for management derived from single-species assessments along with determination of whether adjustments are necessary with predation included in the assessment.

Two major extensions to the base model also are being developed. First, a stochastic feeding model is being incorporated into the MSVPA framework to account for the effects of changes in menhaden population abundance on the diets and consumption patterns of predators. This model will require additional input data on the relative abundance of alternative prey species. Second, the growth and population dynamics of predators (striped bass, bluefish, and weakfish) will be modeled more explicitly to explore and evaluate the effects, if any, of prey quality. This extension will incorporate the effects of prey availability, diet composition, and feeding rates.

In recent years, fishing effort on menhaden has shifted from northerly waters to southern areas; as a result, the Chesapeake Bay has become a center of menhaden fishing. Although recent coastwide stock assessments have characterized the menhaden stock as healthy, concern exists that this characterization does not apply to menhaden in the Bay. Recruitment of Bay menhaden has declined since the 1990s and young-of-year abundance has been low. Low menhaden abun-

dance may cause nutritional stress in predators, such as striped bass. Recent studies suggest that striped bass in the Bay suffer from poor nutrition, evidenced by an increase in the number of diseased fish exhibiting lesions from mycobacteriosis. The Maryland Department of Natural Resources (MD DNR) Pound Net Survey (2002) revealed that 17% of the striped bass had lesions or sores.

The MSVPA analysis of menhaden represents one of the first multispecies modeling efforts of a fish species indigenous to Chesapeake Bay (discussed later is another modeling effort—the Chesapeake Bay Ecopath with Ecosim model). The MSVPA will document quantitatively the simultaneous effects of predation and fishing on the menhaden stock. Although best interpreted on a coastwide scale, these results should provide information to better evaluate the role of menhaden as a forage fish in the Bay. An MSVPA analysis reflecting Bay-specific input data for menhaden, striped bass, bluefish, and weakfish would provide additional insight into management of these species.

### **Size-spectrum Analysis**

A fundamental characteristic of aquatic food webs is conservation of mass through energy conservation via production, respiration, growth, and predation (Jennings et al. 2001). Body size determines these processes, leading to trophic pyramids with the smallest species at the bottom and the largest species on top (Figure 17a).

By turning this pyramid on its side, a

plot results that linearly relates log numbers (or production) to log body size (Figure 17b). Based on the aforementioned law of conservation, perturbations to the ecosystem via removals will cause a change in the line slope. In theory, therefore, it is possible to detect and interpret changes in the structure of an exploited ecosystem by comparing slopes of biomass or abundance (i.e., normalized biomass) in relation to body size. This approach is formally known as size-spectrum analysis.

Size-spectrum analysis has since been adapted and applied in ecological studies ranging from characterization of marine benthic invertebrate assemblages (Schwinghammer 1981, 1983; Saiz-Salinas and Ramos 1999) to harvesting strategies and community structure of fish populations (Pope et al. 1988; Macpherson and Gordoia 1996; Duplisea and Bravington 1999; Kerr and Dickie 2001). Researchers have also used the results of a size-spectrum model (e.g., quadratic regression equations depicting the major biomass domes in a particular ecosystem [Thiebaut and Dickie 1993]) to develop estimates of annual production for the taxonomic groups represented by these domes. The study by Sprules and Goyke (1994) represents a specific example of this application, in which the researchers computed an estimate of annual production for zooplankton in Lake Ontario. Sprules et al. (1991) show that examining the complete biomass size spectrum is possible; they described the pelagic biomass size spectrum including phytoplankton, zooplankton, planktivorous fish, and

piscivorous fish from nine major regions of Lake Michigan in both spring and summer and also estimated the potential annual production of several trophic groups.

Within fisheries, the use of spectral methods has rarely been applied when developing management strategies. One exception is the recent study by Duplisea and Bravington (1999) in which they used spectra models to explore the implications of different harvesting strategies on total yields and community stability and persistence in marine ecosystems. Their analysis indicated potential for application of the method, but counterintuitive fishing strategies emerged for some harvesting questions in a few instances. For example, one might expect that the best strategy for maximizing total yield would specify the harvest of fish at lower trophic levels (i.e., remove biomass from the system by fishing before it is lost to predation up the food chain). Duplisea and Bravington (1999) showed, however, that total yield would be maximized if larger fish were exploited preferentially (i.e., intentionally fishing the larger fish in the ecosystem), since this strategy reduces predation on smaller fish and, therefore, increases their production. Although other researchers within the ICES community have explored the size-spectrum approach as an option for fisheries and ecosystem management (Rice and Gislason 1996; Gislason and Rice 1998; Jennings et al. 2002), additional research is needed to fully characterize its potential.

### *Size-spectra in Chesapeake Bay*

Researchers have not yet used size-spectra analyses and models to develop management strategies for Chesapeake fish. Recently, however, Jung (2002) conducted biomass size-spectrum analyses using midwater trawl catch data to estimate biomass, production, contribution to predators, and recruitment numbers (young of year) for forage fish (primarily bay anchovy). Jung also included analyses of higher trophic-level pelagic and benthopelagic fishes, some of which are piscivores (e.g., weakfish) in the Bay. Jung's analysis indicated that annual, seasonal, and regional differences in size spectra occur in response to changing environmental conditions and these environmental conditions primarily affected recruitment and young of year biomass production. The results may prove useful in development of biomass spectrum models that address fishery management issues.

Multispecies fisheries management is designed, by definition, to incorporate ecosystem processes into management plans. Knowledge of the magnitude of predation on bay anchovy and other forage fish is important, therefore, if multispecies plans for these predator species (e.g., bluefish, weakfish, striped bass) are developed.

### **Ecosystem Models**

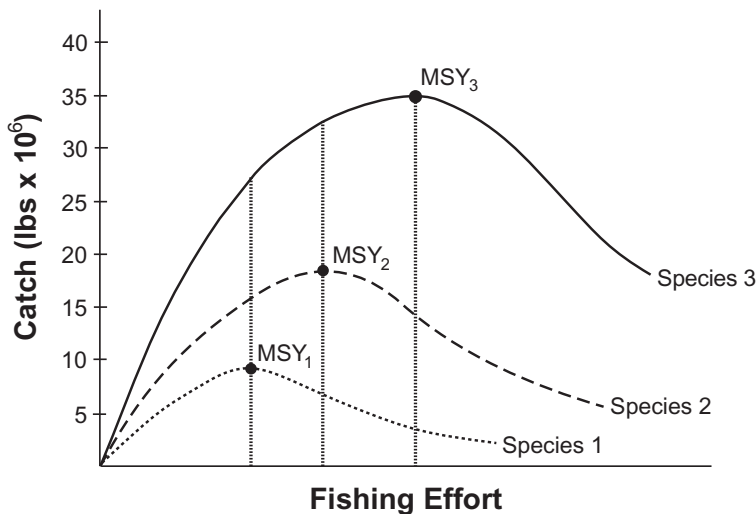
Ecosystem models form another approach to characterize biological interactions in multispecies fisheries. In effect, these models are mathematical representations of whole ecosystems, typically used to elucidate the

**Table 2.** A subset of the potential policy questions motivated by the *Chesapeake 2000* agreement prioritized into the present (P), the near future (NF), and the longer-term future (LTF) based upon the Chesapeake Bay EwE model's ability to address each issue.

Policy Issue	P	NF	LTF
1. How can we bring back oysters tenfold and what are the consequences?	X		
2. How can we increase populations of crabs through predator manipulation or fishery reductions?	X		
3. How many striped bass can Chesapeake Bay support; is game fish restoration prudent given low stocks of forage fish?	X		
4. What are the effects of forage fish in Chesapeake Bay ecosystem dynamics?	X		
5. What defines a healthy Chesapeake Bay or what are trophic limits to production?	X		
6. How might changes in primary productivity affect upper trophic levels?		X	
7. How could SAV be restored and what trophic effects might occur?		X	
8. Can we assess the effectiveness of closed/protected areas?		X	
9. How might land management practices affect the estuarine food web?			X
10. Can we manipulate freshwater input to increase oyster survival?			X
11. How should we fish menhaden for optimal ecosystem function?			X

effects of fishing pressure on the system. Although many of these models are extremely quantitative and employ sophisticated mathematical theory, researchers have used the models primarily for policy exploration and the models have yielded results best interpreted qualitatively. As such, ecosystem models can serve a useful purpose in developing management strategies. Using these models for tactical applications is difficult, however, because accurate parameterization

depends on the availability of demographic data for ecologically valuable species (as opposed to species that are commercially or recreationally valuable); such data are often unavailable. This limitation is important. Nevertheless, in recent years ecosystem models have received increasing attention from fisheries researchers and managers who used them successfully to summarize knowledge and determine properties related to structure and function of aquatic ecosystems worldwide.



**Figure 18.** A hypothetical graph showing a three-species fishery in which all species are caught in the same fishing gear. The productivity of each species differs, leading to different levels of maximum sustainable yield (MSY). The fishing effort (i.e., levels of fishing mortality,  $F$ ) that yields the respective MSYs also differs for the three species. To illustrate the importance of technical interactions, suppose that the multispecies fishery exerts a fishing effort that leads to a mortality rate of  $F_3$ . Fishing at  $F_3$  will cause the abundance of species 1 and 2 to decline to a level at which substantial risk of stock collapse exists. From a fisheries management perspective, reducing fishing effort to either  $F_1$  or  $F_2$  to lower the risk of collapse is desirable. This management strategy is fairly obvious given the graph above; however, independent examination of catch/effort data for each species might not yield as certain a conclusion. Adapted from Houde et al. (1998).

One widely used class of ecosystem models is that which packages Ecopath with Ecosim (EwE) and Ecospace (Christensen et al. 2000). 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 that represent an ecological guild. Researchers can also split them into ontogenetic age or size categories (juvenile, subadult, adult, etc.) if necessary. The data requirements for Ecopath are fairly simple and often obtainable from traditional single-species analytical stock assessment techniques (e.g., VPA). The parameterization of an Ecopath model rests on the satisfaction of two master equations. Equation 2 (below) describes how the biomass production for each group is allocated within the ecosystem over an arbitrary time period term. Using the principle of conservation of matter within a group, equation 3 (below) balances the energy flows of a biomass pool.

$$\text{Production} = \text{catch} + \text{predation} + \text{net migration} + \text{biomass accumulation} + \text{other mortality} \quad (2)$$

$$\text{Consumption} = \text{production} + \text{respiration} + \text{unassimilated food} \quad (3)$$

In general, an Ecopath model requires input of three of the following four parameters: biomass, total mortality, consumption and biomass ratio, and ecotrophic efficiency for each species or biomass pool in a model. The ecotrophic efficiency represents the proportion of the production used in the ecosystem, incorporating all production terms apart from “other mortality” (for more details on Ecopath, including the equations, see Christensen and Pauly 1992; Walters et al. 1997; Pauly et al. 2000).

Although Ecopath can describe an ecosystem, it cannot project the

effects of different management strategies on the structure and function of an ecosystem. Only Ecosim—a time-dynamic simulation module that facilitates policy exploration—can accomplish these types of projections. Ecosim re-expresses the static mass-balanced equations inherent to Ecopath as a system of coupled differential equations (Walters et al. 1997). This system of equations represents the spatially aggregated dynamics of entire ecosystems and is combined with delay-difference, age- and size-structured equations to represent populations with complex ontogenies and selective harvesting of older animals. Summarized, the important computational aspects of Ecosim are

- 1) Parameter estimation based on the mass-balance results from Ecopath;
- 2) Variable speed-splitting methods to simulate the dynamics of both fast (e.g., phytoplankton) and slow (e.g., large predatory fish) biomass groups;
- 3) Explicit incorporation of top-down (i.e., predation) vs. bottom-up control (i.e., food limitation); and
- 4) Flexibility to incorporate age- and size-structure of biomass groups.

One obvious deficiency of EwE is its assumption that the resources, interactions, and subsequent dynamics of an ecosystem are spatially homogeneous. Ecospace—a dynamic spatial version of Ecopath that includes all of the key features of Ecosim—overcomes this deficiency. The details of Ecospace are not presented here, but Walters et al. (1999) and Pauly et al. (2000)

thoroughly describe them. Researchers have formulated several EwE models and used them for policy exploration. Trites et al. (1999) developed an EwE model of the Bering Sea to examine possible explanations for the changes that occurred in the ecosystem between the 1950s and 1980s. Kitchell et al. (1999) used the EwE approach to study the effects of fishing down top predators in the central Pacific. Shannon et al. (2000) used EwE to compare the effects of fishing in the southern Benguela upwelling system under different combinations of bottom-up and top-down control. On a larger scale, Stevens et al. (2000) summarized the direct effects of fishing on chondrichthyans by examining global information on the responses of shark and ray populations to fisheries. They developed Ecosim models of three previously published Ecopath models to simulate changes in biomass of all groups in response to the rapid declines of shark species.

#### *EwE in Chesapeake Bay*

In 2001, the NOAA Chesapeake Bay Office (NCBO), in collaboration with the University of British Columbia (UBC), initiated a workshop series to provide the foundation for construction of an EwE model of Chesapeake Bay. Researchers are developing a large-scale model (~50 species/functional groups) to serve as a “base” and “continuously living” model for future fisheries policy exploration (Table 2).

#### **Technical Interactions**

Although technical interactions are not inherent to food web dynamics,

they are important and relevant to the topic of multispecies fisheries management (Figure 18 provides a detailed description of technical interactions).

### **Multispecies Yield-per-Recruit**

Managers can use single-species yield-per-recruit (SSYPR) models to determine fishing mortality rates that achieve optimal trade-off between the size of the individuals harvested and the number of individuals available for capture. If fishing mortality is too high, then yield will not be optimal since too many individuals will be harvested before having a chance to grow. Conversely, if fishing mortality is too low, the yield will also not be optimal because not enough individuals will be harvested (even though each individual will be large when captured).

Conducting an SSYPR analysis requires an estimate or assumed value for the natural mortality rate, information on growth in weight, and data on selectivity (i.e., age or size at recruitment). Such models generally assume that recruitment—and hence the age-structure of the population—are constant over time and that fishing and natural mortality remain constant once the fish become vulnerable to fishing gear. These assumptions are important and their violation may have adverse effects on model performance; however, practical application of an SSYPR model usually characterizes the effects of different ages at first capture and

varying rates of fishing mortality.

Fishing gear (e.g., trawls, gill nets) used to exploit fish populations are somewhat indiscriminant. If several fish species occupy the same geographic location at a particular time, these fish may be captured in proportion to their relative abundance, subject to the selectivity of the gear. The overall fishing mortality rates of the different species captured can then be interpreted as a function of gear selectivity and culling practices. Typically, the highest  $F$  values are associated with the target species (and size classes); a gradient of  $F$  values that depends on selectivity and post-capture survival (assuming it is not uniform) is associated with bycatch or discarded species.

Researchers use multispecies yield-per-recruit (MSYPR) models to study situations in which several stocks are simultaneously exploited by a single fishing gear. The calculations associated with the approach follow those of single-species models except that the results are summed over all species (see Murawski 1984 for a detailed description of the equations associated with MSYPR). Given this summation, researchers can simulate various regulatory scenarios that reflect different levels of total fishing effort (and thus  $F$  values) and the selectivity of different gear types.

Using MSYPR, it is also possible to accommodate a situation in which several independent fisheries harvest one or more species and stocks (e.g., exposure to multiple fisheries due to seasonal migrations; the use of differ-

ent gear types). In this instance, the fishing mortality rates for each species/stock must be adjusted to reflect the relative contribution by each fishery (see Murawski 1984 for details).

### *Multispecies Yield-per-recruit in Chesapeake Bay*

To date, researchers have not used MSYPR models to study the effects of technical interactions in Chesapeake Bay. Several types of fishing gear have been used historically to harvest several fish species in the Bay simultaneously—most notably pound nets and haul seines (Chittenden 1989). Species typically captured in pound nets and haul seines include striped bass, Atlantic croaker, Atlantic menhaden, and weakfish, making these species candidates for an MSYPR analysis. The results of any MSYPR analysis should be interpreted cautiously, however, since a reasonable risk exists that the assumptions inherent to the model will be violated. As such, characterizing the potential for and effects of assumption violation should become an important component in any MSYPR analysis of Chesapeake Bay fisheries.

### **Multispecies Surplus Production**

Single-species surplus production (SSP) models are typically used to identify the rates of fishing mortality that generate sustainable yields—including the maximum sustainable yield (MSY)—given a population's rate of growth in terms of changes in biomass over time. Due to their simplicity and relatively modest data

requirements (catch and fishing effort), SSP models generally provide a starting point for fisheries stock assessments. The general surplus production model in discrete time takes the form:

$$B_{t+1} = B_t + f(B_t) - Y_t \quad (4)$$

in which  $B_t$  represents the exploitable biomass of a particular species at time  $t$ ;  $f(B_t)$  is a general function describing surplus production (often assumed to be the difference between production and natural mortality) as a function of biomass at time  $t$ ; and  $Y_t$  is the yield to the fishery at time  $t$ .

Schaefer (1954) formulated the first widely used equation for  $f(B)$  from earlier research by Graham (1935). An application of the classical logistic equation for population growth, the Schaefer model is relatively simple and yields a symmetric relationship between surplus production ( $dB/dt$ ) and biomass. Pella and Tomlinson (1969) proposed a generalized extension of the Schaefer model to alleviate the inherent requirement of having a symmetrical relationship between surplus production and biomass. Studies of surplus production related to stock size have shown that non-symmetrical relationships often exist, implying that use of this generalized model may prove desirable.

One of two general modeling strategies is possible when extending the production model approach to estimate multiple stocks production in a multispecies fishery. The first—a temporal multispecies production (TMP) model—evaluates production by applying a single-species model

using the assumption that multispecies fisheries behave as a single-species stock. The term “temporal” is used to define this approach because the production analysis is usually based on combined time series of catch-and-effort data for all species under consideration (i.e., the parameters of  $f(B)$  are estimated from that time-series data). Ralston and Polovina (1982) used this approach to investigate the total production of 13 demersal fish species from the Hawaiian archipelago. In general, they concluded that the approach could prove useful for production analysis in a multispecies fishery.

The second modeling strategy evaluates production over space rather than time. A spatial multispecies production (SMP) model treats the various locations within the total fished area (e.g., islands, reefs) as replicate fisheries and assumes the production from each location is the same (i.e., the parameters of  $f(B)$  are estimated from spatial fisheries data). The assumption remains that the spatially explicit fisheries are in equilibrium. As with the SSP and TMP models, the results of an SMP analysis become unreliable if this assumption is violated.

Koslow et al. (1994) used this approach to study two Caribbean reef fisheries in southern Jamaica and Belize, concluding that SMP models should be used with caution in reef fisheries management due to the high probability of assumption violation. Specifically, Koslow and others noted the nonequilibrium

condition of the fisheries, the heterogeneous mix of species both within and between Jamaica and Belize, the diversity of fisheries targeting various spawning, sedentary, and migratory fish, and the possible differences in productivity among sites as factors contributing to the limited success of the analysis.

#### *Multispecies Surplus Production in Chesapeake Bay*

To date, TMP and SMP models have not been used to develop management strategies for Bay fish. The modest data requirements of these models relative to other multispecies modeling approaches, however, imply some fairly immediate possibilities for development. Since watermen have used pound nets and haul seines to harvest several fish species in the Bay, development of both TMP and SMP models could utilize landings data from these gears. Importantly, the MSY of the species complex in a multispecies production model is not simply the sum of the MSYs of the individual species.

#### **Modeling Summary**

We have reviewed five valuable approaches for investigating various multispecies fisheries questions. Specifically, we considered MSVPA, size-spectra, and EwE models to evaluate the effects of biological interactions, as well as MSYPR and multispecies production models to make inferences about technical interactions. In addition to the techniques described here, other modeling techniques have proved useful in evaluating impacts on marine

communities. Hollowed et al. (2000) reviewed a larger body of multispecies models and described their strengths and weaknesses (as compared to single-species models) in determining the causal mechanisms responsible for shifts in marine ecosystem production. A brief summary of their general conclusions follows.

Hollowed et al. (2000) concluded that multispecies models have a distinct advantage over single-species models since they depict natural mortality and growth rates more realistically. An exception to this lies in the use of single-species models for short-term predictions of large fish species, as trends in predation mortality are not often immediately obvious. With respect to their ability to generate reliable long-term predictions, multispecies models are a work in progress primarily because of their sometimes strong sensitivity to parameter estimates and assumptions about recruitment. Additionally, multispecies models may have the potential to describe the indirect effects of fishing on individual species. Until they are more fully tested and validated, however, relying on general rather than specific model predictions (i.e., qualitative rather than quantitative results) seems more prudent. Undoubtedly, multispecies models that incorporate biological interactions have improved our understanding of fish population dynamics. In some cases, lessons learned from these models have even led to improvements in the single-species models used to characterize the fishing impact on individual species.

## Major Findings

### *Food Web*

The Chesapeake Bay food web has undergone significant historical alterations, primarily due to anthropogenic influences such as eutrophication, overfishing, and habitat degradation over the past three centuries. Eutrophication may drive bottom-up control of food web dynamics, whereas fishing upon top predators likely dominates top-down control.

Food web interactions—the outcome of predator–prey relationships—can have dramatic and substantial effects on the ecosystem’s community structure, including productivity of species supporting important fisheries. The form and magnitude of the effects from altering food web interactions are somewhat unpredictable, both in form and magnitude, due to the high connectivity within and between the benthic and planktonic components of the Chesapeake Bay food web. Connectivity among the food web components must be better understood to avoid individual and aggregate population collapses or extinctions of Bay species.

Major links between and within benthic and planktonic components of the Chesapeake food web include Atlantic menhaden, Atlantic croaker, bay anchovy, blue crab, forage fish (e.g., bay anchovy), spot, and Atlantic croaker. Researchers have only identified a few keystone (e.g., blue crab) or dominant (e.g., oyster) species in Chesapeake Bay. Further research must identify such species as they may

exercise control over community structure and productivity out of proportion to their abundance and dominant species may be the major contributors to energy flow and biomass production in aquatic ecosystems.

Some food web interactions that are not normally regarded as predator-prey or consumer-prey interactions may be consequential in the food web and population dynamics of key species (e.g., disease in oyster, bycatch mortality for endangered or threatened sea turtles and birds of prey).

### *Modeling*

The five modeling approaches reviewed in this element may prove useful in addressing many multispecies fisheries questions. Specifically, MSVPA, size-spectra, and EwE models can evaluate the effects of biological interactions; MSYPR and multispecies production models can make inferences about technical interactions.

In addition to models described here, other modeling techniques could be used to evaluate the impacts on marine communities. Hollowed et al. (2000) reviewed a larger body of multispecies models and described their strengths and weaknesses (as compared to single-species models) for determining the causal mechanisms that induce production shifts in marine ecosystems.

Hollowed et al. (2000) concluded that multispecies models have a distinct advantage over single-species models

in that they depict natural mortality and growth rates more realistically.

An exception lies in the use of single-species models for short-term predictions of growth and mortality in large fish species in which trends in predation mortality are not always obvious. Regarding reliable long-term predictions, multispecies models should be considered works in progress due to their strong sensitivity to parameter estimates and assumptions about recruitment. In addition, multispecies models may have the potential to describe the indirect effects of fishing on individual species quantitatively. Until these models are more fully tested and validated, however, relying on qualitative rather than specific model predictions remains prudent.

Multispecies models that incorporate biological interactions have improved our understanding of fish population dynamics. In some cases, the lessons learned from these models have led to improvements in the single-species models used to characterize the impact of fishing on individual species.

## **Panel Recommendations**

### *Management*

- 1) Develop life cycle diagrams and food webs for target species; use them to define important food web linkages and validate food web models.

Identify the major predator-prey interactions, including all significant sources of food and mortality without ignoring atypical sources (e.g., disease, bycatch) and noncommercial species.

Document beneficial aspects of food web interactions, such as the potential benefits of bycatch as food for endangered, threatened, and overexploited species (e.g., sea turtles). Consider vital prey species that potentially are affected by increases in the abundance of the target species. In examining food web interactions of the target species, explore the likelihood that food web (energy transfer) approaches may fail to identify dynamically important linkages (e.g., trophic cascades and keystone species).

2) Distinguish between anthropogenic and natural processes that affect water and habitat quality and thus trophic interactions, such as pollution effects on water quality, watershed influences, hydrodynamics, and variation in environmental processes.

Both anthropogenic and natural causes—or some combination of the two—can alter food web dynamics. It is important to recognize the causes of variability before undertaking management actions intended to either shift the balance among predator and prey species or promote the productivity of prey resources by appropriate controls of fishing on target species.

3) Use multiple models and varying data sources to explore the Chesapeake Bay ecosystem and the ways in which fishing may affect the food web dynamics and production of target species.

Each modeling approach may serve a unique purpose. Run alternative food web models (e.g., Ecopath with

Ecosim) when developing FMPs to understand linkages between food webs, fish habitat, environmental changes, and fisheries production. To detect robust responses to changes in target species abundance, develop several models within each class of food web model (e.g., multispecies stock assessments, ecosystem models), when possible, to facilitate model comparison.

#### *Needed Research and Development*

4) Conduct field investigations to determine and quantify major predator–prey interactions and significant sources of food and mortality.

Predator–prey dynamics are at the heart of interactions among species that affect abundance and production. Such interactions have dramatic and substantial effects on community structure and may influence the yields of Bay fisheries. At present, managers can use the fundamental knowledge of food web structure in a precautionary manner, but major research must proceed to ensure that multispecies fisheries management in the Bay is confidently implemented.

5) Conduct modeling and field investigations to determine food web (energy transfer) approaches to identify and quantify the effects of dynamically important linkages (e.g., trophic cascades and keystone species).

Do trophic cascades and keystone species exist in Chesapeake Bay? Evaluate existing Bay-area fishery-independent and fishery-dependent databases as sources for inputs to

multispecies models. Integrate these databases to reflect a baywide scale.

- 6) Investigate the connectivity among components of the food web to better understand and avoid the risk of individual or aggregate extirpation of Chesapeake Bay species.

The form and magnitude of effects of alterations in food web interactions are somewhat unpredictable due to the high degree of connectivity within and between the benthic and planktonic components of the Chesapeake Bay food web.

- 7) Investigate anthropogenic (e.g., hypoxia) and natural (e.g., climate and weather) processes that affect water or habitat quality and, therefore, trophic interactions.

Understanding how natural processes control or destabilize food web relationships (in addition to fishing effects) is important. Research on variability in food consumption by target species, in relation to environmental factors and under varying environmental conditions, will help address this issue.

- 8) Compare and contrast the various modeling approaches of food web dynamics. Several modeling approaches (e.g., EcoPath and EcoSpace, multispecies virtual population analysis) are available to address food web dynamics. Researchers should apply and evaluate more than one model concurrently.

Testing and comparing modeling approaches to assess model performance and to understand the

causes of differences in model results remain important. Thorough comparative modeling research will lead to rigorous and robust model applications for evaluating food web relationships.

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