One of the goals of fishery management is to sustain fisheries of individual exploited species. A key to developing ecosystem approaches to management is to extend this goal to ecosystem sustainability by focusing on sustaining relationships between species (including humans) within complex adaptive ecosystems that are robust to random disturbance and yet prone to rapid, irreversible state changes under certain conditions. In this summary of research supported by the AFSC Status of Stocks and Multispecies Assessment Program, we review the history of commercial exploitation in the Gulf of Alaska from 1740 through the present day within the context of ecosystem sustainability. Further, we describe the development of quantitative ecosystem models that were developed for fisheries management in the GOA using two approaches: 1) a food web approach with dynamic equations describing predator-prey interactions as has been applied in many other fished marine ecosystems, and 2) a complex systems modeling approach that has been applied in many biological, social, and physical systems, but has not yet been applied in fished marine ecosystems.

Using the food web approach, we identify and classify relationships between fisheries and fished species in the GOA food web, and dynamic relationships between predator-prey interactions, fishing, and climate change over the history of commercial exploitation. Using the complex systems approach, we identify both static and dynamic sources of robustness in the GOA ecosystem and also potential ecosystem thresholds where the state of the ecosystem is prone to rapid change. Some potential thresholds relate to the network properties of food web structure, while other thresholds relate to fishing intensity interacting with dynamic predator-prey functional responses in the ecosystem. Combining these and other modeling approaches with a realistic accounting of uncertainty can support fishery sustainability in the ecosystem context, allowing managers to consider relationships and to operate within both single-species and ecosystem-level thresholds.

Ecosystem sustainability

Ecosystems have been viewed on one extreme as purely chaotic, untamed nature, and on the other extreme as purely physical systems with predictable equilibrium states. A developing concept of ecosystems as complex adaptive systems lies between these extremes; the ecosystem as a complex adaptive system has behavior which is recognizably patterned and yet not fully predictable. Seeing the ecosystem as a complex adaptive system provides necessary balance—neither extreme concept of nature as pure chaos or as a controllable machine is useful or realistic for ecosystem-based management.

Sustainability has been defined and redefined—culturally, mathematically, and legally—as humans have exploited and often depleted desirable natural resources. We suggest that the most powerful union of ecosystem and sustainability combines understanding of the defining characteristics of complex adaptive systems with the objective of identifying and sustaining healthy relationships within and between the interconnected spheres of ecosystem, economy, and society. To promote sustainability via ecosystem-based management, we need to identify vital relationships in a marine ecosystem. Then we need to determine a range of policy options that protect the infrastructure of relationships so that adaptive capacity is maintained for the future. Both the ecosystem and the economy depend on it.

GOA exploitation history: 1740-2005

There are three major periods where ecology, economy, and society interact in the GOA commercial fishery exploitation history: Russian colonial (1741-1867), American colonial (1868-1958), and Alaska statehood (1959-present). The Russian colonial period was characterized by heavy sea otter
and fur seal exploitation, with an offshore fishery by Americans for right whales. This early exploitation had devastating effects on the hunted populations (and on Native Alaskans, as well). Otter, seal, and whale hunting from shore stations continued under American colonial rule while new fisheries for salmon, herring, and halibut developed. Soon after Alaskan statehood, large-scale offshore whaling and fishing commenced by foreign nations, resulting in the largest biomass removals ever recorded during the 1960s: 1.7 million metric tons (t) of whales and 1.3 million t of Pacific ocean perch, along with a combined 1.1 million t of halibut, herring, salmon, crabs, and shrimp. During statehood there were also significant fisheries milestones: the Fishery Conservation and Management Act of 1977 extended U.S. management jurisdiction out to 200 miles past the coastline, with the full domestication of offshore groundfish fisheries in 1990. After 1977, whaling had effectively ceased, and fisheries were dominated by groundfish and salmon catches.

In viewing the exploitation history of the GOA (Fig. 1) within the context of ecosystem sustainability, we see emergent patterns of economic, social, and biological relationships, and a general lack of fit to the classical idea that ecosystems (or fisheries, or economies) are controllable machines. We see a series of exploitative waves with similar characteristics but applied to different components of the ecosystem. With each historical period, the cumulative exploitative waves actually crest higher, with different combinations of species compared with previous eras. These patterns suggest the international exploitation by distant water fleets, displaced workers sending money back home, product (furs, whale oil, baleen, canned salmon, herring meal, fresh dressed halibut, frozen groundfish) leaving the area. The process is to extract product, then export earnings.

Throughout history, heavy exploitation has been a direct cause of stock decline. This has been proven repeatedly in fisheries and other resource management case histories. Stopping exploitation, however, has not necessarily brought stock recovery. Historically, regulation by national governments was generally too little and too late to ensure the sustainability of any of the early territorial fisheries. Fisheries sustainability was enforced only by economics, such as the expense and difficulty of operating in remote Alaska. Improved technology and organized capital investment increased exploitative capacity and often led to rapid depletion of fish and mammal populations; in some cases, ending exploitation before regulation took place (e.g., shore-based whaling). Importantly for sustainability in the ecosystem context, it seems clear from this history that allowing simple economics to regulate exploitation is damaging to both the resource and the economy. For example, in the early 20th century the Pacific salmon fisheries, a powerful industrial monopoly with a powerful lobby, managed itself into a resource disaster in the quest for increasing profits and decreased competition. More recently, the Pacific ocean perch fishery of the early 1960s occurred prior to modern fishery regulations and severely overfished the population, forcing fleets to move on to different species. The Pacific ocean perch stock, while now considered healthy, has never recovered to pre-1960s population levels. In the classical theory of fishery management, changes in fishing effort control populations, so depletion and recovery are expected and predictable. However, in the theory of an ecosystem as a complex adaptive system, there is no central source of control. Equilibrium is not the default state and reversibility is not guaranteed.

The relationship of fishing with a marine ecosystem, however, can be characterized beyond the immediate and obvious removal of fish in trade for money. Static and dynamic food web models are valuable tools to perform systematic analysis of hypotheses for the various relationships of fishing, climate, and feeding ecology in the GOA.

**Standard food web models**

We built a static mass balance ecosystem model of the GOA using algorithms based on Ecopath methodology to evaluate relationships between species and how they affect mortality and production. The GOA food web model (Fig. 2) includes area- and time-specific production and consumption parameters based on research surveys and single species stock assessments that characterized the state of the system in the early 1990s. It also includes explicit juvenile groups for major groundfish and pinniped species and substantial taxonomic detail for benthic, pelagic, bird, and marine mammal groups. Here, we present food web modeling results for four case study species: Pacific halibut, longnose skates, walleye pollock, and squids. We use the food web model to present species relationships, evaluate roles as predators or prey, and evaluate fishing mortality relative to predation mortality to deter-
amine the extent of potential control of mortality by fishery managers.

Food web modeling expands the conventional view of a fishery and its direct effect on the population of its target species by picturing fisheries as predators within the ecosystem. In the food web context, the halibut longline fishery is clearly the apex predator in the GOA, and the pollock trawl fishery is also a high trophic level (TL) predator (Fig. 2). The halibut longline fishery represents the largest single source of mortality for both halibut and an incidental catch species, the longnose skate (Fig. 3). Both halibut and longnose skates are high TL predators themselves, with few natural predators, so fishing mortality is a larger component of the total explained mortality than predation mortality. However, the high volume pollock fishery causes relatively little of the lower TL pollock’s total

Figure 1. Commercial exploitation of fourteen species groups in the Gulf of Alaska, 1750 – 2000, in tons removed (top panel) and in percentage of total tons removed (lower panel). Exploitation waves start with sea otters and fur seals, switch briefly to salt cod, and then move to salmon when canning technology reached Alaska in 1880. Herring and halibut waves followed simultaneously, while whale catch peaked in the 1960s along with rockfish. The crabs and shrimp wave peaked and receded in the 1980s; the current exploitation wave rides the groundfish complex along with a resurgence of salmon.
Figure 2. Visual representation of the GOA food web in the early 1990s. Boxes are labeled with an abbreviated group name representing each modeled species or functional group, and box size is proportional to the biomass of that group. Species groups are arranged vertically by trophic level (TL, y axis) and horizontally by rough association with benthic (left) or pelagic (right) energy flow pathways. Pathways between each group are represented by gray lines, with line width proportional to the size of annual biomass flow.
mortality (Fig. 3). Further, despite being responsible for the largest bycatch of squid of any GOA fishery, the pollock trawl fishery contributes an insignificant portion of squids' estimated total mortality in the GOA (Fig. 3). These food web derived comparisons of trophic level and the relative contributions of fishing and predation mortality to total mortality may help prioritize management efforts to control fishing mortality where it matters most (i.e., high TL commercial and nontarget species) and allow consideration of alternative strategies where changing fishing mortality may not contribute greatly to changes in total mortality (predation-dominated commercial and nontarget species).

Examining the food web relationships of commercially important species enhances single species management in at least two ways. First, an understanding of food web relationships for a fished species suggests potential sources of variability in mortality and production not currently accounted for in single species stock assessments. Second, any strong relationships between fished species identified by food web modeling may imply that separately managed species might benefit from more coordinated management. For a fished predator species such as halibut, food web modeling generally supports the single species stock assessment assumption of constant natural mortality, because halibut have few natural predators and the majority of explained halibut mortality is from fishing. However, the diet composition of halibut reveals a dependence on a single prey item, pollock (Fig. 4), which has a declining population in the GOA. This implies that future halibut production might be negatively affected by dependence on pollock, an idea which cannot be addressed using single species population modeling. While halibut biomass has remained high over the course of the 1990s, a dramatic reduction in halibut weight-at-age has been observed in recent years. This decline in production was attributed to a climate regime shift. The GOA food web model suggests that this change in halibut production might be related to halibut's observed dependence on declining pollock. The static food web cannot display diet changes over time, but it can suggest that halibut be monitored for diet shifts to alternative prey or additional changes in production if pollock continue to decline.

Figure 3. Comparison of mortality sources for Pacific halibut (upper left), longnose skates (upper right), walleye pollock (lower left), and squids (lower right) as estimated from the GOA food web model.
For fished prey species such as pollock, food web modeling shows that the overwhelming majority of explained mortality is from predation rather than fishing (Fig. 3). This suggests that for pollock, reducing fishing mortality may have little impact on their population trajectory, contrary to conventional fishing theory. It also suggests that increased fishing mortality might have a greater than expected effect if the population collapses under the combined effects of high predation mortality and increased fishing mortality. A further implication of the GOA food web model is that if pollock’s predator populations change substantially, then predation mortality would likely change with them; in other words, the single species stock assessment assumption of constant natural mortality for pollock is not supported by food web modeling. Although food web modeling implies potential shortcomings in the single species assessments for halibut and pollock, it can also be used to address those shortcomings by suggesting coordinated monitoring and management efforts for the two species. At present, halibut and pollock fisheries are managed separately by different agencies (the International Pacific Halibut Commission and National Marine Fisheries Service (NMFS)), with independent stock assessments. An understanding of the food web relationships for the interdependent halibut and pollock might be used to provide early warning for future changes in productivity for halibut or for mortality for pollock in each individual assessment.

Moving beyond the static food web model, we can use a dynamic ecosystem model to evaluate different hypotheses regarding the relationships between fishing history, climate change, and predator-prey interactions in determining biomass trajectories for important species in the GOA. This dynamic model is based on the equations in the dynamic multispecies food web model Ecosim, but has been implemented independently at the Alaska Fisheries Science Center to improve model flexibility and statistical properties. Perhaps the most significant result from attempting to reconstruct biomass trajectories with the model is that the simple idea at the basis of fisheries management theory, that populations exist in equilibrium with fishing mortality, is not supported. In this model, the historical biomass of the ecosystem cannot be recovered from the current biomass simply by eliminating fishing. Some change in productivity, either at the population level or at the ecosystem level, must be included to force populations initialized from early 1990s data to “recover” to prefishing biomass levels over the course of a century or more.

The best available information about biomass trajectories for twelve important species groups ranging from marine mammals through commercially exploited fish and invertebrates includes the outputs of other models as well as field survey information. There are several existing hypotheses linking the Pacific Decadal Oscillation (PDO) to biomass trajectories for several GOA species, including salmon and halibut. Other studies have suggested that productivity of key species may be crucial to explaining dynamics for the ecosystem, including Pacific ocean perch (a dominant species prior to heavy fishing in the 1960s), herring (a key forage species with a century-long history of heavy exploitation), and pollock (the dominant commercial forage species today).

We developed an experimental design comparing biomass and catch trajectories predicted from the ecosystem model with the best available information from the GOA for six hypotheses of ecosystem control. The hypotheses are

1. Historical fishing alone (with default predator-prey interactions) explains biomass trajectories.

2. Historical fishing and a specific set of predator-prey interactions explain biomass trajectories.

3. Historical fishing, a specific set of predator-prey interactions, and higher historical productivity of Pacific ocean perch and herring explain biomass trajectories.

4. Historical fishing, a specific set of predator-prey interactions, higher historical production
A historical fishing and climate patterns (with default predator-prey interactions) explain biomass trajectories.

6. Historical fishing, climate patterns, and a specific set of predator-prey interactions explain biomass trajectories.

We evaluated fits of ecosystem model trajectories to the data using the Akaike Information Criterion (AIC). Fits were poorest for hypotheses 1 and 5, suggesting that fishing and climate alone do not explain ecosystem dynamics; at a minimum, fishing and specific sets of predator-prey relationships are required to explain ecosystem dynamics. Hypothesis 2 was supported only for halibut, with poor fits of ecosystem model trajectories for many other species. Hypotheses 3 and 4 improved model fits for several species, with hypothesis 4 having the best overall AIC, and the best fits for pollock, cod, thornyhead rockfish and juvenile Steller sea lions (Fig. 5). Hypothesis 6 had the best fits for four different species: arrowtooth flounder, sablefish, herring and Pacific ocean perch (Fig. 6). However,
forcing with climate resulted in an extremely poor fit for salmon.

The results of this analysis demonstrate that some species dynamics can be explained well by some hypotheses, but that no single hypothesis explains all species dynamics, suggesting that in the GOA, there is no single main driver of the ecosystem. Both “top-down” control by fishing and “bottom-up” effects either for individual species or for the entire system are necessary to explain ecosystem dynamics. Furthermore, different groups are best explained by different control hypotheses, which in turn imply very different predator-prey relationships within the ecosystem. If long-term sustainability of commercial species is the primary goal, management cannot afford to assume that only one type of forcing (fishing vs. keystone species vs. environmental) is dominant in the GOA, or that one set of “best fit” parameters should be used in forecasting. It seems appropriate to introduce multiple modeling approaches that incorporate a realistic range of uncertainty as well as all feasible hypotheses rather than attempting to choose between them.

Figure 6. Best model fits (lines) to biomass time series (points) for the GOA ecosystem model forced with fishing, and the hypothesized Pacific Decadal Oscillation (PDO) forcing of primary producer groups from 1901 to 2002. Biomass is reported as a density in tons per square kilometer. Fitting to vulnerability parameters corrected most species extinctions, as in the fishing only model, with the notable exception of salmon (a failure which causes this model to have the lowest AIC in model comparisons). Herring and POP time series had better fits to the model forced with PDO driven primary production than to the models forced with hypothesized recruitment time series. Pollock had slightly worse fits to this model than to the one forced with the pollock stock assessment time series. Fits to arrowtooth flounder and sablefish were best in this model.
Complex systems food web models

Identifying historical and current food web relationships, exploitation history, and climate influences is the first step towards developing a fishery management policy to sustain vital relationships in the GOA. The second step is to address the maintenance of adaptive capacity for the future; this requires an understanding both of the species relationships and of the potentially complex behaviors of the full ecosystem under alternative policy options. Now we shift the emphasis from identifying relationships between system components to identifying structural and dynamic system properties which imply thresholds where system behavior changes abruptly and possibly irreversibly. Complex adaptive systems can, when perturbed, experience rapid phase transitions between multiple stable states. Identifying and mapping potential system level thresholds, especially thresholds related to changing fishing intensity, should assist fishery managers in avoiding policies which might reduce future adaptive capacity or cause rapid ecosystem reorganization. We begin with a static “network model” of the food web to identify structural properties.

Diverse disciplines ranging from computer and social sciences to epidemiology study how the structure (topology) of complex systems affects their function. In recent years, graph theory and network analytical concepts are providing valuable insights into system behavior in several areas. Networks are simplified models of relationships within a system, where the components in the network are called “nodes” and the connections between them are called “links.” The simplest network type is a regular lattice which is characterized by perfect order, with identical numbers and types of links between nodes. This network type clearly oversimplifies natural systems, but it has some properties in common with other more realistic network types. Three other structural types of networks have been described, each with different implications for system behavior and tolerance to perturbations: random networks, small-world networks, and scale-free networks. Mathematically, the regular lattice and random network types represent the extreme ends of a range of possible network configurations from most to least ordered.

While random structure was originally the default network model for many natural systems, random connections between links make networks less realistic in terms of information flow between nodes and sensitivity to node failure. Disconnecting a small proportion of nodes causes a random network to fragment. The small-world network structure has certain dynamic properties observed in natural systems related to the efficiency of information flow through the network. The small-world property (described as “six degrees of separation” in sociology) ensures close connections between otherwise distant groups of nodes by a few key links between groups that are not found in random networks. Scale-free network models were developed to explain the observed “scale free” or power law distributions of links per node observed in many real networks, which are unlike the distributions found in random networks. The most important property of the scale-free network is robustness to the failure of a small pro-

Figure 7. (upper) Food web constructed from the GOA food habits database, where each species is a node (dots) and each predator-prey interaction is a link (lines). The four “hubs” apparent in the figure are cod, pollock, halibut, and arrowtooth flounder. (lower) Degree distribution for GOA food web; frequency of nodes with degree k. The node with 80 links is arrowtooth, the two nodes with 120 links are pollock and halibut, and the node with over 160 links is cod, which is why they are highly connected “hubs” in the network.
portion of nodes, but there is a threshold between robustness and fragility where a previously stable, connected structure may suddenly fragment under certain conditions. (Scale-free networks such as the Internet have been found to be robust to the random failure of nodes, but are highly vulnerable to failure of the rare highly connected nodes.)

The GOA food web network constructed from the NMFS food habits database (Fig. 7) displays several of the small-world and scale-free properties found in other complex networks. The small world property suggests that in the GOA, impacts on a single species may be transferred through much of the food web due to its small-world average path length. The error tolerance/attack vulnerability scale-free network property is easy to translate into a practical management context: don’t spend significant resources worrying about chance species extinctions due to fishing or environmental change, because the scale-free food web is inherently robust to these events. However, knowing which are the highly connected nodes (identified as cod, halibut, pollock, and arrowtooth flounder) suggests that extra vigilance be given to protecting these species from fishing effects to prevent single species fishing impacts from translating into network fragmentation, especially if they are already commercially fished species (as cod, halibut, and pollock certainly are). Overall, network modeling implies 1) that elimination of some single species may greatly perturb the food web’s structure and 2) that the food web structure is robust to random species extinction but likely to reorganize if a highly connected species is removed.

We further explored the robust yet vulnerable nature of complex systems using a dynamic ecosystem model to explore a range of potential species interactions in the GOA and determine how fishing might affect these ecosystem dynamics. Within the food web-based ecosystem model, each species interaction is characterized by a complex predator-prey functional response, which can encompass behaviors such as seeking shelter from predators or foraging more actively, and the effects of predator satiation or consumption constraints due to the handling time required to eat individual prey. Since the numerical values of a few parameters determine the qualitative shape of each functional response, we can explore diverse kinds of predator-prey interactions by regarding those parameters as “dials” and changing them. Certain parameter values of the functional response can lead to extreme ecosystem dynamics ranging from excessive stability to chaos. The “true” functional response describing each predator-prey interaction in the ecosystem is unknown and difficult to measure. Therefore, selecting ecosystem model parameters controlling the functional response (and therefore determining ecosystem model dynamics) is problematic, especially because these parameters can be so influential.

Here, we randomly sampled from the full range possible for each parameter and test the validity of the resulting parameter set by determining whether all species in the ecosystem can survive and coexist over time; if so, the ecosystem is “successful.” This method requires no a priori knowledge of functional response parameters, yet results in feasible parameter sets which produce viable ecosystems. To test what effect fishing might have on the range of possibilities for the parameters, we simulated different levels of fishing intensity on the system. For each different level of fishing intensity, we sampled parameter space to see whether the overall range of functional response parameters—the “fraction of parameter space” allowing survival and coexistence of species—changes with different levels of fishing in the ecosystem. For each fishing intensity level, we find a different parameter “success rate”, with success rate defined as the fraction of good sets among all random parameter sets tested. We interpret higher success rates of good parameter sets to mean a higher likelihood that all species avoid extinction. Conversely, a fishing intensity that yields a lower ‘good parameter success rate’ is more likely to cause extinction of some species. Sampling parameter space in this fashion, we can evaluate the reliability of predictions that no species will go extinct from food web models whose food web links are likely correct, but in the face of broad ignorance about the strengths and functional forms of those links.

There were three important conclusions to this study. First, the GOA marine ecosystem model tolerated an extremely wide range of variation in the functional response parameters for nearly all species, implying substantial system level robustness to changes in the details of individual species interactions. In each of the fishing experiments, a large number of ecosystems sharing very similar biomass characteristics were produced and maintained over a 50-year simulation from functional response parameter sets drawn at complete at random. The similarity of the random ecosystems from each fishing experiment is particularly striking given that the parameter sets appear unrelated to each other.
Second, there are a few key species groups in the GOA with less robustness to variation in certain functional response parameters, and at least two of these are commercially fished species. Constraints related to the handling time parameter for pollock and cod were clearly present, suggesting that it is difficult to maintain all species in the ecosystem if consumption is constrained for either of these species. Similar constraints developed for additional species groups under heavy fishing. In addition to pollock and cod, Pacific ocean perch and other rockfish, nontarget species such as sleeper sharks, and longnose skates, and even low trophic level groups such as pelagic microbes were intolerant to the full effects of handling time in the heavy fishing experiments. This sensitivity was not present for these groups in the other fishing experiments, suggesting that fishing can have impacts on populations not just through direct mortality, but also through the indirect effects on feeding interactions. Reduced tolerance to consumption constraints for predators may be a sign of a stressed population, indicating that they must always increase consumption with prey availability to avoid extinction.

Third, and most important, there is a clear threshold effect between moderate and heavy exploitation rates where fishing fundamentally constrains the robustness of the ecosystem, and this threshold is not a linear function of fishing effort (Fig. 8). We find that as fishing effort rises gradually from light to moderate fishing, system robustness declines only gradually until, as fishing effort crosses the threshold, ecosystem robustness plummets sharply. Beyond this threshold fishing level, it becomes difficult to meet a simple ecosystem-level management objective of preventing extinction, and system characteristics become much less predictable than in conservatively fished or unfished systems. Overall, heavily fished ecosystems appear likely to reorganize into a new state which is unpredictable from the current state, a characteristic consistent with the concept of ecosystems as complex adaptive systems.

Conclusion

One purpose of this research has been to develop intuition about the GOA marine ecosystem using ecosystem model scenarios, so that management may move beyond sequential concentration on single species to a fuller ecosystem level of policy evaluation. Fishery management has previously assumed that single fish stocks independently responded to changing fishing mortality by changing their productivity in a predictable manner. This predictable response was then used to balance today's yield and economic benefit against tomorrow's stock productivity in order to promote sustainable yield. Our food web modeling has shown that in addition to fishing mortality, predator-prey interactions and environmental fluctuations are necessary to explain historical species trends. Thus, in the ecosystem context, there are factors influencing productivity that extend well beyond fishing mortality. Our complex systems models have shown that static and dynamic food webs have thresholds where the loss of certain species and/or increased fishing intensity may lead to radical changes in species composition—ecosystem reorganization. Initiating ecosystem-based fishery management means considering species relationships and system reorganization potential along with standard single species resource management. Integrating these concepts will help us make more effective management decisions now and in the future to promote fishery sustainability at the ecosystem level.

Figure 8. Model random ecosystem success rates (surviving systems / total drawn) for each fishing experiment and functional response parameterization. Success rates were higher overall in the more complex parameterization where a vulnerability parameter was drawn for each predator-prey link, and lower overall in the simpler parameterization where a vulnerability parameter was drawn for each predator to govern all of its prey interaction links. Both parameterizations had comparable success rates for no fishing, light fishing, and moderate fishing scenarios, but much lower success rates for heavy fishing scenarios across the system (3xF) or targeting rockfish (70xF). Including random variation in primary production (PP variability series above) lowered success rates slightly for the vulnerability by link parameterization, but the overall pattern appeared similar.