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A Mass-Balanced Model of Trophic Flows in Prince William Sound: Decompartmentalizing Ecosystem Knowledge

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Abstract

Just as real-world food webs contain complex interactions among species, so too must scientists and others interact to describe food webs in realistic ways. The most useful ecosystem models are constructed through collaboration among a wide range of experts. Collaboration among Prince William Sound (PWS), Alaska, researchers resulted in a mass-balanced Ecopath model of trophic flows including all ecosystem components (explicitly or implicitly). This study was conducted to describe functional interactions among components, and to reveal thermodynamic constraints of these interactions, thus enabling further refinement of contributed estimates as well as dynamic simulations of ecosystem perturbations.

Since the 1989 *Exxon Valdez* oil spill (EVOS) in Prince William Sound, and adjacent areas, research teams focused on the status of particular biological components of the PWS ecosystem, changes to those components, and the effects of EVOS. Some research groups investigated the effects of EVOS on larger segments of the PWS ecosystem, but a system-wide analysis was not undertaken until the current model was constructed. Estimates of basic population parameters were lacking for several biological components of the ecosystem, but the Ecopath approach enables refinement of knowledge of uncertain groups based on the constraints of interrelationships among groups. The whole-system model described herein can be used by managers, schools, or local communities for learning, knowledge refinement, or simulation of environmental disturbances such as oil spills or increased fishing. Ecopath modeling through multiway collaboration is presented as a broadly accessible tool for restoration and resource planning with the potential to be highly community-based.

> *Only fluency across the boundaries will provide a clear view of the world as it really is.*
>
> E.O. Wilson, Consilience: The Unity of Knowledge, 1998

Introduction

It is increasingly apparent that single-species approaches to fisheries management fail in all but the most fortuitous circumstances (Wilson et al. 1994, Roberts 1997; also see Laevastu et al. 1996). This realization provides increased impetus for resource managers to adopt a more ecologically sophisticated logic. For example, components of ecosystems interact with each other, the actions of resource users affect nontarget components of ecosystems, resource users can influence the "biotic integrity" of an ecosystem (NMFS 1998), and natural changes in certain ecosystem components can cause changes in other components, which are often unpredictable. Incorporation of such whole-ecosystem considerations into resource decision-making is called "ecosystem-based management," in which human activities are managed within the context of a naturally dynamic and integral ecosystem (Langton and Haedrich 1997, NMFS 1998; also see Juda 1996, Okey and Harrington 1999).

Such nice ideas are not challenging to discuss; the real key to achieving ecosystem-based management in decision-making forums is the application of integrative analytical tools. The first tool needed is one that describes interactions of the components of a defined ecosystem, and the constraints that might exist among those components. For example, thermodynamic (energy flow) constraints can limit the sizes of populations, either absolutely or in conjunction with other limiting factors like predation or recruitment. The second analytical tool needed for the transition to ecosystem-based management is one that can be used to predict the effects of changes in one ecosystem component on other components. These tools should be comprehensive enough to provide a cohesive picture of the defined ecosystem, in as accurate a manner as possible, while retaining adequate simplicity to enable a wide range of interested parties to comprehend and use the model. Most importantly, these tools can function optimally when parallel collaborative structures enable maximum flow of ecosystem knowledge.

A mass-balanced trophic model of the Prince William Sound ecosystem was constructed using the user-friendly Ecopath software, with the collaborative contributions of a working group of experts from the region. This is a static model that includes all biotic components of the PWS ecosystem, either implicitly or explicitly, in a possible scenario of interrelationships (trophic energy flows among components). The data in the model were then analyzed in dynamic simulation routines called Ecosim and Ecospace to predict indirect effects of simulated perturbations on the biotic system. This modeling approach is discussed in the methods section below.

The purpose of this paper is to point out the natural necessity for broad collaboration to achieve (1) realistic descriptions of whole ecosystems, and (2) functional policies and "ecosystem-based management" of human activities (defined in Okey and Harrington 1999). We illustrate this necessity for collaboration by describing the methods used to construct the PWS model. This paper is about collaboration, not Ecopath modeling per se.

Our premise is that human knowledge of the ecosystem is, to a large degree, compartmentalized among individuals, research teams, institutions, and other groups. This is especially true within the modern milieu of western culture and science. We suggest that the most realistic description of an ecosystem can be constructed by de-compartmentalizing knowledge through collaborative efforts such as the one described herein, and through everyday communications and working relationships. Furthermore, traditional ecological knowledge of native communities may prove invaluable for achieving a fuller understanding of ecosystems, as this knowledge may be less compartmentalized, albeit generally less quantifiable.

The science conducted subsequent to the EVOS has been criticized for failing to maximize opportunities for knowledge gathering as the result of political and legal constraints (Keeble 1991, Wheelwright 1994, Paine et al. 1996). Our efforts to construct a balanced trophic model of PWS revealed that reliable estimates of basic information such as biomass, production and consumption rates, and diet composition are lacking for many groups. One explanation for this paucity of information is that EVOS research was not guided by a system-wide analytical framework. Another is that some components of the ecosystem have simply not been studied in depth because the ecosystem is complex. Notwithstanding these alternative explanations, a considerable amount of information has been collected about the biota within Prince William Sound during the years since the spill (Spies et al. 1996). Moreover, significant efforts have been made to describe, in detail, larger functioning segments of the PWS ecosystem to reveal system-level effects of EVOS (Cooney 1997, Duffy 1997, Holland-Bartels et al. 1997). These programs are the source of much of the available knowledge of the PWS ecosystem, but a comprehensive, system-wide synthesis had not been undertaken until the current model was constructed (see contributions in Okey and Pauly [1998] for a more detailed description of the model).

The mass-balanced trophic model of Prince William Sound was constructed to integrate and synthesize what is being learned from the various research and monitoring projects within the *Exxon Valdez* oil spill (EVOS) restoration program, and to enable insight into "the effects of the oil spill and the long-term restoration and management of injured resources and services from an ecosystem-level perspective," as desired by the EVOS Trustee Council (1996:53). A collaborative synthesis of compartmentalized information can optimize ecosystem-level insights into the impacts of EVOS and other anthropogenic stressors. Moreover, the EVOS Trustee

Council stated that existing PWS data sets "need to be integrated in a simple [cost-effective] model to benefit long-term resource management," and "the restoration program will increasingly focus on an integrated, ecological approach." The goals of our study are to achieve these stated objectives.

Methods

The Ecopath Model of Prince William Sound

The balanced trophic model of PWS was constructed to describe the most likely flow scenario during the period from 1994 to 1996. A quantitative description of the whole trophic structure of PWS and adjacent waters and the relationships among the different species and groups inhabiting the area will place the results of individual EVOS projects into a realistic context and enable marine resource policy planning on an ecosystem level (multispecies as opposed to single species). The PWS model has unique potential as its 50 defined ecosystem components makes it, by far, the most explicit Ecopath model to date. There are many possible examples of its use; a PWS Ecopath model can be used to reveal of shifts in trophic structure in the wake of the oil spill that might be hindering the recovery of seabirds and marine mammals. Likewise, a quantitative analysis of the relationships between seabird foraging and hatchery-released fish will help to identify the ecological role of the hatchery program. Also, it may help track pollutants as they move through the food web (Dalsgaard et al. 1998). The versatility of the Ecopath system allows it to produce a fast and cost-effective overview of any part of the system. The basic idea of this project is that the use of a mass balance model such as Ecopath will allow easy identification of areas of trophic flux that will be of interest to those involved in policy making and restoration.

Constructing the PWS Model

The collaborative process of constructing a balanced trophic model of the PWS ecosystem consisted of four components: (1) a scoping period to identify ecosystem components and experts, (2) workshops, (3) coordinated e-mail and telephone communications, and (4) an edited volume that provided a venue for authored contributions. Initial identification of components and contributors was accomplished through inputs from EVOS program scientists, conversations with other experts, and our knowledge of the PWS marine ecosystem and the scientific literature.

Three meetings occurred over a 9-month period: a preparatory working lunch held in conjunction with the 1998 EVOS restoration workshop in January 1998; a model specification workshop during March 2-4, 1998, at which invited experts provided initial estimates of biomass, production, consumption, diet composition, migration, and spatial distributions; and an evaluation workshop on October 5, 1998, at which participants evaluated the balanced model and initial analyses to refine strategies of future model iterations and analyses.

At the model specification workshop, parameters were contributed within the context of modifying a pre-existing, preliminary model of PWS, constructed from existing literature sources (Dalsgaard and Pauly 1997, Pauly et al. 1998b). This format of building upon an existing, simpler model served three purposes: (1) anticipating skepticism regarding construction of a realistic whole-ecosystem model, (2) avoiding pressure for commitment by contributors early in the process, and (3) ameliorating a seemingly daunting challenge by refining an existing model rather than starting from scratch.

Facilitated communication among working group participants was crucial to keep participants coordinated within the context of the whole interactive ecosystem, and the edited volume of authored sections enabled many experts to contribute data and invest time without sacrificing recognition. Table 1 shows that contributors from a broad range of affiliations contributed to the integration of knowledge about a broad range of ecosystem components.

Contributors provided estimates for each of the following parameters:

1. Biomass in wet weight units and expressed as density (t per km^2) for PWS as a whole (9,059 km^2).

2. The P/B ratio (production/biomass). In Ecopath-type models, this is equivalent to an instantaneous rate of total mortality (i.e., Z; per year).

3. The Q/B ratio (consumption/biomass). This is a population-weighted estimate of food consumption per unit biomass (per year), or *ration* for an average-sized individual.

4. Exports from the system consist of catches (here in t wet weight per year) and animals leaving the system.

5. Information for a group in which diet fractions add up to 1.

When available, contributors provided seasonal means allowing for consideration of seasonal oscillations. They were also asked to quantitatively indicate increasing or decreasing trends as well as uncertainty by providing confidence intervals or likely minimum and maximum values.

Temporal Simulations with Ecosim

Beyond the uses of static representations of the PWS ecosystem, the data in Ecopath files were used in dynamic simulations using the Ecosim approach of Walters et al. (1997). Ecosim models allow rapid exploration of the predicted consequences of natural or anthropogenic disturbances on all components of an ecosystem simultaneously over a specified time period (typically 10 years). These could include changes in fishing, anthropogenic disturbances like another oil spill, or natural changes in agents of physical forcing. Other changes in resource use or potential management actions can likewise be simulated.

Hypothetical Scenarios for Simulating Perturbations

After the balanced trophic model of PWS was constructed, hypothetical "what if" scenarios were simulated using Ecosim. These scenarios were contributed by B. Spies, B. Wright, and A. Gunther at the model specification workshop:

1. What if fishing pressure on herring increases or decreases; what if there is one stock of herring? two? three?
2. What if somebody decides to fish sandlance or capelin? this is probably far-fetched, but model simulations would likely show important trophic impacts of removing important forage fishes.
3. What if an earthquake raises the upper 10 m of intertidal above sea level?
4. What if PWSAC goes broke and the hatcheries close?
5. What if there is another oil spill?
6. What if human impacts from the road to Whittier result in damage to intertidal habitats in the western part of PWS?
7. What if recreational fishing pressure removes 90% of the rockfish from PWS?
8. What if there is a major warm-water episode for 2 years with the upper 200 m of water over the shelf in the GOA is elevated by 2ºC ?
9. What if the bloom and sustained productivity lasts only for 3 weeks instead of the usual 12 weeks in PWS ?
10. What if the harbor seals continue to decline at 8% per year ?
11. What if Dungeness crab return to PWS?
12. What if salmon prices drop or increase?
13. What if pollock disappear from PWS?
14. What if salmon farming were allowed in PWS?
15. What if a road were established to Cordova?
16. What if cruise ship traffic increases into Cordova?

Spatial Simulations with Ecospace

The recently developed Ecospace routine (Walters 1998, Walters et al. 1998) was used to simulate changes in spatial distributions of Prince William Sound groups starting with information on habitat preferences and spatial distributions of habitats and organisms provided by contributors (also see Okey 1998). Ecospace simulates dynamic, two-dimensional redistribution of ecosystem components based on trophic interactions (flow) among organisms, their relative preferences for spatially specified habitats,

Table 1. Some Prince William Sound ecosystem component groupings and associated contributors.

Ecosystem component	Contributor	Affiliation
Cetaceans	Craig Matkin	North Gulf Oceanic Soc., Homer
Sharks	Lee Hulbert	NMFS Auke Bay Laboratory
Pinnipeds	Kathy Frost	ADF&G, Fairbanks
Cetaceans and pinnipeds	Rod Hobbs	NMML, NMFS, Seattle
Pacific halibut	Bob Trumble	IPHC, Seattle
Adult arrowtooth flounder	Mark Willette	ADF&G, Cordova
Shallow large epibenthos	Tom Dean	Coastal Resources Associates, Vista, CA
Walleye pollock	Mark Willette	ADF&G, Cordova
Miscellaneous fish groups	Tom Okey	UBC Fisheries Centre, Vancouver
Seabirds and raptors	Bill Ostrand, David Irons	USFWS, Anchorage
Adult salmon	Slim Morestead (consulted)	ADF&G, Cordova
Juvenile salmon fry	Tom Kline	PWS Science Center, Cordova
Nearshore demersal fishes	Tom Dean	Coastal Resources Associates, Vista, CA
Sea otter	J. Bodkin, D. Monson, G. Esslinger	USGS-BRD, Anchorage
Squid	Jay Kirsh	PWS Science Center, Cordova
Forage fishes	Evelyn Brown	UAF Institute of Marine Science
Deep epibenthos	Tom Okey	UBC Fisheries Centre, Vancouver
Adult Pacific herring	John Wilcock (consulted)	ADF&G, Cordova
Sea ducks	Dan Esler	USGS-BRD, Anchorage
Juvenile Pacific herring	Robert Foy	UAF Institute of Marine Science
Jellyfish	Jennifer Purcell	Horn Point Lab, Cambridge, MD
Small benthic infauna	Stephen Jewett	UAF Institute of Marine Science
Nearshore zooplankton	Robert Foy	UAF Institute of Marine Science
Offshore zooplankton	Ted Cooney	UAF Institute of Marine Science
Deep large infauna	Tom Okey	UBC Fisheries Centre, Vancouver
Shallow small epibenthos	Tom Dean	Coastal Resources Associates, Vista, CA
Shallow large infauna	Tom Dean	Coastal Resources Associates, Vista, CA
Phytoplankton	Peter McRoy (consulted)	UAF Institute of Marine Science
Macroalgae and eelgrass	Tom Dean	Coastal Resources Associates, Vista, CA
Forage fish diets	Molly Sturdevant	NMFS Auke Bay Laboratory
Birds eating herring eggs	Mary Anne Bishop	Pac. NW research station, USFS, Cordova
Recreational catches	Scott Meyer	ADF&G, Homer
Commercial catches	Bill Bechtol	ADF&G, Homer
Preliminary model of PWS	J. Dalsgaard, D. Pauly	UBC Fisheries Centre, Vancouver
“What if” scenarios	B. Spies, B. Wright, A. Gunther	AMS; NMFS Juneau; AMS

and their movement rates and vulnerability to predators in the various specified habitats.

Results

Workshop participants helped define the ecosystem and its components, they contributed estimates for the input parameters listed above, and they provided information on spatial and temporal changes. Figure 1 shows the trophic levels and the relative biomasses of biotic components of PWS based on the contributed estimates to the trophic flow model (trophic flows are left out of Fig. 1, as they are too numerous to display in this format). This model and its graphical representation represents a likely scenario of energy flow, based on the assumption of equilibrium in the system.

The structure of trophic flows provides an indicator of knowledge flow and a guide for researcher interactions when refining the parameter estimates for a group. Figure 2 identifies all of the direct flows connected to a single group in the model (in this case, adult Pacific herring). Ideally, the parameter estimates for a given group are derived empirically and have a high degree of accuracy and precision, but in reality, there are varying degrees of uncertainty among groups. Inconsistencies in energy flow between connected groups are indicated when the Ecopath model is unbalanced. These highlighted inconsistencies enable researchers to revisit the data and refine the model in a systematic way. This refines the realism of the overall model as well as estimates for individual groups. If a particular group is "unbalanced" within the model (i.e., when the ecotrophic efficiency is greater than 1; "ecotrophic efficiency" is the proportion of production by a group that is either consumed or exported), this may indicate that biomass or production/biomass values for the group are underestimates, or that consumption by other groups has been overestimated. Thus, the researcher for a group can use trophic flow connections as a guide to collaborative interactions in order to refine the information for a group.

Ecosystem components extracted from other trophic positions reveal unique trophic flow patterns that indicate different knowledge flow structures for refinement and learning. The relative magnitudes of trophic flows are not shown in these figures, but optimal knowledge flow structures would also account for magnitude of flows.

One Ecosim simulation is presented as an example of the usefulness of the collaborative approach; Fig. 3 shows functional responses of some groups to an aggressive fishery on sandlance in PWS, as trajectories of biomass changes. The model predicts that both seabirds and avian predators (birds that eat seabirds) would decline in response to such a fishery, while other groups would increase.

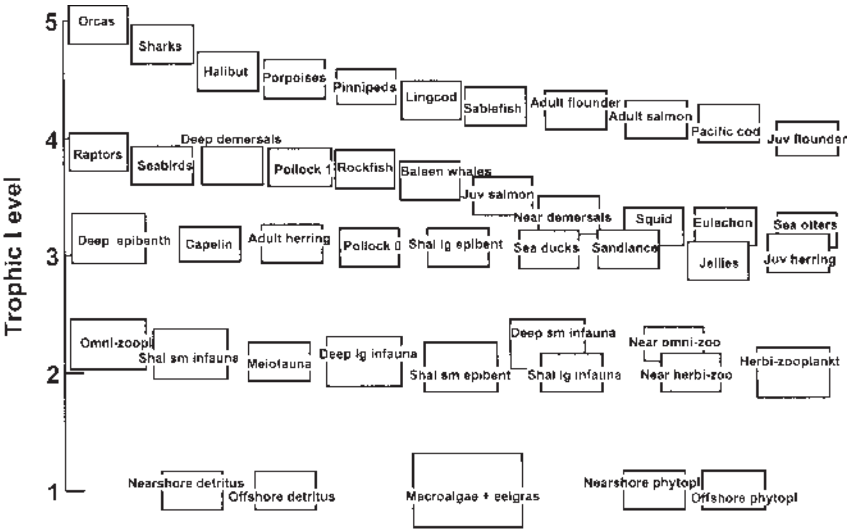

Figure 1. Components of the balanced trophic model of Prince William Sound, Alaska, displayed on a trophic level scale. Box size represents the log relative standing biomass of each component. Trophic flows are not displayed here, as there are too many connections for this format.

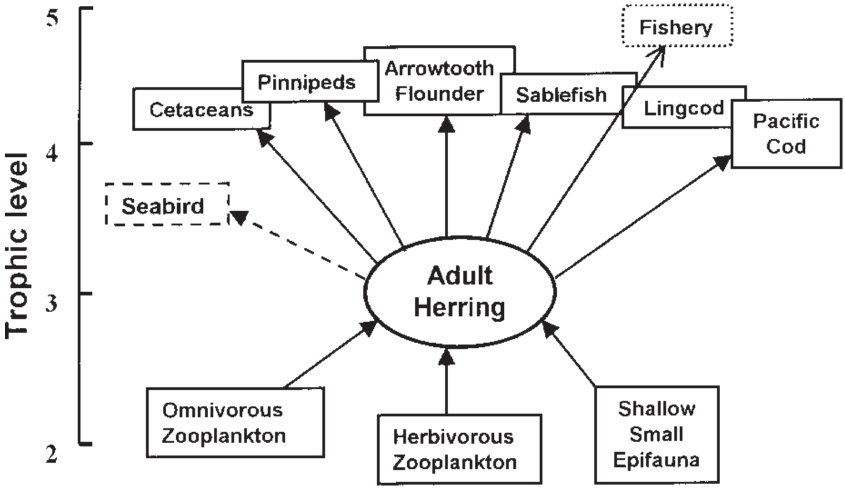

Figure 2. A mid-trophic-level component (adult Pacific herring) extracted from the overall food web along with directly connected components. Known trophic flows among components serve as indicators of knowledge flow among experts to optimize refinement of information about the group and its interrelationships (e.g., refine model input parameters).

When the same Ecosim scenario is used in the Ecospace routine, components are redistributed in two-dimensional, habitat-specified space at the relative biomasses revealed by the Ecosim run. Thus, a comparison of the "equilibrium" and "sand lance fishery" scenarios reveals different predictions of spatial distributions as well as temporal trajectories.

Discussion

Trophic interactions in an ecosystem are also flows of energy, which vary in rate and magnitude among connections (between the various components) and in time and space. We contend that ecosystems can be best understood when flows of ecosystem knowledge closely resemble flows of energy. Pathways to optimize knowledge flow for one ecosystem component should be based on the trophic flows immediately surrounding that component. Ecosystem-based trophic models, like Ecopath, integrate previously disparate ecosystem information through a system of knowledge flow that resembles trophic flow. This method was used to synthesize a cohesive picture of an apparently compartmentalized ecosystem.

Several EVOS-funded projects, notably the Alaska Predator Ecosystem Experiment (APEX), the Nearshore Vertebrate Predators (NVP) project, and the Sound Ecosystem Assessment (SEA) project, are devoted to the biology and ecology of distinct groups of organisms, sometimes including their prey, their predators, or both. As a result of these programs, the resolution of information is high for some ecosystem components. However, resolution is low for other components. Use of an Ecopath model allows all components of the defined ecosystem to be included and balanced (while accounting for imports and exports). This approach enables modification and verification of distinct components, as well as insights into whole ecosystem structure and function. Within the Ecopath framework, the precise information gained from the large investments in some research programs results in increased knowledge of less-studied components. This knowledge refinement is optimized through an appropriate knowledge flow structure.

This approach can be used to gain a better understanding of individual resource components and their potential trajectories in an ecosystem context, in addition to ecosystem structure and function. These trophic flow models can also be used to accurately map the fate and transport of contaminants within a food web (Dalsgaard et al. 1998).

A mix of reluctance and enthusiasm was encountered during our attempts to initiate a collaborative synthesis of ecosystem knowledge in Prince William Sound using the Ecopath approach. Some of the initial reluctance was linked with skepticism about the Ecopath approach. However, feedback from participants indicates a higher degree of enthusiasm and acceptance of the approach, as well as increased interaction and discussion among research groups, now that a face-to-face workshop was conducted.

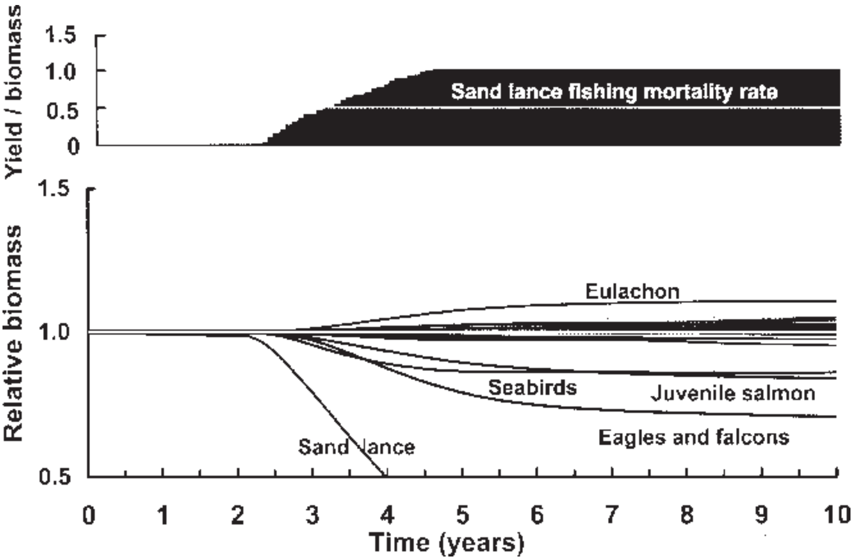

Figure 3. Ecosim simulation of the response to an aggressive sand lance fishery showing biomass declines in seabirds (which prey on sand lance), juvenile salmon, and avian raptors (which depend on seabirds and salmon). Eulachon, a competitor of juvenile salmon and a prey of seabirds, increases as seabirds decline. Aggregation of seabirds into one group masks the magnitude of declines in seabird species that are particularly dependent on sand lance. The functional responses predicted by Ecosim integrate the relative trophic forces in an ecosystem. These functional responses, rather than the absolute magnitude of responses, are useful for resource decision making and research planning. This sand lance example is a relatively simple one; some simulations predict more broad and dramatic responses.

Aside from technical skepticism about a particular analytical approach, reluctance to collaborate in an ecosystem context, in general, is linked to aspects of human behavior, such as social group dynamics and perceptions of territory. Behaviors reinforcing reluctance to collaborate are natural and adaptive, but offset by other motivations that reinforce collaboration. Based on our experience with this synthesis, we suggest that reluctance to collaborate can be overcome by redefining working communities and territories to resemble ecosystem structure. We also suggest that this can be done through workshops, collaborative reports, and other venues of knowledge flow patterned after energy flows in ecosystems.

The initial PWS model was constructed through the collaboration of members of the scientific community in the region, and it is planned to also integrate traditional knowledge from native communities. The representation of knowledge and the knowledge flow structures of these communities, however, differ in fundamental ways from the knowledge structure of the scientific community. Examination of these differences will aid in the development of optimal collaborative structure for understanding the ecosystem.

Some overlap exists between these two knowledge systems, and thus, some opportunity exists for integration, as elegantly demonstrated by Johannes (1981) in the South Pacific. The potential of incorporating traditional knowledge is further underscored by the richness of information attainable by examining lists of local common names, as discussed by Palomares et al. (1999). We suggest that tremendous potential exists for the integration of traditional ecosystem knowledge into current science and management structures through the type of collaborative modeling approach outlined in this paper, and using analytical tools like the Ecopath approach to constructing trophic models of historical ecosystems to be used as benchmarks. This has been discussed by Haggan (1996, 1998) and Pitcher (1998), and has been achieved by contributors to Pauly et al. (1998a). Failure to include traditional knowledge in such a process certainly limits the realism of the model, as well as its ultimate effectiveness as a management tool.

One potential outcome of Ecopath modeling activities in PWS is community-based resource management and policy development. By this we mean resource management that functions well because it is appropriately, and constructively, influenced by stakeholder communities and other trustees. The future success of oil spill restoration and resource management planning will be optimized through the participation of stakeholders, especially when venues for participation are functional, educational, and collaborative. We suggest that community-based management naturally occurs in parallel to ecosystem-based management that is achieved through knowledge flow structures that resemble ecosystem structures, as explored during this collaborative approach.

A great deal can be learned from Ecosim simulation models to aid resource managers in making decisions that affect the development of these communities. Perhaps even more importantly, the outputs and implications of Ecosim model runs are easily grasped by anyone because of the friendly user interface and graphics that are clear and intuitive. To encourage the process of ecosystem-based management, the model of PWS will be widely disseminated among the public as well as among managers. A CD-ROM version of the PWS model is available for distribution to interested organizations and institutions, including schools through the *Exxon Valdez* Oil Spill Trustee Council and appropriate trustee agencies. This CD-ROM also includes a local/traditional language database of the marine organisms of PWS and beyond. In addition, a locally enriched, customized version of "FishBase," the global, computerized encyclopedia of fishes, will also be made available on the worldwide web (see MacCall and May 1995 and www.fishbase.com).

In this paper we have outlined an iterative process. Knowledge about trophic interactions must exist before optimal knowledge flow structures can be indicated by trophic structure. Knowledge flow structures suggested by this process can then be used to refine the input parameter estimates, and thus increase the realism of the model. As the realism of the model increases, the tool becomes more useful for resource assessment and management, as well as research scoping and planning. At the same time, interest in the approach increases within the communities that are aware of the model. This in turn continues to increase model realism and applications. In this sense, the Ecopath approach has the potential of becoming a focal point for a living synthesis of ecosystem information.

Acknowledgments

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