ECOSYSTEMS OF THE PAST: HOW CAN WE KNOW SINCE WE WEREN'T THERE?

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ABSTRACT

Most reconstructions of historic abundances for marine organisms have been done on a species by species basis. It is argued here that assembling such reconstructions and working at the ecosystem level makes it more feasible to evaluate the consistency of historic estimates. If we construct ecosystem models of past ecosystems based on present ecology and historic exploitation patterns, we can use information about system form and function to evaluate past abundances. This can in turn be used to describe the parts of the systems for which we do not have information. A modeling approach, Ecopath, which has been used for such ecosystem reconstructions is presented, and it is discussed how it can be used for historic and pre-historic reconstructions. Application is exemplified through a case study of the Strait of Georgia ecosystem, British Columbia, Canada, where ecosystems models were constructed to represent the present, a hundred, and five hundred years ago. The model construction was part of a multidisciplinary project, including fisheries ecologists, marine historians, archaeologists, economists, along with fishers and others with local knowledge of a system and its history who, jointly parameterized, evaluated and discussed the models and the ecosystems they represented. The reconstruction serves to provide a baseline for evaluation of present day ecosystems and the human impact on these.

INTRODUCTION

Humans have exploited the living resources of the seas for thousands of years and have altered their ecosystems throughout this period (see Pitcher, 2001, for a recent review). Information about past ecosystem composition is sparse as quantitative information on marine populations rarely go back more than a few decades, or in the form of time series of catches a few hundred years at the best.

Human exploitation tends to remove top-predators through 'fishing down the food web' eventually leading to a concentration on prey species (Pauly *et al.*, 1998a). Where we have time series spanning the history of exploitation, we often find that the abundance of upper trophic level species decrease with 1-2 orders of magnitude (MacIntyre *et al.*, 1995), e.g., in the Gulf of Thailand where the depletion of the resources was relatively well described (Christensen, 1998). Often, however, we do not have time series at our disposal, and humans tend to evaluate based on personal impressions, not on records from the past. This leads to a 'shifting baseline' syndrome (Pauly, 1995), which has implications for how fisheries management is viewed. Where it in general has been appropriate to focus on 'sustainable development' for humans, this goal is not necessarily appropriate for marine ecosystems. The overwhelming majority of marine populations are severely depleted (Ludwig *et al.*, 1993), and focusing on how to sustain such depleted states is shortsighted. Instead focus should be on rebuilding ecosystems as a new goal for fisheries management (Pitcher and Pauly, 1998). The question then becomes, how can we then know what it is we want to reconstruct, i.e., what was out there before we started fishing?

As a starting point recall the ecology textbooks from our university days. Eugene P. Odum (1971) in his 'Fundamentals of Ecology' described how ecosystems develop over time. An example could be a clear-cut, nutrient-rich meadow in a temperate climate zone; depending on conditions such a system may develop into a full-grown deciduous or conifer forest in the course of a few hundred years. The development is not deterministic, but depends on chance and circumstances; still, we have expectations to how the forest may look over time from now and for hundred of years to come, given that we leave it to itself, and that there are enough bits of forests around to supply seeds.

In a similar way we have expectations to how marine ecosystems may develop if we leave them undisturbed for a length of time. Such expectations build on how ecosystems 'mature' over time. Quantifying a series of ecosystem indices (see Table 1), Christensen (1995) ranked 41 published mass-balance models of aquatic ecosystems in term of their maturity *sensu* Odum. The study included representations of ecosystems before and after a major disturbance, and it was concluded that disturbance tend to lead to a decrease in system maturity.

Table 1. Major tendencies describing the development incurred during ecosystem development, based on a selection of Odum's (1969) 24 attributes of maturity. These ecosystem indices can all be quantified using the Ecopath model.

Ecosystem attributes	**Developmental stages**	**Mature stages**
Gross production/biomass	High	Low
Biomass supported / energy flow	Low	High
Total organic matter	Small	Large
Niche specialization	Broad	Narrow
Size of organism	Small	Large
Mineral cycles	Open	Closed
Nutrient exchange rate, between organisms and environment	Rapid	Slow
Role of detritus in nutrient cycling	Unimportant	Important
Nutrient conservation	Poor	Good

Our knowledge of past systems is indeed incomplete, and we therefore need to utilize the circumstantial evidence that may be available. An important part of this may come from considerations of ecosystem maturity. We can assume undisturbed ecosystem to be mature *sensu* Odum. The implications of this are that all niches should be filled; that a major part of the energy flows should be through detritus-based food webs; that primary production should be efficiently utilized; that the total system biomass/energy throughput ratio should be high, etc. (Christensen and Pauly, 1998). Based on this and on an assumption of mass-balance, i.e., where the available prey production has to meet the food required by predators, and on whatever information may be available from historical sources on past exploitation and its resource base, we can assemble a picture of the ecosystem as it may have been. Further, by using a variety of tools, we can validate that the picture is indeed consistent with the available information and constraints set by resource ecology and thermodynamics.

Reconstruction as outlined here relies on an ecological modeling approach, which will be described in more detail below. Its use will further be demonstrated using the Strait of Georgia, British Columbia, Canada, as an example of how models of past ecosystems can be constructed. Model construction relies heavily on input from a diverse array of sources, including fisheries ecologists, marine historians, archaeologists, economists, along with fishers and others with local knowledge of a system and its history. As such, it is one of a few existing methodologies where multi-disciplinarity is a requirement and not just wishful thinking.

ECOSYSTEM MODEL CONSTRUCTION AND EVALUATION

Mass-balance modeling: Ecopath

The approach described here for reconstruction of ecosystems relies heavily on mass-balance ecosystem modeling. This implies the main assumption (or truism) that the energy uptake for a given ecosystem group has to balance the energy expenditure. For any given group this can be expressed:

Consumption =
production + respiration + unassimilated food
...1)

We may in turn express the production term of this equation as:

Production=
predation + catch + migration + biomass accumulation + other mortality
...2)

These equations serve as the backbone (master equations) for an ecosystem modeling approach and software called Ecopath with Ecosim (Christensen and Pauly, 1992; Pauly *et al.*, 2000), which has been widely used for modeling of marine ecosystems over the past decade. In total more than 2500 scientists in 125 countries have registered as users of the software (freely distributed through *www.ecopath.org),* and some 150 models have so far been published based on the approach. In the Ecopath approach, the second master equation is used to link predator and prey based on the fact that the predation term can be calculated as the sum of the consumption by all predators.

If we as an example know that a top predator consumes 10 $t\cdot km^2\cdot year^{-1}$ based on its biomass and consumption rate, and if we from diet studies know that this consists of, say, 40% zooplankton and 60% anchovies, we can calculate that the top predator will consume 6 $t\cdot km^2\cdot year^{-1}$ of anchovies. This information, derived independently of the information we may have on anchovy production can be used as an element in the second master equation to estimate the total production of anchovies.

If we describe all groups in an ecosystem, and we know all catches, etc., we can set up a set of linear equation corresponding to Equation 2. With perfect knowledge, this gives us n equations (if there are n groups in the system) with no unknown parameters. The system of equations would be overdetermined. In the real world we do not have perfect knowledge, and we instead can leave one of the parameters in Equation 2 as unknown for each group in the ecosystem. This leads to n equations with n unknown.

The unknown parameter for each equation, (i.e., for each ecosystem group) can in theory be any of the terms in Equation 2. Most application of Ecopath so far have, however, set the parameter for which we have least knowledge and least possibility of estimation to be the unknown. The parameter in question is the term called 'other mortality', which describes the production terms not covered by the other terms of the equation, e.g., mortality due to disease or old age. The other mortality will be a small term in most cases, and where we do not have information about either the biomass, production or consumption rate of a group, we can leave such a parameter as unknown, and input an assumed value for other mortality, (e.g., 5% of production). The Ecopath software will then balance all the flows in the system and in the process calculate whatever parameter has been left unknown for each group. The result is that we always end up with a balanced model of the flows in the ecosystem, even if we do not know everything about all parts of the system. [Note that in practice, other mortality is related to 1-EE, with EE being the 'ecotrophic efficiency', see the contributions in this volume].

The mass-balance constraint should, as hinted to above, not really be seen as a questionable assumption but rather as a filter. One gathers all possible information about the components of an ecosystem, of their exploitation and interaction and passes them through the 'mass-balance filter' of Ecopath. What comes out in the other end is a possible picture of the energetic flows, the biomasses and their utilization. The more information used in the process and the more reliable the information, the more constrained the picture will be.

If we for example know the biomass and consumption rate of zooplankton, we can calculate how much phytoplankton they require on an annual basis. If we do not have an estimate of primary productivity we have to take the estimate of primary production required to feed the zooplankton at face value and use it as basis for our estimate of the primary production. If, however, we have an estimate of the primary production we can compare demand and supply, and if they do not match, we can start examining the reliability of the estimates in more detail. We would also question if there are other populations in the ecosystems that should be considered. This illustrates that the more information we have, the more constrained our model will be, and the more comfortable we can feel about the predictions that may later originate from the model. It should also be clear that when we compare estimates of demand and supply at the ecosystem level, we add a dimension to the data evaluation process, a dimension that is not addressed when working only at the population level.

Addressing uncertainty

Some major advantages of the modeling approach outlined above include that it relies on readily accessible data of the type routine gathered and analyzed by fisheries scientists and marine biologists, and also that it is fairly simple to construct a model even if one has only incomplete information about the resources. A consequence of this is that it is in practice always possible to construct an ecosystem model of a given area even in data-sparse situations. But how good is the model then?

There are formal ways of describing the uncertainty involved in the model construction and parameterization. For this Ecopath, relies on two independent, but inter-linked approaches. The first is a module where the pedigree of all the input parameters can be defined (Table 2). Each type of pedigree is associated with a confidence interval, and once the pedigrees have been described a different module applies a Monte-Carlo technique to generate a large number of parameter representations sampling at random from the confidence intervals of the input parameters. Each of the model realizations are evaluated using a series of mainly physiological constraints, and statistics from the accepted runs are then gathered to derive parameter confidence intervals for input as well as for estimated parameters. Using a sampling-importance-resampling scheme in a Bayesian context, the confidence intervals can be further constrained (McAllister *et al.*, 1994). Further, a formal sensitivity analysis evaluates all possible input-output combinations highlighting where consideration of input parameter uncertainty is most required. Jointly, these approaches make evaluation of model uncertainty both explicit and transparent, yet it remains a relatively simple and versatile approach.

Table 2. Example of options for definition of pedigree for diet compositions in Ecopath. For each group in an ecosystem one of these options is used to define the pedigree of the diet. The confidence intervals (Cf.int.) are default values, and can be changed during input. They are used to describe parameter uncertainty in the balanced ecosystem model.

Option	**Cf.int (%)**
General knowledge of related group/species	±80
From another model	±80
General knowledge for same group/species	±60
Qualitative diet composition study	±50
Quantitative but limited diet composition study	±30
Quantitative, detailed, diet composition study	±10

Reconstructing historic states

The starting point for reconstruction of historic states will preferably be based on the present state of the given ecosystem. We have considerable information about global fish resources, their biology and ecology, most notably through database on finfishes called FishBase, available online at *www.fishbase.org*. Using FishBase, it is possible to extract a list of all species occurring in any given area along with direct access to a good deal of the parameters required for ecosystem modeling. With this background, with information of other key components, (e.g., primary productivity from SeaWIFS data, and on cephalopods from *www.cephbase.org*), and with knowledge of the exploitation of the resources (see *www.fao.org* and *www.fishbase.org* if local information is not readily available), the foundation for the model construction is laid.

Once the present day model is constructed, the next task is to draw up a list of ecosystem species or groupings for the historic state. This includes considerations of whether there are additional groups to be included or, for that matter, if there may be groups in the present models that have been introduced, or for other reasons may not have been there in past times.

The next step is to gather historic information about utilization and abundance of the ecosystem species or groupings. We may not know very much about the fishing operations of centuries ago, but there are traces left to be picked up – as presented for the Strait of Georgia below (see also Mackinson, this vol.).

Where we can construct time series of human exploitation we have the basic information at hand needed to estimate population sizes using assorted tools from the battery of stock assessment methodologies developed over the past century, see, e.g., Smith (1994), and Hilborn and Walters (1992). With such information construction of ecosystem models using Ecopath becomes straightforward.

The data requirements for the model construction are:

- A list of ecosystem species/groups;
- Historic catch levels and, where available, also size composition of catch;
- Abundance estimates for as many groups as possible;
- Consumption rates for all groups (present day rates acceptable); and
- Diet compositions for all groups (present day diets acceptable).

Ranges are acceptable for all input parameters, apart for time series.

Model construction includes a balancing stage, during which the internal consistency (demand vs. supply, physiological constraints) of the input data is checked in detail. This feeds back to the input data, and serves to identify where there are problems that requires further attention or changes to the input parameters. The resulting model, after having passed the mass-balance filtering procedure, will be internally consistent, and the uncertainty related to all parameters will be explicit.

Once a draft historic model has been constructed, balanced and evaluated, a series of analyses can be conducted to examine compatibility with known time series where such are available. This is done using the time-dynamic simulation model Ecosim (Walters *et al.*, 1997; 2000), which in turn can be used as an extra loop feeding back to the parameterization process described above.

Reconstructing the unfished state

As described above, it is by far the easiest to construct a model when information is sparse – as it will be when dealing with pre-historic states. We are, in such situations, much less constrained by prior knowledge during model construction, but of course it is at the cost of the model being less reliable compared to where we have a richness of information. Let us as an example consider how the ecosystem of the Strait of Georgia may have looked two thousand years ago. How would we go about constructing such a model?

We should first of all consider how the climate might have been: warmer, colder, or similar. Such information is readily available, e.g., from tree growth rings. Based on this we can choose an ecosystem structure that is fitting for the climate, and we can draw up a list of ecosystem groups that may have been present. In addition to extant groups this would include humpback whales, sea otters and Steller sea cows, groups that once served important ecological roles in the Strait. We can assume that there was some fishing in coastal areas, and that this was concentrated on the larger species, that pinnipeds would have been exploited, etc. We can also assume that the biomasses of the top predators would have been considerably higher than presently.

Further, we can assume that the total primary production should have been roughly similar to the current level. This sets a limit for the amount of basic food that was produced, and hence for how much we can 'blow' up the ecosystem, and still have enough to feed the intermediate consumers required to sustain high biomasses of top predators. Obviously, different assumptions would produce different results, and we can through comparisons of the results evaluate how sensitive the findings are to each of the assumptions.

Christensen and Pauly (1998) used a similar approach to estimate how much two present day ecosystem models (of the Gulf of Mexico and the Central Eastern Pacific) could be increased given no fishing and much higher levels of the top predators. They concluded that it would be possible to increase the biomass of top predators by an order of magnitude or more, which in turn would require a six to seven times increase in overall consumer biomass, and that present day primary production would be able to sustain this. Comparing fifteen ecosystem indicators for the two ecosystem states, the present and the pre-historic, they also concluded that all of the indicators pointed to the pre-historic states as being more mature *sensu* Odum (see above) than the present day systems.

A more rigorous form of reconstruction is possible using the Ecosim model of the Ecopath with Ecosim software (see Walters *et al.*, 1997; 1999; 2000). Taking as basis a (historic or present day) model, and adding a very low abundance of groups that would have been present in the pre-historic ecosystem, a simulation can be run where the fishery is reduced to the limited pre-historic level. The simulation is run until a new ecosystem state is reached. This state, in turn, can be output as an Ecopath model and used for comparing with the historic states.

If abundance estimates are available, or can safely be assumed for some groups the simulations can be forced to accommodate these as absolute values, adjusting abundance of all other groups for consistency, but doing so within the limits set by available primary production. Using this approach it is possible to generate a representation of the pre-historic information that is consistent with all available information about the biology and ecology of the ecosystem resources, as well as with what is known of the resource utilization over time.

RECONSTRUCTION OF ECOSYSTEMS: THE STRAIT OF GEORGIA

The ecosystem used here to exemplify reconstruction of ecosystem is the Strait of Georgia, a semi-enclosed area along the western coast of Canada, several hundred kilometers long and up to fifty kilometers wide. Based on a three-month pilot project followed up by a multidisciplinary workshop, three ecosystem models were constructed (Pauly *et al.*, 1998b) to describe the current state of the Strait of Georgia, how it may have looked a hundred years ago (before the onset of commercial fisheries), and five hundred years ago (before first contact of native people with Europeans and the expansion of the fur trade). Prior to the project, workshop material in form of ecological studies of all important (energetically as well a commercially) fish species as well as of all other important ecosystems groupings, from primary producers to seabirds and whales was collated and analyzed. Information on presence, exploitation and abundance of living organisms were obtained from historical records, newspapers, fisheries statistics, linguistic and archaeological (including petroglyphs and pictographs) studies, and environmental knowledge from aboriginal people and fishers living around the Strait.

The quantitative information gathered was used to prepare initial ecosystem models for the two more recent time periods. A two-day multidisciplinary workshop subsequently reviewed the material and assessed the suitability of the ecosystem models for the reconstruction process. The purpose of the model construction is to describe policy options for management, including an evaluation of the gains that may be obtained from rebuilding the ecosystem populations to levels comparable with the historic baseline values, and comparing this with what may obtained by preserving the status-quo, which we may call ‘sustainability’ or ‘preserving misery’ (Pitcher, 1998).

The methodology for ecosystem reconstruction described here has been under development for several years, and in summary relies on three principal components: (1) identification of data sources and descriptions of stocks, interactions, and exploitation; (2) construction of ecosystem models giving representative time snapshots; and (3) policy exploration for management. These components are described in more detail below.

INFORMATION SOURCES FOR ECOSYSTEM RECONSTRUCTION

As outlined above the data sources to be used for ecosystem reconstruction are diverse and include information with a high variation in precision and uncertainty. It should be stressed, however, that by using a variety of information and by applying triangulation to the extent possible the consistency of the data can be checked, and this can in turn be used to direct the model building and evaluation by adding measures of uncertainty to all input data irrespective of the source.

For the Strait of Georgia case, and indeed for this type of ecosystem reconstruction in general the types of information introduced below are of interest (Wallace, 1998b).

Exploitation time series

For marine ecosystems in general the by far most important form of human impact is through fishing, whaling, and other ways of extracting living resources. Information on such extraction is also the most important type of data required for ecosystem modeling, and fortunately enough, it is for many systems possible to create extensive databases documenting the extraction in historical times. In developed countries, fisheries statistics are often available from the second half of the nineteenth century, (even if they may be buried in paper piles, and out of sight for present assessments), while extractions in earlier times may need to be reconstructed based on indirect information.

For the Strait of Georgia, the most valuable source of historical catch information was a series of reports by the regional Inspector of Fisheries, published annually from 1875-1944. The reports described the amount of fish caught, the district where the catches come from, and gave a summary of major events in the fishery for the year. Later catch series mainly came from the publications of the Department of Fisheries and Oceans. In addition, there are a number of published time series for individual species. Figure 1 presents an overview of the species/groups and time periods for which time series were available for the Strait, and is intended to demonstrate that a variety of sources are indeed available, and that these together gives information about a good deal of the ecosystem resources.

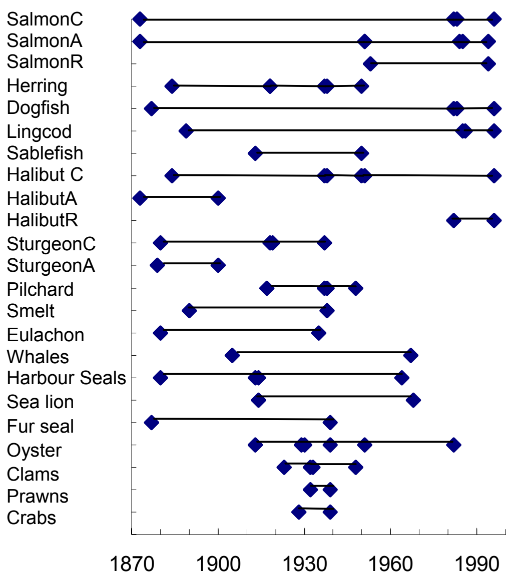

Figure 1. Overview of time series used for reconstruction of the Strait of Georgia ecosystem. 'C' indicates commercial, 'A' aboriginal, and 'R' recreational fishery. Based on Wallace (1998a; 1998b).

Once time series for the exploitation of the commercially important populations have been assembled it is possible to use standard fisheries assessment techniques to obtain population stock estimates, e.g., using virtual population analysis or age synthesis models. Stock estimates are of importance as input parameters for the ecosystem models.

Historical and archeological sources

Explorers tend to describe what they see, and later readers often try to discredit what may seem incredible abundances. Some for example have wondered if Eric the Red excelled in Public Relation or whether the climate of 'Greenland' was different when he advertised. Many will tend to buy the PR explanation, if only due to the "shifting baseline syndrome" described by Pauly (1995). However, historic accounts, carefully evaluated, may indeed be used to evaluate past distributions and abundances.

Where accounts give details of exploitation, e.g., the amount extracted using a given gear in a given time, or abundances in the form of sightings per time, (e.g., for birds or marine mammals), it is possible to use standard fisheries assessment methodologies to derive estimates of catches or abundances (see, e.g., Jackson *et al.*, 2001). These in turn may be useful for 'anchoring' other parts of the ecosystems as described in more detail below.

The most important source about historic diets comes from archaeological studies of middens. In the Strait of Georgia these have for instance shown that salmon and shellfish were the most important seafood for the native populations, and also that bluefin tuna in prehistoric time were caught in the Strait (Mitchell, 1988).

An additional historical source exists along the coast of British Columbia in form of petroglyphs and pictographs created by native or 'First Nation' people. As described by Williams (1998), petroglyphs and pictographs may be used to provide information of human interaction with animal and fishes over a long time span. Indications are that the images may be coded using a coherent visual language, a language now forgotten, but perhaps open to decoding.

Printed media

For the reconstruction of the Strait of Georgia ecosystem, newspapers from the late 1800s proved a valuable source. Most notably, the whaling industry was regularly described, and an estimate of the whale populations of the strait was obtained from these sources. Further, photographs were used to provide information about presence of certain species in the area, and in the case of rockfish (*Sebastes* spp.), even to produce an estimate of catch per fisher per hour, i.e., catch per unit effort or CPUE.

Printed maps and charts provided information about past occurrences and importance of ecosystem groupings, e.g., 'Porpoise Bay' indicating the porpoise may have once been abundant in a given area. Where cross-validation of sources is possible, i.e., where several independent sources are consistent, this form of information may be used to indicate that a group was present and probably abundant, and that it should therefore be included in historic ecosystem models for the area under consideration.

Traditional environmental knowledge

An important part of the Strait of Georgia project was to combine quantitative information about ecosystem resources with traditional aboriginal knowledge, and to use this combination to improve the ecosystem models. As part of this a series of interviews were held with First Nation elders to describe the activity, and to obtain information about the ecosystems and their exploitation (Salas *et al.*, 1998).

The interviews focused on deriving information about what the main resources in the Strait of Georgia were, and whether these resources were exploited. A species list was drawn up prior to the interviews, and the elders were questioned about each of the species included. Information about the fisheries focused on their intensity, on their character (commercial vs. subsistence), and on whether there were any management systems and trading networks in place. Also, information was sought about population size and the level of consumption of marine resources, along with information about observed changes in their abundance and the potential causes. The interviews confirmed that the First Nation people have considerable knowledge of their environment, and that such knowledge can indeed be of use for improving the understanding of the ecosystems and their use.

Information synthesis and evaluation

The Strait of Georgia project started out by gathering the information introduced above, and subsequently two initial ecosystem models were constructed to describe the present state and the state prior to the expansion of commercial fisheries, i.e., of the late 19th Century. With this as background material, a two-day workshop was held with participants from a variety of disciplines and with the purpose of discussing species abundance at present, a hundred years ago, and five hundred years ago, before the expansion of the fur trade.

The workshop started out with presentations of the methodology, of the draft ecosystem models and their assumption, of factors contributing to environmental regime shifts, of oral traditions and cultural protocols among First Nations, of resource abundance and development of fisheries, and an evaluation of past salmon abundance. As conveyed through this shopping list, the intention with the presentation was to give an overview of the information gathered and of how it could be used by the participants.

The participants subsequently split randomly into two groups, both tasked with the same challenges:

- Evaluate which species may have been lost from the Strait of Georgia during the last 500 years;
- Draw species distributions plots for the cases where the distribution may have changed radically over time;
- Evaluate the abundance of the major ecosystem groups relative to their present abundance;
- Examine the draft ecosystem model and evaluate if the list of groups included should be modified, e.g., by adding, merging or splitting groups;
- Identify information sources for past aboriginal harvest of non-salmon species;
- Suggest methods to improve the approach and discuss how to improve the incorporation of traditional knowledge.

The working groups spent most of the time available on discussions of the third of the points above, the previous abundances of the major ecosystem groups. Interestingly, the conclusions reached by the two groups were very similar, lending some degree of objectivity or at least ‘convergent subjectivity’ to the process.

The cooperation between a diverse group of ecosystem stakeholders, including government and academic researchers, fishers and First Nation people observed during this study was free of conflicts. This is due to the objective of the work having been to seek visions for how the ecosystem resources should be managed in the long-term, and is an example of what has been termed ‘patrimonial mediation’ (Babin, 1999). We infer from this that it is crucial, when seeking to settle a conflict, to start by discussing and agreeing on the long term, and only subsequently work backwards towards the present and its more pressing issues.

Based on the workshop recommendations, further information was gathered on missing pieces and additional analysis were performed. With this as background, the two initial ecosystem models were improved, and a third, tentative, model describing the state prior to contact between First Nation people and Europeans was constructed. The methodology and the findings are described in more detail by Pauly *et al.* (1998b).

This ‘Back to the Future’ methodology has been applied since then to one additional area, Hecate Strait also in British Columbia (Beattie *et al.*, 1999). A new multidisciplinary project at a larger scale currently applies the methodology in a comparative fashion to an ecosystem at the Canadian west coast and one at the Canadian east coast (Pitcher *et al.*, 2002).

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