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Mass-Balance Models of North-eastern Pacific Ecosystems

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Mass-Balance Models of Northeastern Pacific Ecosystems

Fisheries Centre, University of British Columbia, Canada

Dedicated to the memory of Professor P.A. Larkin

Mass - Balance Models of
North-eastern Pacific Ecosystems:
Proceedings of a Workshop held at the Fisheries Centre
University of British Columbia, Vancouver, B.C., Canada,
November 6-10, 1995

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ABSTRACT

A one-week workshop was held at the Fisheries Centre, UBC, from November 6-10, 1996, during which ten invited participants, mainly from the scientific community in British Columbia, Alaska and Washington, and Fisheries Centre faculty and graduate students assembled the elements required for preliminary mass-balance models of trophic fluxes in the Alaska Gyre, on the shelf off southern British Columbia, and in the Strait of Georgia.

Such mass-balance models were urgently required, as no systematic attempt had been made to verify that commonly-cited biomass, production and consumption rate estimates published for various critical marine groups in these three systems (e.g. salmon, marine mammals), were mutually compatible. The construction of these mass-balance models not only allowed verification (or correction) of previously published flux and biomass estimates, but also identification of major gaps in knowledge, and cost-effective estimation of some of the previously unknown rates and biomasses required for assessment of marine carrying capacity in the Northeastern Pacific.

Each workshop participant covered a functional group and its associated fluxes: phytoplankton and primary production, zooplankton and secondary production, major fish species and their fisheries, marine mammals and birds and their food consumption.

Model construction was performed using the well-documented Ecopath approach and software, previously applied to over eighty aquatic ecosystems throughout the world, and of which a pre-release Windows-based version was applied during the workshop.

This report documents the parametrization of the three above-mentioned models through short contributions authored by the participants, the construction and validation of these (still) preliminary models, then presents suggestions for their future development and uses.

Director's Foreword

Researchers from academia, government scientists and graduate students gathered at the UBC Fisheries Centre from November 6th-10th 1996, in order to construct the first mass-balance models of three marine ecosystems in the North-east Pacific: the Alaska Gyre, the shelf of southern British Columbia, and the Straight of Georgia. This report presents the result of the workshop as preliminary Ecopath models of these three systems.

Traditional fishery science conspicuously failed to take account of ecosystem interactions and for many years the single species stock assessment reigned supreme. Evaluation of the impact of harvesting on predators and prey was often considered unnecessary: an interesting but purely academic exercise. Many, including the late Peter Larkin himself, doubted this wisdom, and a few pioneering souls dared to invent multispecies models or tried to model the energy flow in whole ecosystems. But, by emulating single species population dynamics, multispecies fishery models rapidly became over-parametrized and immensely data-hungry, while ecological ecosystem modellers went down ever more esoteric pathways, losing the mathematically ungifted on the way. Also, it soon became clear that whole-ecosystem models driven by primary production were swamped by flows to and from the microbial components of the ecosystem that are gigantic in relation to exploited fish. They were also swamped by massive uncertainty concerning the nature and dynamics of those microbial flows.

By concentrating on components of the system that were well described, a clever short cut was invented by Dr. Jeffrey Polovina from Hawai'i in the early 1980s. Ecopath is a straightforward ecosystem modelling approach that balances the budget of biomass production and loss for each component by solving a set of simultaneous linear equations. (The Ecopath approach is the only ecosystem model to obey the laws of thermodynamics!) Simple data on diet, biomass, production and consumption to biomass ratios is all that is required, so that preliminary models can be quickly constructed from data already published or easily available.

Ecopath's potential was recognized and was championed at an early stage by Dr Daniel Pauly at ICLARM, Manila. This resulted in a series of workshops run world-wide, a further development of the method, with more rigorous mathematics by Dr Villy Christensen from Denmark, and eventually, to the enhanced model published as Ecopath II in 1992. Initially applied to a coral reef ecosystem by J.J. Polovina, over 80 Ecopath models covering a wide range of marine and freshwater systems have now been constructed world-wide, most of them in the developing world. It is something of a paradox that this new approach should be used last in developed areas of the world where the best data sets are available. The power of the approach, which unites the developed and developing world, lies in making cross-system comparisons possible.

The three Ecopath models in this report are preliminary and will doubtless need to be refined with better and more precise data from the systems concerned. That can come later. But another, unexpected and exciting, output arose from the workshop. This was the first version of Ecosim, a set of routines added to Ecopath by Dr Carl Walters from the Fisheries Centre in cooperation with

Dr Villy Christensen and Dr Daniel Pauly. Ecosim comprises a dynamic simulation of the effects of altering fishing mortality on selected components of the ecosystem. This technique, which allows the investigation of the impact of fishing on the whole ecosystem, will be formally published in 1997 in Reviews in Fish Biology & Fisheries. This new tool promises to be the first that could be practically employed in ecosystem management.

Mass-Balance Models of North-eastern Pacific Ecosystems is the seventh in a series of workshops sponsored by the UBC Fisheries Centre. The workshop series aims to focus on broad multidisciplinary problems in fisheries management, to provide an synoptic overview of the foundations and themes of current research, and attempts to identify profitable ways forward. Edited reports of the workshops are published in Fisheries Centre Research Reports and are distributed to all workshop participants. Further copies are available on request for a modest cost-recovery charge.

I thank UBC's Vice President of Research and the Department of Fisheries and Oceans Canada for sponsoring the workshop, and I am indebted to the late Dr Peter Larkin for sufficient shaking of their trees for the money.

Tony J. Pitcher

Professor of Fisheries

Director, UBC Fisheries Centre

FOREWORD

There are four reasons why Daniel Pauly might have asked me to make some introductory remarks for this workshop.

First, I helped raise some funds to support the workshop. It wasn't as much as I would have liked to raise, nor as much as Daniel could have made good use of. But it was enough to warrant a place on the program. I would like to acknowledge a contribution of $10,000 from the University of British Columbia and a matching contribution from the Department of Fisheries and Oceans Canada.

Second, for several years now, Daniel has bent my ear about Ecopath, initially at the International Center for Living Aquatic Resources Management (ICLARM), and more recently here at UBC. I have read about Ecopath and formed some opinions about its usefulness for fisheries management, but I have to admit I have never really come to grips with this approach, and I suspect that others might feel the same. To get that feel that comes with using a model, a workshop seemed a good idea. That is the second reason.

The third reason is that in recent years my attention has been much drawn to the Gulf of Alaska and the Eastern Bering Sea. This attraction stems in part from an interest that goes back to the days when I was involved in International North Pacific Fisheries Commission activities that has been rekindled by interactions with Lee Alverson (whose energies and whose capacities for generating enthusiasms are well known).

The fourth and final reason relates to my current involvement in the North Pacific Universities Marine Mammal Research Consortium which I helped set up three years ago. The Consortium is engaged in research that is at present concerned with the decline in abundance of Steller sea lions in the Gulf of Alaska, but in its initial conception, the Consortium was encouraged to view the Steller sea lion question and other marine mammal issues in broad ecosystem contexts. So what more natural than to encourage a workshop on an Ecopath model of the Gulf of Alaska?

On behalf of the Consortium, I would like to add my welcome to that of Dr. Pitcher and wish you every success in the workshop. I regret that I will not be able to participate to the extent that I had hoped but I will drop in to the workshop during the week as I have the opportunity. Onward and Upward!

P.A. Larkin

North Pacific Universities Marine Mammal Research Consortium

Preface and Acknowledgments

The proceedings presented here pertain to a workshop held on November 6-10, 1995 and, given our other commitments, we had to limit our editorial interventions, as we wanted the proceedings to appear no more than a year after the event.

Thus, what is presented here largely consists of texts written by the workshop participants before and/or during the workshop, the major exceptions being contributions written in the Fall of 1996 by the editors, by J.J. Polovina and by N. Haggan, and presenting updates of recent developments concerning the construction and interpretation of Ecopath models, and their integration in physical and cultural contexts.

As a result, most readers should be able to find more pertinent references than we used, and probably more accurate parameter values than were available during the workshop, and incorporated into what must be viewed, therefore, as preliminary models. But then again, this was one of the main purposes of the exercise: to construct models that could serve as a basis for subsequent, more detailed work.

To encourage this, we will make available to anyone interested a copy of the Ecopath software, and of the files generated during the workshop (contact D. Pauly: pauly@fisheries.com, or V. Christensen: v.christensen@cgnet.com)

We dedicate these proceedings, modest as they are, to the memory of Professor P.A. Larkin, who passed away on July 10, 1996, and who made possible the workshop upon which these proceedings are based.

We take this opportunity, finally to thank all those who made the workshop and this proceedings what they are now; Dr. Pitcher, the Director of the Fisheries Centre, for his support, Ms Rattana "Ying" Chuengpagdee, for her superb organization of the event, Ms Pamela Rosenbaum, for keeping us within our budget, Ms Sandra Gayosa, of ICLARM, for typing much of the first draft of this document, Mr Nigel Haggan for his assistance in shaping it into a whole, the participants - including the Fisheries Centre graduate students - for their enthusiasm, and UBC and DFO for funding the workshop and the publication of this report.

Daniel Pauly

and

Villy Christensen.

Vancouver, October 1996

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INTRODUCTION

(Daniel Pauly and Villy Christensen)

Rationale For Mass-Balance (Trophic) Models

Over the last decades, there have been massive changes of the oceanic regime in the North Pacific. These changes have resulted in increase of some major resource species, notably several species of salmon off British Columbia (B.C.) and Alaska (Beamish and Bouillon 1993), and hake off B.C. (Pitcher, this vol.). Decreases in other species, e.g., lobsters in Hawai'i have been attributed to the same climatic changes (Polovina et al. 1994).

Oceanographers, fisheries scientists and marine biologists have been tracking these changes, sometimes together, more often separately. Their common goal has been to predict future oceanographic regimes and, based thereon, the likely futures of major resources species. This research has yielded excellent results.

However, the "trophic context" of key species in north Pacific ecosystems has been largely neglected, at least since T. Laevastu and colleagues' heroic attempt at a spatially-structured simulation model of the entire Bering Sea (see Laevastu and Larkins 1981). Trophic context, as defined here encompasses food consumption and requirements of key species, and their contribution to the diet of predators. Dealing with the trophic context of resource species provides powerful insights for estimation of biomasses and of the fluxes that occur between them. It thus provides an independent way to validate published estimates of biomasses and/or fluxes.

However, most marine and fisheries scientists have to date preferred to work on single species, or on interactions among few species, rather than to model entire ecosystems. There are many reasons for this, but the most prevalent is that "ecosystems modeling" is perceived as a specialized and long-term activity, leading to large, unwieldy products, perhaps best illustrated by the Bering Sea model alluded to above.

Practical demonstrations of the power and versatility of the Ecopath approach may help to shift emphasis to whole-system attributes, increasingly required in an age of global change.

The Ecopath approach and software

The Ecopath approach is based on the work of J.J. Polovina (1984), of the US National Marine Fisheries Service (Honolulu Laboratory). The present authors, both then at the International Center for Living Aquatic Resources Management (ICLARM) in Manila, Philippines, developed and adapted Polovina's work to a user-friendly and versatile software package for personal computers. This software allows for rapid construction and verification of mass-balance models of ecosystems (Christensen and Pauly 1992a, 1992b).

The key steps to construct a model are to:

i) Identify the area and period for which a model is to be constructed;

ii) Define the functional groups (i.e., "boxes") to be included;

iii)Enter a diet matrix defining all trophic linkages by expressing the fraction that each "box" in the model represents in the diet of its consumers;

iv)Enter the food consumption, production/biomass ratio and/or biomass, and fisheries catches, if any, for each box;

v) Balance the model, i.e., modify entries (iii & iv) until input = output for each box;

vi)Compare model outputs (network characteristics, estimated trophic levels and other features of each box) with estimates for the same area during another period, or with outputs of the same model type from other, similar areas, etc.

These steps are simple provided that basic parameters are available. Numerous well-documented Ecopath applications to aquatic ecosystems already exist, ranging from aquaculture ponds and flooded rice paddies to shelf systems (see Pauly and Christensen 1993, and contributions in Christensen and Pauly 1993). Other models exist which represent the North Sea (Christensen 1995), and George's Bank. Indeed, the latter model was constructed by a group of Canadian scientists (from DFO and other institutions) during a workshop run by V. Christensen, similar to the one reported upon here, and held in St. John's in late 1993.

The workshop and its outputs

The workshop was held November 6-10, 1995, at the Fisheries Centre, UBC. There were some twenty-four participants: mainly members of the scientific community in British Columbia, and the states of Alaska and Washington, US, Fisheries Centre faculty and graduate students. Dr. Polovina was invited for the workshop to benefit from his pioneering work on Ecopath, and more recently, on regime shifts in the North Pacific gyre (Polovina et al. 1994, 1995).

Identification of key scientists was helped by discussions of the mass-balance approach at the March 1995 UBC Fisheries Centre workshop on "Impact of Changes in North Pacific Oceanographic Regimes on Coastal Fisheries." Aside from the travel arrangements, preparatory work included the briefing prospective participants on the data to be assembled, the compilation of a preliminary database and assembling relevant publications. Also, the Ecopath "module" taught (by D.P.) in September-October 1995 at the Fisheries Centre as part of "Fish 504"used the Strait of Georgia as an example, thus preparing the students to participate in the workshop, which became an element of their course.

The first day of the workshop proper was devoted to a formal review of the concepts behind the Ecopath approach (Box 1) and informal presentations and discussions on its various features, both positive and negative. The following multi-authored text presents the following:

- Estimated "summer" biomasses of the major components in three marine ecosystems: the Alaska Gyre, on the shelf of Southern B.C., and in the Strait Georgia;
- Mass-balance models describing the trophic flows in these three ecosystems, and largely pertaining to the late 1980s;

- Parameter estimates for the construction of "winter" models for these same areas, and hence for studying seasonal cycles;
- A basis for comparisons with similar ecosystems in other parts of the world; and, most importantly:
- A basis for formulating hypotheses about the likely effect of future changes of oceanographic and/or fisheries regimes on food webs and biomasses of key species in the three model areas .

We hope these results will be seen as useful by the scientific community in the Pacific Northwest, and contribute to a renaissance of studies linking ecological models and applied fisheries work. We also hope that the overview of ecosystems we present here will also lead to more consideration of local knowledge on their interrelationships of their component species (see Haggan, this vol.).

Box 1 Basic equations, assumptions and parameters of the Ecopath approach.

The mass-balance modelling approach used in this workshop combines an approach by Polovina and Ow (1983) and Polovina (1984, 1985) for estimation of biomass and food consumption of the various elements (species or groups of species) of an aquatic ecosystem (the original "ECOPATH") with an approach proposed by Ulanowicz (1986) for analysis of flows between the elements of ecosystems The result of this synthesis was initially implemented as a DOS software called "ECOPATH II", documented in Christensen and Pauly (1992a, 1992b), and more recently in form of a Windows software, Ecopath 3.0 (Christensen and Pauly 1995, 1996). Unless noted otherwise the word "Ecopath" refers to the latter, Windows version.

The ecosystem is modeled using a set of simultaneous linear equations (one for each group i in the system), i.e.

Production by (i) - all predation on (i) - nonpredation losses of (i) - export of (i)= 0, for all (i).

This can also be put as

$$P_i\text{-}M2i - P_i(1\text{-}EE_i) - EX_i = 0 \qquad 1)$$

where P_i is the production of (i), $M2_i$ is the total predation mortality of (i), EE_i is the ecotrophic efficiency of (i) or the proportion of the production that is either exported or predated upon, $(1\text{-}EE_i)$ is the "other mortality", and EX_i is the export of (i).

Equation (1) can be re-expressed as

$$B_i{*}P/B_i - \Sigma_j B_j{*}Q/B_j{*}DC_{ij}\text{-}P/B_i{*}B_i(1\text{-}EE_i)\text{-}EX_i = 0$$

or

$$B_i{*}P/B_i{*}EE_i - \Sigma_j B_j{*}Q/B_j{*}DC_{ij} - EX_i = 0 \qquad ..2)$$

where B_i is the biomass of (i), P/B_i is the production/biomass ratio, Q/B_i is the consumption/biomass ratio and DC_{ij} is the fraction of prey (i) in the average diet of predator (j).

Based on (2), for a system with n groups, n linear equations can be given in explicit terms:

$$B_1P/B_1EE_1 - B_1Q/B_1DC_{11}\text{-}B_2Q/B_2DC_{21} - ...\text{-}B_nQ/B_nDC_{n1} - EX_1 = 0$$

-
-

$$B_2P/B_2EE_2 - B_1Q/B_1DC_{12} - B_2Q/B_2DC_{22} - ...\text{-}B_nQ/B_nDC_{n2} - EX_2 = 0$$

-
-

$$B_nP/B_nEE_n - B_1Q/B_1DC_{1n} - B_2Q/B_2DC_{2n} - ...\text{-}B_nQ/B_nDC_{nn} - EX_n = 0$$

This system of simultaneous linear equations can be solved through matrix inversion. In Ecopath, this is done using the generalized inverse method described by MacKay (1981), which has features making it generally more versatile than standard inverse methods.

Thus, if the set of equations is overdetermined (more equations than unknowns) and the equations are not consistent with each other, the generalized inverse method provides least squares estimates which minimize the discrepancies. If, on the other hand, the system is undetermined (more unknowns than equations), an answer that is consistent with the data (although not unique) will still be output.

Generally only one of the parameters B_i, P/B_i, Q/B_i, or EE_i may be unknown for any group i. In special cases, however, Q/B_i may be unknown in addition to one of the other parameters (Christensen and Pauly 1992b). Exports (e.g., fisheries catches) and diet compositions are always required for all groups.

A box (or "state variable") in an Ecopath model may be a group of (ecologically) related species, i.e., a functional group, a single species, or a single size/age group of a given species.

ALASKA GYRE MODEL

The Marine Ecosystem of the Gulf of Alaska

(Jeffrey Polovina)

The Alaska Gyre is an extremely important part of the North Pacific: it is the ecosystem where most salmon from the Pacific Northwest accumulate the energy that enables them to swim back to the stretch of the river or brook where they once hatched.

Compared to earlier decades, there is a significant body of biological evidence to suggest that the carrying capacity of the Gulf of Alaska has increased since the late 1970s. Changes have occurred at several trophic levels from zooplankton to at least salmon. This is possibly due to changes in the intensity of the Aleutian Low Pressure System (McFarlane and Beamish 1992; Beamish and Bouillon 1993; Brodeur and Ware 1992; Polovina et al. 1995).

A comparison of zooplankton abundance in the Gulf of Alaska between 1956-1962 and 1980-1989 showed a doubling of summer zooplankton biomass, pelagic fish, and squid abundance in the latter period (Brodeur and Ware 1992). Trends in North Pacific salmon production follow changes in the Aleutian Low Pressure Index from 1925-1989 (Beamish and Bouillon 1993). Above average North Pacific salmon catches occurred during 1925-1945 and 1977-1989, when the Aleutian Low Pressure System was more intense than average. Below average salmon catches occurred during 1946-76 when the Aleutian Low was weaker than average.

As the late 1970s represent a transition period from low to high carrying capacity, our trophic model of the Alaska Gyre system should focus on the 1980s, and describe the ecosystem characteristics of this latter period.

Lower Trophic Levels

(Jenny Purcell)

The data presented here originate mainly from the SUPER (SUbarctic Pacific Ecosystem Research) project, (see Miller et al. 1988) and were sampled during May-June and August 1984, 1987 and 1988 at two locations - Station P (50° N; 145° W) and Station R (53° N; 145° W). All standing stock estimates, integrated to a depth of 80m, and initially expressed in terms of $\text{mgC}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$, were converted to g wet weight $\text{m}^{-2}\cdot\text{year}^{-1}$ through a wet weight : carbon ratio of 10:1.

Bacteria

Biomass and production data for bacteria were taken from Kirchman et al. (1993; Tables 1 and 2, respectively):

- Biomass 1.1 gC m^{-2}= 11 g wet weight m^{-2};
- Production 55.6 mg C m^{-2} day^{-1} = 203 g wet weight m^{-2} year^{-1};
- P/B = 18.45 year^{-1} ;

- Carbon consumption (taken for 0 - 80 m from Table 1 in Simon et al. 1993).

Thus, we have 75.5 mgC m^{-2} day^{-1} = 276 g wet weight m^{-2} $year^{-1}$, or Q/B = 25 $year^{-1}$, which is low such small organisms.

Phytoplankton

Chlorophyll *a* biomass (from Table 2 in Frost 1993) was converted to carbon using to the ratio of 60:1. Chlorophyll biomass is rather constant over the year (Miller et al. 1991). Thus we have:

- Biomass 25.3 mgChl.·m^{-2} = 15.2 g wet weight·m^{-2};
- Production 728.4 mg C m^{-2} day^{-1} = 2659 g wet weight·m^{-2} $year^{-1}$;
- P/B = 175 $year^{-1}$.

Futher, data may be found in Welschmeyer et al. (1993).

Microzooplankton

Biomass and ingestion rates of microzooplankton are from Strom et al. (1993; Tables 1 and 2, respectively):

- Biomass 170.4 mgC m^{-2} = 1.7 g wet weight m^{-2};
- Ingestion 98 mgC m^{-2} day^{-1} = 358 g wet weight m^{-2} $year^{-1}$;
- Q/B = 0.6 per day or 210 $year^{-1}$.

The diet consists of 75% phytoplankton and 25% bacteria and other microbes.

Small herbivores

Density estimates for eight species of copepods were adapted from Table 1 in Dagg (1993), based on data collected with a MOCNESS net (243 µm mesh). Dagg et al. (1989) report biomasses of 85 µgC for *Neocalanus plumchrus* and 624 µgC for *N. cristatus* (see also Frost 1987). Densities were converted to carbon using 85 µgC, assuming that most copepods were small. Herbivore biomass is about 15 g m^{-2} in the summer and about 4.5 g m^{-2} in the winter (Richard Brodeur, pers. comm.). Thus, we have:

- Biomass 535.6 copepods m^{-3} (80 m depth) = 29,272 copepods m^{-2}, or = 25 g wet weight m^{-2};
- Copepod ingestion of phytoplankton was estimated from Figure 12 in Dagg (1993), as: 943.8 µgChl. m^{-2} day^{-1} = 2067 g wet weight m^{-2} $year^{-1}$.

Clearance rates of protozoans by *N. plumchrus* and *N. cristatus* were averaged from data in Gifford (1993). All copepods were assumed to clear protozoans at the same rate (this may be an overestimate, see Landry et al. 1993). Thus:

Ingestion of protozoans 1.8 µgC $copepod^{-1}$ $hour^{-1}$ = 192 g wet $weight^{-2}$ $year^{-1}$, and Q/B is thus 90.4 $year^{-1}$.

Adding phytoplankton and protozoans gives a total copepod ingestion rate of 2,259 g wet weight·m^{-2} $year^{-1}$, and the diet based on the ratio of those consumption rates is 91.5% phytoplankton and 8.5% (bacteria-rich) detritus.

Salps and gelatinous herbivores/omnivores

The major species of salp is *Cyclosalpa bakeri*, and the following, adapted from Purcell and Madin (1991) and Madin and Purcell (unpublished data), refer only to that species, though *Salpa fusiformis* also occurs in the area. Salps were not present in the May cruises of SUPER, but were in August. Overall, salp may occur only 3-4 months per year in the Alaska Gyre. *Cyclosalpa bakeri* is extremely delicate, and its biomass and related parameter are unlikely to have been estimated in any other studies. The values are:

- Biomass 804 mgC m^{-2} = 8 g wet weight m^{-2};
- Total ingestion 66.3 mgC m^{-2} day^{-1} = 242 g wet weight·m^{-2} $year^{-1}$; and
- Q/B = 30 $year^{-1}$.

The diet consists of 53% phytoplankton and 40% microzooplankton and 7% detritus.

Further data on the metabolism and growth of *Cyclosalpa bakeri* may be found in Madin and Purcell (1992), and in Cooney (1987, 1988) for zooplankton in general.

Carnivorous Zooplankton, Jellies and *Velella*

(Mary Arai)

Carnivorous Zooplankton at Station P

Populations of chaetognaths at Station P were estimated from Forbes et al. (1988). Standing stock in May was 2,078 individuals·m^{-2}. The standing stock graphed in Terazaki and Miller (1986) show a later summer maximum approximately double that for May.

Terazaki and Miller (1986) estimated generation times of 6-10 months; thus, with three spawning periods at Station P, P/B is at least 1.5 $year^{-1}$, and we assume it here to be twice as high.

The diet consists mainly of small herbivorous zooplankton (see Sullivan 1980).

Carnivorous Jellies

The numbers of *Aglantha* were derived from data in Forbes et al (1988) for May 1984. This value is probably an underestimate as it is approximately one-third of the value in Arai and Fulton (1973) for 1971. The estimate also does not include siphonophores, which, in 1971, were approximately two-thirds as abundant as *Aglantha* (Marlow and Miller 1974).

Numbers were converted to wet weight using a value of 83.2 mg/animal (Ikeda 1972). Thus, biomass = 9.1 g·m^{-2}, with winter populations similar to those in May (Arai and Fulton 1973).

On the high sea, there is one more generation of *Aglantha* than inshore. P/B is therefore = 1+ predation rate, and probably ranges from 2 - 4 $year^{-1}$.

A first estimate of ingestion rate, derived from Purcell and Grover (1990) is Q/B = 110 $year^{-1}$, which appears to be very high, perhaps excessively so. Therefore, Q/B is estimated from an assumed food conversion efficiency of 0.3. The diet is assumed to consist of small herbivorous zooplankton.

Table 1 Data for establishing a length-weight relationship in *V. velella*[a].

Length	Weight	Length	Weight	Length	Weight
8	50	19	360	25	710
11	110	21	420	26	490
15	200	22	480	27	880
15	210	22	520	28	880
16	280	22	670	28	990
17	340	23	600	29	840
18	270	23	650	31	940
18	310	23	660	32	1400
18	360	24	810	36	1590
18	370	-	-	-	-

a) based on hydroids sampled in May 1986, stored in 5% formalin, , and measured (mm and mg wet weight) in October 1996.

By the Wind Sailor Velella velella

Velella velella is a hydroid which form floats with sails, hence its common name, "By the Wind Sailor". Like coral, *V. velella* contain symbiotic algae (Hovasse 1923; Taylor 1971; Holland and Carré 1974), but they also feed on euphausiid and fish eggs (Bieri 1961). The ratio of food intake *vs.* energy supply from the algal symbionts is not known. Growth to float length of 10 cm occurs from January to April; along the California coast, a second generation occurs from July to September (1977).

The northern limits of *V. velella* distribution roughly correspond to the convergence of subarctic waters with the mixed waters of the Alaska current (Savilov 1961), and hence the distribution of *V. velella* swarms is very irregular in space and time (see also Bieri 1977, and Arai 1992). For example, in 1957, seven swarms appeared at ocean weather station "PAPA" (50° N, 145°W) in February, May and October. Thus, biomass estimates are not provided for the Alaska Gyre system, nor for the southern B.C. shelf, where *V. velella* also forms large aggregations off the B.C. coast.

For the B.C. coast, population numbers as length categories for spring populations in neuston tows are given in Arai et al. (1993). Pertinent stations for the 30-300 m shelf are LB2-11 and LC 2-8. A length-weight relationship being necessary to analyze these data, but none having so far been published, 28 preserved specimens of *V. velella* were measured and weighted for the purpose of deriving such relationship (Table 1).

From these, the relationship

$$W = 0.48 \cdot L^{2.26}$$

was established, using a linear regression of the log(W) against the log(L) values, whose correlation is r = 0.981. This relationship may be used to convert observed lengths of *V. velella* into weights. However, the narrow range of sizes used to derive the relationship must be considered, as well as a weight loss following preservation, of perhaps 30-50 %.

Initial Estimates on Krill

(Astrid Jarre-Teichmann)

Euphausia pacifica, *Thysanoessa longipes*, and *T. inermis* are the most important euphausiid (krill) species in the central northeast Pacific, (Mauchline and Fisher 1969). *T. inspinata* occurs further south than *T. longipes*, and the northern boundary of its distribution lies south of 50° N. *T. raschi* is more common on the shelf than offshore.

T. longipes and *T. inermis* live for 2-3 years (Mauchline 1980), while *E. pacifica* lives for at least 2 years (Tanasichuk 1995). Most species mature at about one year of age (Mauchline 1980). Lindley (1980) estimated $Z = 0.8$ year^{-1} for 2-year old *T. inermis*. Total mortality (Z) estimates for *E. pacifica* range from $Z = 0.6\text{-}1.9$ year^{-1} on the shelf of B.C. (Ron Tanasichuk, Nanaimo, pers. comm.) to $Z = 3.0$ year^{-1} in the California Current (Mullin 1969) and $Z = 8.7$ year^{-1} off Oregon (Mauchline 1980). $Z = 3.0$ year^{-1} was chosen as an initial estimate for the present modelling study. This may turn out to be conservative if juvenile stages of krill are to be explicitly included in this box.

E. pacifica grow rapidly during summer (Lasker 1966), but as in other organisms, growth stagnates for several months during winter (Ron Tanasichuk, Nanaimo, pers. comm). Consequently, if a typical summer situation is to be represented on an annual basis, the initial P/B ratio should be set at 5-6 year^{-1}.

In general, the diet of both *T. longipes* and *E. pacifica* consists of detritus, diatoms, dinoflagellates, tintinnids, chaetognaths, larvae of echinoderms, amphipods, and crustaceans (Mauchline 1980), i.e., of phytoplankton, small zooplankton and detritus. However, a quantitative breakdown was not available. Euphausiids are known to be predominantly filter feeders, although some hunting has been observed (Mauchline and Fisher 1969; Lasker 1966). A diet composition of 85% phytoplankton, 5% zooplankton, and 10% detritus may be assumed.

A population of *E. pacifica* uses about 9% of the assimilated carbon for somatic production over the entire life of its constituent individuals; mature animals use another 9% for gonadal production, whereas the somatic production of juveniles can be as high as 30% (Lasker 1966). Therefore, the net efficiency of *E. pacifica* was assumed at 20%, in line with the estimates of Lasker (1966) that 62-87% of the assimilated carbon is respired. Lasker also estimated an assimilation coefficient of 80% for *E. pacifica* fed with nauplii, but, as the assimilation efficiency of omnivores is generally lower than that of carnivores (Welsh 1968), an assimilation coefficient of 70% is suggested, close to the estimates of other cold-water zooplankton of 65% (Schnack et al. 1985). This leads to a gross efficiency of 12.6%. It should be noted that this value is considerably higher than the estimate of 5.4% for *Euphausia superba* based on the energetic model of Clarke and Morris (1984) and the annual P/B ratio of Siegel (1986).

In the absence of biomass estimates for the Alaska gyre, krill biomass can be computed, based on an ecotrophic efficiency of 95%, which emphasizes the role of krill as food in the ecosystem. Also, the *total* zooplankton biomass estimate of 34.5 g m^{-2} at an oceanic station in the northeastern Pacific "transition zone" in the late 1980s (Richard Brodeur, pers. comm.) may serve as a guiding value for balancing the summer model.

Salmon in the Ocean

(Leonardo Huato)

The northeastern Pacific ocean supports numerous stocks of six anadromous salmonids species: coho, *Oncorhynchus kisutch;* chinook, *O. tshawytscha;* sockeye, *O. nerka;* steelhead, *O. mykiss;* chum, *O. keta;* and pink, *O. gorbuscha* (Healy 1993; Ignell and Murphy 1993). Table 2 presents freshwater, estuarine and ocean residence times for 5 of these 6 species:

Sockeye, pink and chum salmon migrate into oceanic waters. On their return, they pass throughout the coastal domain without feeding. All mortality can be attributed to predation as there is no US or Canadian commercial fishing during their oceanic phase. Coho and chinook remain in coastal waters. Table 3 presents instantaneous mortality estimates for the estuarine and oceanic phases.

Table 2 Freshwater, estuarine and ocean residence times for salmonids (Pearcy 1992).

Species	Freshwater	Estuary	Ocean
Coho	0 - 4 years	days	0.5 - 1.5 years
Chinook	0 - 2 years	days	0.5 - 6 years
Sockeye	0 - 2 years	days	1 - 5 years
Chum	days-weeks	weeks	2 - 4 years
Pink	days-weeks	days	1.6 years

Table 3 Estuarine and oceanic mortality rates (Z; year^{-1}) for salmon, by stage (based on Bradford 1995, and Ricker 1976).

Species	**Smolt-Adult** (Estuaries)	**Adult** (Ocean)
Coho	2.32 ± 0.06	1.32
Chinook	-	0.42
Chum	4.92 ± 0.12	1.64
Sockeye	2.78 ± 0.07	0.92
Pink	3.68 ± 0.12	2.45

Biomass or densities are not reported in the literature. For steelhead, biomass was set at 0.1 $t \cdot km^{-2}$, and P/B at 1 year^{-1}. For the other species (except chum), biomass was estimated using total catch and total mortality (Z; year^{-1}), and harvest rate (annual catch in numbers/population size), as follows:

- Current year run size = total catch / harvest rate; and
- Size of the cohort in the previous year = current year run$\cdot e^{Z}$.

For chum, the catch was assumed to be composed of 30% of individuals of age 4 and 70% of age 3 individuals. Thus, the total number of age 4 is given as:

- $N_4 = 0.3 \cdot$total catch/harvest rate;
- $N_3 = (0.7 \cdot$total catch/harvest rate$) + N_4 \cdot e^{Z}$;
- $N_2 = N_3 \cdot e^{Z}$; and
- $N_1 = N_2 \cdot e^{Z}$ (Table 4).

Total catches were obtained by pooling US and Canadian catches in numbers, then converting to biomass using mean body weights at age.

Table 4 Numbers and biomass of sockeye, pink and chum salmon in the Alaska Gyre (U = harvest rate; Z = total mortality; year^{-1}).

Sockeye			Pink			Chum		
U = 0.6			U = 0.7			U = 0.55		
Z = 0.92			Z = 2.45			Z = 1.65		
Catch = 50 million			Catch = 72 million			Catch = 12 million		
Numbers at age (10^6)	Weight (kg)	Biomass (t)	Numbers at age(10^6)	Weight (kg)	Biomass (t)	Numbers at age(10^6)	Weight (kg)	Biomass (t)
83	3	250	101	1.7	172	6.5	6	3.9
209	0.72	151	588	0.3	176	49	3	147
525	0.11	57.7				253	.11	.28
Density (t·km^{-2}) = 0.109			Density (t·km^{-2}) = 0.083			Density (t·km^{-2}) = 0.051		

The exploitation rates used here were kindly provided by Carl Walters (pers. comm.). Sockeye catches are from the early 1980s and stem from Burgner (1991); pink catches are as reported by Heard (1991) for the years 1980-1989; chum catches stem from Salo (1991) and pertain to the early 1980s.

The area of the Northeast Pacific (i.e., Alaska Gyre) over which the biomass was assumed to be distributed was 4,205,000 km^2, and 30,000 km^2 for the shelf and shelf edge of southern B.C. (from the Southern tip of Vancouver Island up to the Southern tip of the Queen Charlotte Islands, and from depths of 30 to 300 m; see Pauly, this vol.). Table 4 presents catch numbers used in the calculation and estimated biomasses of sockeye, pink and chum salmon.

As stated above, chinook and coho do not have an oceanic phase, i.e., they are only coastal residents. Catches for this species are for DFO statistical areas 11-27 (Table 4).

Diet composition varies with location, season and length of the fish, and Table 6 gives a first example. The "other" category in that table includes identified preys for pink, sockeye, coho and steelhead, and unidentified preys for chum. As chum, with their large stomachs, are known to be specialized to feed on coelenterates (Arai 1988), it may be assumed that the large fraction of their unidentified food consisted of jellyfish.

Table 5 British Columbia chinook and coho catches from statistical areas 11 - 27 from 1980 to 1989 (U = harvest rate; Z = total mortality; year^{-1}; source: DFO, B.C. Catch Statistics Reports).

Coho			Chinook		
U = 0.4			U = 0.4		
Z = 2.32			Z = 0.42		
Catch = 1,666,667			Catch = 100,000		
Weight (kg)	Numbers at age(10^3)	Biomass (t)	Numbers at age(10^6)	Weight (kg)	Biomass (t)
20	250.	5000	4.17	3	12,500
10	380	3805	42.4	1	42,398
2	579	1158	--	--	--
0.1	881	88	----	--	--
Density (t·km^{-2}) = 1.830			Density (t·km^{-2}) = 0.335		

Table 6 Diet composition (% weight) of pink, sockeye, chum, coho and steelhead in the Subarctic Northern Pacific (from LeBrasseur, 1966).

Pred.\Preys	Amphipods	Squid	Fish	Other
Pink	15	75	10	-
Sockeye	20	75	2	3
Chum	1	2	-	97
Coho	-	100	-	-
Steelhead	2	95	1	2

Table 7 presents another example.

Table 7 Diet composition of chinook salmon, in % volume (based on 30 g fish caught off Vancouver Island Healey 1991).

Prey Species	%
Herring	30
Sand Lance	18
Pilchard	7
Anchovy	4
Rockfish	2
Other fish	9
Euphausiids	25
Squids	4
Other invertebrates	1

Healey (1978) also reported on the food and feeding habits of coho salmon in the Strait of Georgia, based on fish with fork lengths of 11.6 - 28.1 cm. The stomach contents were composed of herring, sand lance and unidentified fish remains (32%, by volume); amphipods (33%) and crab megalops (26%). Stomach content as percentage of body weight varied between 0.4% and 1.5%.

Mesopelagics

(Jenny Purcell)

Mesopelagic fishes in the Gulf of Alaska are a multispecies group, characteristically found between 150 - 500 m during the day and between 150 m and the surface at night (Gjøsaeter and Kawaguchi 1980). *Stenobrachius leucopsarus* is the dominant species in trawl catches. Other frequently caught species include *Diaphus theta*, *Tarletonbeania crenularis*, and *T. macropus* (Gjøsaeter and Kawaguchi 1980).

The density of the mesopelagic group in the Gulf of Alaska is estimated at 4.5 $t{\cdot}km^{-2}$ (Gjøsaeter and Kawaguchi 1980). An estimate of P/B for the group, of 0.7 $year^{-1}$, is obtained from the von Bertalanffy growth parameter K = 0.34 $year^{-1}$ for *S. leucopsarus* (Gjøsaeter and Kawaguchi 1980) using an M/K ratio of 2.0.

Important dietary items include copepods, euphausiids, ostracods, amphipods, and small decapods (Gjøsaeter and Kawaguchi 1980). The food consumption of *Diaphus taaningi* was estimated at 0.8% body weight day^{-1}, or 3 x body weight $year^{-1}$ (Baird et al 1975).

Sharks

(Jeffrey Polovina)

The principal oceanic sharks in the Gulf of Alaska are the salmon shark (*Lamna ditropis*) and the blue shark (*Prionace glauca*). Salmon sharks are year-round residents. An estimate of natural mortality for a close relative of the salmon shark, the porbeagle (*Lamna nasus*) is 0.18 $year^{-1}$ (Aasen 1963). Blue sharks are summer visitors which migrate north from transition zone waters (Brodeur 1988). Natural mortality range for blue sharks is 0.18-0.24 $year^{-1}$ (Nakano and Watanabe 1992), which suggests an estimate of P/B of about 0.2 $year^{-1}$ for both species.

Salmon sharks appear to feed primarily on coho, sockeye, pink, and chum salmon but may also consume mesopelagics and other pelagic fishes (Brodeur 1988; Compagno 1984). Blue sharks feed on squid, mesopelagics, saury, and pomfret (Brodeur 1988; Compagno 1984). While food consumption is not known for the salmon or blue sharks, for the mako shark it has been estimated at 3% body weight per day or about 10 times body weight year^{-1} (Stillwell and Kohler 1982).

The densities of salmon shark and blue sharks in the Gulf of Alaska are not known. As a lower bound, the density of sharks, principally blue and salmon, caught as by-catch in the squid driftnet fishery in 1990, is estimated at 0.05t·km^{-2} (Bonfil 1994). Blue sharks are absent from the Gulf of Alaska in winter. Hence, based on ratios of salmon shark to blue shark in the bycatch, the winter shark biomass is probably only one fourth of the summer value (Bonfil, 1994).

Miscellaneous fishes

(P. Livingston)

Pomfret (Brama japonica)

The pomfret is an epipelagic fish species occurring in the subarctic zone of the North Pacific in summer, but apparently not in winter (Brodeur 1988). Relative abundance in the Alaskan Gyre region during the 1980-89 period was lower than in the 1955-58 period (Brodeur and Ware 1995). Northward movement occurs during summer and pomfret reach the northern part of the Gulf of Alaska by September and retreat to the south to spawn during winter i.e., they appear to follow the northward movement of the 10° C isotherm (Trumble 1973). Small pomfret (<30cm FL), are not found north of 44° N in July (Pearcy et al.1993). Pomfret are usually the most abundant non-salmonid fish in the subarctic region of the North Pacific.

The diet of pomfret, as summarized by Brodeur (1988), consists mainly of cephalopods and fish which, in the majority of studies, comprised over 50% of the diet by weight. Other preys, contributing from 11 to 49% of the diet by weight, were euphausiids, amphipods, and decapods. Pearcy et al. (1993) found that squids made up over 75% of the prey volume. Usually, small *Gonatus* spp. (DML <60mm) were found in pomfret taken in the northern Gulf of Alaska. Myctophids were the most frequently occurring fish in the diet of pomfret in the Gulf of Alaska north of 45° N, but saury were also found. Here, diet percentages by weight were estimated using information in Pearcy et al. (1993), leading to the following: 75% small squid; 3% amphipods; 8% mesopelagics; 4% saury; 5% carnivorous zooplankton; 5% large herbivorous zooplankton.

Population-weighted food consumption (Q/B) was estimated as 4.28 year^{-1} using equation (3) of Pauly et al. (1993b), an asymptotic length (L_∞; TL) of 61 cm based on Eschmeyer et al (1983), and data in Shimazaki (1989), from which an asymptotic weight (W_∞) of 3859 g at a temperature of 12° C was obtained.

P/B was estimated to be 0.47 year^{-1} by entering a longevity of 9 years (Savinyck and Vlasova 1994) into the empirical equation of Hoenig (1983), which links longevity and Z, here assumed equal to P/B (see Allen 1971).

Jack mackerel (Trachurus symmetricus)

Jack mackerel distribution is bounded by the 11° C isotherm (Brodeur 1988), and thus ranges further north in summer than in winter. Catch data by Brodeur and Ware (1995) shows that jack mackerel were not exploited during the 1980-89 period in the Alaska Gyre.

The diet of jack mackerel, summarized by Brodeur (1988), consists primarily of euphausiids, which make up over 50% of stomach content by weight, the rest being contributed by copepods, decapods, pteropods, cephalopods, and fish.

Key parameters are $P/B = 0.5$ year^{-1}, and $Q/B = 7.0$ year^{-1} (Jarre-Teichmann and Christensen, in press).

Saury (Cololabis saira)

Saury is the dominant small pelagic fish in the subarctic zone in summer (Brodeur 1988). This species is not well-sampled by the gill nets used on the high-seas, and its abundance is not known (Brodeur and Ware, 1995). Saury exhibit a preference for water temperatures in the 15-18° C range (Kasahara 1961), and is not present in the Alaskan gyre during winter.

The diet of saury consists primarily of copepods, which comprise over 50% of the stomach contents by weight. Euphausiids, amphipods, decapods, and fish contribute the rest (Brodeur 1988). Also, we have (from Hughes 1974): $L_\infty = 35$ cm (TL), $K = 0.34$ year^{-1}, and $M = P/B = 1.6$ year^{-1}.

A Q/B value of 7.9 year^{-1} was obtained using the empirical model of Palomares and Pauly (1989), with $W_\infty = 193$ g (Hughes 1974), a mean habitat temperature of 15°C, and a caudal fin aspect ratio of 2.

Daggertooth (Anotopterus pharao)

Welch et al. (1991) present evidence showing that *Anotopterus pharao*, a specialized member of the order Myctophiformes (Fam. Anotopteridae) reaching some 85 cm (TL), attacks adult Pacific salmon (*Oncorhynchus* spp), and may be able to ingest juveniles.

They further report that, "as up to 12% of adult sockeye salmon returning to British Columbia bear slash marks, the potential significance of *A. pharao* as a cause of mortality for juvenile salmon needs to be evaluated".

Unfortunately, no data appear to exist on the abundance of *A. pharao* in the North Pacific, or on its diet, and it is thus difficult to follow up on this suggestion here.

Marine Mammals

(Andrew Trites and Kathy Heise)

Thirteen species of marine mammals feed in the Gulf of Alaska gyre during summer and winter. These were grouped into five categories: pinnipeds, toothed whales, baleen whales, beaked whales and killer whales (resident and transient). Estimates of mean body weight (wet, i.e., live weight) for males and females of each species were obtained from Trites and Pauly (in prep.). Population estimates were obtained from published sources or educated guesses based on the best available information, such as Northridge's (1991) global population estimates. Unless otherwise stated, individual ration (R, in % of body weight day^{-1}) was estimated for each species and sex using:

$$R = 0.1 \cdot W_{i,s}^{0.8}$$

where $W_{i,s}$ is the mean body weight in kg of species (i) and sex (s), 0.8 is from Eq. 23 in Innes et al. (1987), and 0.1 is a downward adjusted value (from 0.123 in Innes et al.), which account for the difference between ingestion for growth and ingestion for maintenance.

Estimates of daily ration ranged from 1.7% of body weight in a 6,100 kg minke whale (107 kg day^{-1}), to 5% of body weight per day in a 32 kg harbour porpoise (1.6 kg day^{-1}), and are compatible with present knowledge of the biology of large and small marine mammals (Bonner 1989). Dietary composition was determined from stomach and fecal remains reported in published sources for each species (e.g., Perez 1990). Dietary composition for pinnipeds, toothed whales, baleen whales and beaked whales was set equal to the mean diet of the species within the grouping, weighted by the relative population abundance and daily ration estimates for each species.

Detailed summer and winter population and prey composition data for all 13 marine mammal species are summarized in Appendix 1, Tables A - C. Additional information concerning the assumptions and estimates used for each species of marine mammal in the Alaskan gyre is given below.

Pinnipeds

Northern fur seals and northern elephant seals are found in the Alaska gyre in both summer and winter. A third species, the Steller sea lion, feeds in the gyre during winter. The maximum rate of population growth for northern fur seals and other pinnipeds is believed to be about 12% (Small and DeMaster 1995). The P/B ratio was therefore set at 6%, half of the maximum.

Northern fur seals (*Callorhinus ursinus*) from the Pribilof Islands numbered 1,019,192 in 1994 (Small and DeMaster 1995). Their annual migration extends from the Bering Sea to the coastal waters of California. Much of the population migrates through the Western Gulf of Alaska from April to July (Bigg 1990). Between 10% and 25% of the population feed in the Alaska Gyre on their return to the breeding islands in the Bering Sea (10% in April, 25% May, 23% June, and 20% July, as calculated from the number of fur seals sighted in all areas of the north Pacific during pelagic surveys shown in Figure 8 of Bigg (1990). This represents 13% of the total population over the 6 summer months or 130,000 fur seals per month. 5,000 fur seals were assumed to be present from October to March, given that few, if any, appear to be in the gyre during winter (Bigg 1990). The ratio of males to females was assumed to be 1:4 in both seasons. Mean body weight of males (30.2 kg) and females (25.3 kg) were taken from Trites and Pauly (in prep.).

Dietary information was based on stomach contents from fur seals shot at sea from 1956 to 1972 (Perez and Bigg 1981, 1986). The Gulf of Alaska gyre corresponds to Area 16 of the fur seal pelagic survey (Table 19 of Perez and Bigg 1981) where, in the summer, the animals eat predominately squid (78%), salmon (11%), rockfish (8%), and pollock (3%). While no animals have been collected in the gyre during the winter, it is reasonable to assume that a few must feed here.

Without dietary information it was assumed that the animals had consumed a generic diet, taken from Pauly et al. (1995).

Northern elephant seals (*Mirounga angustirostris*) make biannual migrations from the breeding beaches in California to deep waters of the Gulf of Alaska (DeLong et al 1992; LeBoeuf 1994; Stewart and DeLong 1994, 1995). Males go further north than females and may feed in the Alaska Gyre for 30-50 days of each trip, before returning south. It was assumed that 40% of the male population spent up to one month in the gyre in the summer and another month feeding in the area in winter. Given the current population estimate of 127,000 elephant seals (Stewart et al. 1994) and an assumed sex ratio of 50%, approximately 4,000 males should be present in each of the 6 months of summer and winter.

In the absence of dietary information for elephant seals feeding in the Gulf, it was assumed that they ate 40% small squid, 20% dogfish, 10% rockfish, 10% sablefish, 10% hake and 10% miscellaneous demersal fish, based on dietary composition estimates from elephant seals sampled in California (Antonellis et al. 1984). Mean body weight was taken from Trites and Pauly (in prep.).

Steller sea lions (*Eumetopias jubatus*) breed on offshore rocks and islands from California to northern Japan. They generally feed within 20 km of shore during summer, but venture several hundred km during winter (Merrick 1995). The western Gulf of Alaska population numbered approximately 15,000 in 1994 (Trites and Larkin 1996) and has declined by over 65% since 1980. Winter diet is not precisely known, but was assumed to consist of 15% squid, 20% small pelagic fishes (capelin, mackerel, herring), and 65% large pelagic fishes (mostly pollock), based on dietary information compiled by Merrick (1994). Mean body weight was taken from Trites and Pauly (in prep.).

Baleen Whales

Three species of baleen whales are found in the Alaska gyre during summer months: blue, fin and sei whales. Minke and humpback whales are primarily coastal species (Leatherwood et al. 1982; Jefferson et al. 1993) and were not considered to occur in significant numbers in the gyre. All of the baleen whales show seasonal movements into southern latitudes in winter months (Leatherwood et al. 1982), and are not present in the gyre in winter.

The maximum rate of population increase assumed for baleen whales is 4% (Reilly and Barlow 1986) and production was estimated to be 2% (half of r_{max}). Much of the information on distributions and diet was obtained through historical whaling accounts from the coast of Japan, the Gulf of Alaska and the coast of British Columbia (see, e.g., Scammon 1874; Townsend 1935; Nemoto 1959; Nichol and Heise 1992).

Blue whales (*Balaenoptera musculus*) wintering off the coast of California and Mexico number 1,700 (Small and DeMaster 1995), but no estimates are available for populations summering further north. The Gulf of Alaska is the northern limit of the range of blue whales (Jefferson et al. 1993). An evenly distributed summer population size of 1,700 animals (range 1,000-3,000) was assumed.

Blue whales consume 40 g of food per kg of body weight per day during the summer feeding season and increase their body mass by 50% (Lockyer 1981b). Dietary information obtained from historical whaling accounts from Japan and British Columbia show blue whales to feed primarily on euphausiids (95%) and occasionally on copepods (5%) (Nemoto 1959; Nichol and Heise 1992).

Fin whales (*Balaenoptera physalus*), like blue whales, extend their feeding range into the Gulf of Alaska during the summer months. Fin whales increase their weight by an estimated 30% over the summer months, with a daily ration of about 40g per kg body weight (Lockyer 1981b). Dietary information obtained from historical whaling accounts indicates that fin whales feed on euphausiids (75%), copepods (20%), and fish (5%) (Nemoto 1959, Nemoto and Kawamura 1977, Nichol and Heise 1992).

Fin whales, once the most abundant baleen whale in the world's oceans (Evans 1987), were commonly taken by whalers, but are presently listed as endangered (Small and DeMaster 1995). Current population estimates range from 17,000 to 20,000 in the North Pacific (Evans 1987; Gambell 1985a).

Sei whales (*Balaenoptera borealis*) are primarily an offshore species with an estimated population of 14,000 animals in the North Pacific (Gambell 1985b). Like other baleen whales, they move into cooler waters in summer to feed and move into lower latitudes in winter to breed. It was assumed that they feed at approximately the same summer feeding rate as do the other baleen whales (4% of body weight$\cdot$day^{-1}, Lockyer 1981b). Based on historical whaling data, sei whales feed primarily on copepods (80%), followed by small squid (5%) euphausiids (10%) and small pelagic fish (5%) (Nemoto 1959; Nichol and Heise 1992).

Toothed Whales

Dall's porpoises, killer whales and sperm whales are found in the Alaskan gyre in summer. The maximum rate of population increase for all toothed whales is believed to be 4% (Reilly and Barlow 1986) and annual production was estimated to be 2% of biomass (half of r_{max}).

Sperm whales (*Physeter macrocephalus*) are found in the gyre in summer only, and all individuals are mature males. Much of the information available on the distribution and diet of sperm whales was obtained through historical whaling accounts from the coast of Japan, the Gulf of Alaska and the coast of British Columbia (e.g. Townsend 1935, Nichol and Heise 1992). According to Townsend (1935), sperm whales north of 49° N were "stragglers" from the breeding groups of sperm whales found further south. It was assumed that 2,000 sperm whales were present in the Pacific north of 45° N in summer. The average weight of mature sperm whales in the Antarctic was 27.4 t, and they consumed approximately 3% of their biomass per day (Lockyer 1981a). These parameters were assumed to apply to the mature males found in the gyre in summer.

Diet information from the Gulf of Alaska was not available, and thus, historical records of the stomach contents of 501 whales harvested off the west coast of Vancouver Island (Nichol and Heise 1992) were used here. They indicate that sperm whales feed primarily on large squid (80%), but also consume small squid (5%). Fish were also consumed, notably the ragfish *Icosteus aenigmaticus* (15%).

Resident killer whales *(Orcinus orca)* in British Columbia and in Prince William Sound, Alaska eat fish (Bigg et al. 1990; Heise et al. 1992; Ford et al. 1994). Approximately 238 resident whales live in the Gulf of Alaska and the Bering Sea. Diet information from stomach contents is not available for this area, but there are many reports of killer whales raiding commercial longline gear in the Gulf of Alaska and in the Bering Sea. Based on this, and on studies of killer whales from other areas, resident killer whales in the Gulf of Alaska gyre are assumed to eat primarily salmon (80%), as well as large (10%) and small pelagics (10%). The winter diet is assumed to contain less salmon (60%), and an increased number of large and small pelagics (20% each). Adjusting for the age structure of the killer whale population and the caloric value of prey, Barrett-Lennard et al. (1995) estimated that male and female killer whales consume 84.6 kg and 84.1 kg respectively of food per day, which is slightly higher than would be predicted from the empirical equation of Innes et al. (1987).

Olesiuk et al. (1990a) estimated a production of 2.92 % year^{-1} for resident killer whales in British Columbia, while Small and DeMaster (1995) used r_{max} = 4%, a value that is considered conservative for most cetaceans (Reilly and Barlow 1986). Thus, we assume a P/B ratio of 2% for resident killer whales. Barrett-Lennard et al. (1995), based on data in Bigg et al. (1990), estimated the sex ratio of female to males to be 0.64:0.36. Mean body weight estimates are 2,587 kg for males and 1,973 kg for females (Trites and Pauly, in prep.).

Approximately half of the 88 transient (mammal-eating) killer whales that utilize the waters of western Alaska and the Bering Sea (Barrett-Lennard et al. 1995) are assumed to occur in the Gulf of Alaska. While no diet information is available from stomach contents of whales in this area, it is reasonable to assume that it is similar to transients from other areas. Based on Barrett-Lennard et al. (1995), summer diet was assumed to comprise 50% toothed whales (predominantly Dall's porpoises), 40% baleen whales and 10% pinnipeds. In winter, it was assumed that transients spent more time foraging in nearshore areas, yielding an estimated population of only 22 animals, and a diet composition of 60% toothed whales and 40% pinnipeds. The sex ratio for resident and transient killer whales was assumed to be the same (0.64:0.36 female : male). Marine mammal prey has higher caloric value than that of fish (Perez 1990), and Barrett-Lennard et al. (1995) estimate that male and female transients consume 73 kg of prey per day.

Dall's porpoises (*Phocoenoides dalli*) are widely distributed throughout the north Pacific. Hobbs and Lerczak (1993, in Small and De Master 1995), estimated an abundance of 106,000 animals for the Gulf of Alaska. Applying a correction factor for vessel attraction (0.2, based on Turnock and Quinn 1991) gives a population abundance estimate of 21,200 (range 15,000-30,000) for the Gulf of Alaska. This estimate was used for both summer and winter models because Dall's porpoises do not appear to show strong seasonal movements (Green et al. 1992). Mean body weight estimates for males and females were 63.1 kg. and 61.4 kg, respectively (Trites and Pauly, in prep.).

The food consumption of Dall's porpoises was estimated from the equation presented above, adapted from Innes et al. (1987). The diet of Dall's porpoises from the Gulf of Alaska is not known, but Klinowska (1991) lists Pacific mackerel, sardines, saury, and squid as occurring in the diet of animals taken in the western north Pacific. The diet composition retained here is based on the stomach contents of 28 animals taken off the coast of Japan, analyzed by Wilke et al. (1953), and consisting of mesopelagics (70%), small squid (20%) and small pelagics (10%).

Beaked Whales

The maximum rate of population increase for all toothed whales is believed to be 4% (Reilly and Barlow 1986) and the production for beaked whales was set at half this value.

Baird's beaked whales (*Berardius bairdii*) are the largest of the beaked whales and may attain lengths of up to 14 m, and ages of up to 84 years (Rice 1986; Klinowska 1991). Barlow et al. (1995) estimate a total of 19 Baird's beaked whales off the coasts of California, Oregon and Washington. As the species is primarily pelagic, an evenly distributed population of 10,000 was assumed across their range (from Jefferson et al. 1993). However, most animals in the north Pacific move south in winter (Tomilin 1957). The sex ratio of adult Baird's beaked whales appears to be strongly biased towards males; for example, only 3 of 24 whales caught off Coal Harbour between 1948 and 1967 were females (Rice 1986). A male to female sex ratio of 3:2 was assumed.

Rice (1986) found primarily medium-sized squid in the stomachs of animals harvested by California whalers. Klinowska (1991) cites benthic fish and cephalopods in the stomachs of animals harvested in the western Pacific. Tomilin (1957) reports a predominance of squid in the diet, with rockfish, skate and sardines occurring less frequently in animals harvested by Soviet whalers. A diet composition of 35% large squid, 30% small squid, 25% large pelagics and 10% small pelagics was assumed.

Stejneger's beaked whales (*Mesoplodon stejnegeri*) inhabit cold temperate and subarctic waters, rarely ranging below 45° N in the eastern north Pacific (Jefferson et al. 1993). They are one of the more common species found stranded in Alaska (Zimmerman 1991), but are rarely seen at sea. It was assumed that Stejneger's beaked whales are present year round in the Gulf of Alaska gyre because there is no seasonality to the strandings. Given no reliable population estimates are available for this species, density was based on an estimated population size of 1,000 averaged across the entire area of their distribution, which agrees with the order of magnitude estimate of Northridge (1991). Diet is primarily squid if one can trust the two stomach contents reported in Klinowska (1991), and the information in Tomilin (1957).

Cuvier's beaked whales (*Ziphius cavirostris*) are perhaps the most abundant of the beaked whales, with an almost cosmopolitan distribution. Barlow et al. (1995) estimate 886 animals off the coasts of Washington, Oregon and California. A population size of 1,000 animals was assumed with no seasonal changes in the distribution or feeding behavior. Tomilin (1957) reports squid in the stomach of one specimen. which, in the absence of more information, was assumed to be the sole prey of this species.

Seabirds in the Alaskan Gyre

(John Kelson, Yoshihiko Wada and Suzann Speckman)

Sooty and short-tailed shearwaters dominate the avifauna on the outer coast of the Gulf of Alaska, both numerically and in terms of biomass. A variety of prey species are used by seabirds in the Gulf; of these, capelin, sand lance, and euphausiids are of greatest importance. Trophically, seabirds in the Gulf range from near primary consumers to third-order carnivores (Sanger 1987), ingesting an estimated 1,120,000 t during the 120-day summer period (DeGange and Sanger, 1986). The P/B ratio of these birds could not be estimated using the data at hand, and was assumed = 0.1 $year^{-1}$, based on contributions in Christensen and Pauly (1993). Values express an average for the summer months, from April to September (see also Wahl et al. 1989). Body weights were obtained mainly from Palmer (1962), but in some cases, they were estimated from length and related to similar species. Body weights and diet compositions for petrels, jaegars, phalaropes and albatrosses were combined, assuming that body size and prey species were similar. A few rare prey species were omitted from the diets, as were unusual feeding events, such e.g., as a glaucous-winged gull eating an ancient murrelet.

Table 8 summarizes our population estimates, which lead to an overall biomass of $0.0055 t \cdot km^{-2}$, and to Q/B = 101 $year^{-1}$. Table 9 presents the diet composition of seabirds in the Alaska gyre; see Wada (this vol.) for the estimation of consumption rates.

Table 8 Biological and population statistics of marine birds in the Alaska gyre.

Species	**Body weight**	**Daily ration**	**Q**	**Population**	**Consumption.**
(Unit)	(kg)	(% W)	(kg $year^{-1}$)	($N \cdot km^{-2}$)$^{-}$	($kg \cdot year^{-1} km^{-2}$)
Cassin's auklet	0.15	35.2	19.3	0.010	0.19
Common murrelet	0.8	27.4	79.9	0.010	0.80
Arctic terns	0.15	35.2	19.3	0.250	4.82
Tufted puffin	0.6	28.6	62.6	0.010	0.63
Horned puffin	0.55	28.9	58.1	0.010	0.58
Black-footed albatross	3.09	22.3	252.1	0.060	15.12
Jaegars	1	26.5	96.6	0.110	10.63
Sooty shearwater	0.79	27.4	79.1	3.500	276.76
Short-tailed shearwater	0.46	29.7	49.9	0.550	27.46
Northern fulmar	0.78	27.5	78.2	1.800	140.80
Glaucous-winged gull	1.16	25.9	109.6	0.400	43.84
Mottled petrel	0.35	31.0	39.6	0.550	21.77
Fork-tailed storm-petrel	0.048	41.7	7.3	1.610	11.77
Leach's storm-petrel	0.048	41.7	7.3	0.550	4.02
Black.-legged kittiwake's	0.2	33.7	24.6	0.060	1.48
Phalaropes	0.03	44.8	4.9	0.005	0.02
Sums	-	-	-	**9.49**	**560.69**

Table 9 Diet composition of seabirds in the Alaska gyre.

	Food items[a]							
Bird Species	**Crust.**	**Ceph.**	**Cop.**	**Euph.**	**Dec.**	**S. pel.**	**L. pel.**	**Benth.**
Cassin's auklet	-	1.1	76.7	3.5	14	4.7	-	-
Common murre	-	0.1	-	3.2	1	74.5	11.7	-
Arctic terns	0.1	-	-	95.6	0.1	2.9	-	0.1
Tufted puffin	-	7.8	-	11.2	-	80.6	0.6	-
Horned puffin	0.2	1.2	-	0.5	-	98	0.1	-
Black-footed albatross	-	100	-	-	-	-	-	-
Jaegars	-	-	-	-	-	90	10	-
Sooty shearwater	0.2	26.6	-	1.5	-	71.8	-	0.1
Short-tailed shearwater	0.1	2	-	72.4	-	23.6	0.1	1.8
Northern fulmar	0.7	96.3	-	0.2	-	2.2	0.6	0.2
Glaucous-winged gull	0.2	-.	-	0.4	0.3	95.4	-	1.6
Mottled petrel	-	70	-	20	10	-	-	-
Fork-tailed storm-petrel	-	60.7	-	22.3	3	4.2	1.7	1.3
Leach's storm-petrel	-	70	-	20	10	-	-	-
Black-legged kittiwake's	0.6	0.1	-	10.4	0.2	79.9	1.2	2.2
Phalaropes	-	10	30	30	30	-	-	-
Overall contr. (%)	**0.3**	**44.74**	**0.021**	**5.93**	**0.47**	**47.79**	**0.4**	**0.34**

a) Crustaceans, Cephalopods, Copepods, Euphausiaceans, Decapods (crabs), Small pelagics, Large pelagics, Benthos.

Balancing the Alaska gyre model

(Villy Christensen)

Only few modifications had to be made to the input data in order to balance the Alaska gyre model.

One of these was the introduction of a “squid box”, suggested by their importance in the diet of various groups. However, given the scarcity of information on squids biomass and related parameters in the North-eastern Pacific, this box was based largely on model-generated constraints, i.e., squid production was estimated from the requirements of squid predators. Other inputs were a Q/B value set at 15 year^{-1}, and a diet composition composed of 40 % herbivorous zooplankton, 40 % krill, 5% crustaceans other than krill, 5 % squids (i.e., cannibalism) and 5 % pelagic fishes.

Another modification was to account for the fact that the marine mammals could not accommodate the predation pressure exerted by the transient killer whales. This was corrected by making 75% of killer whale diet be an import, i.e., the transient orcas feeding in the Alaska gyre system are assumed to take 75% of their food outside of that system. This may or may not be a good assumption – what matters is that, with the data available, this was a possible solution. Another solutions may be that the number of killer whalers was overestimated.

Table 10 Basic parameters for the Alaska gyre model. (Estimated parameters are shown in brackets). Biomasses are given in t·km^{-2}·year^{-1}, while production/biomass (P/B) and consumption/biomass (Q/B) are both annual rates. EE is the ecotrophic efficiency, expressing the proportion of the production that is lost to exports or predation mortality.

Group	Biomass	P/B	Q/B	EE
Phytoplankton	15.200	175.00	0.0	(0.95)
Bacteria	11.000	18.50	25.0	(0.45)
Microzooplankton	1.700	63.00	210.0	(0.93)
Small herbivor. zooplankt.	25.000	27.00	90.0	(0.22)
Salps	8.000	9.00	30.0	(0.00)
Carnivorous zooplankton	(0.579)	3.00	10.0	0.95
Jellies	9.100	3.00	10.0	(0.02)
Krill	(4.648)	3.00	15.0	0.95
Squids	(2.630)	3.00	15.0	0.95
Other crustaceans	(1.683)	4.00	13.3	0.95
Pink	0.083	2.45	12.2	(0.35)
Sockeye	0.109	0.92	4.6	(0.71)
Chum	0.051	1.64	8.2	(0.84)
Steelhead	0.100	1.00	5.0	(0.80)
Mesopelagics	4.500	0.70	3.0	(0.62)
Small pelagics	1.894	1.60	7.9	(0.95)
Sharks	0.050	0.20	10.0	(0.05)
Large fish	(0.718)	0.47	4.3	0.95
Pinnipeds	0.072	0.06	16.9	(0.65)
Toothed whales	0.097	0.02	5.4	(0.78)
Baleen whales	0.256	0.02	14.6	(0.24)
Beaked whales	0.003	0.02	7.5	(0.00)
Orca (transient)	0.001	0.02	12.1	(0.00)
Marine birds	0.006	0.10	101.0	(0.00)
Detritus	0.000	-	-	(0.27)

The ecotrophic efficiencies of the marine mammals is generally on the high side. This may indicate that their production (biomass and/or P/B) is underestimated, or that the predation is overestimated, as discussed above.

The basic parameters for the model are given in Table 10, while detailed diet compositions are given in Appendix 1, Table E. The flowchart of the model is given in Figure 1, while Figure 2 presents the mixed trophic impacts within the Alaska gyre ecosystem.

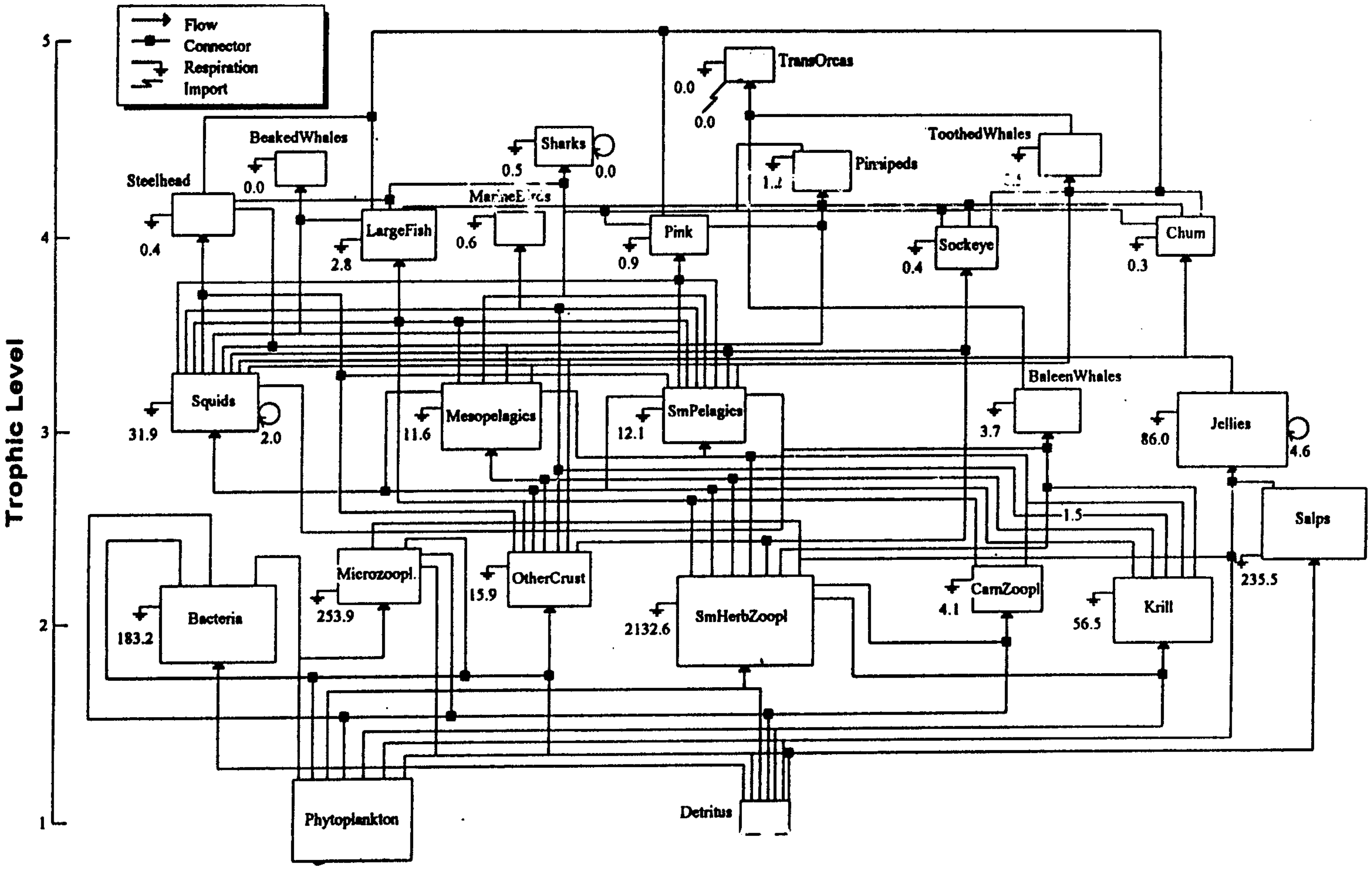

Figure 1 Flow chart of trophic interactions in the Alaskan gyre system. All flows are expressed in t·km^{-2}·year^{-1} and all biomasses in t·km^{-2}; minor flows are omitted, as are all backflows to the detritus. Note that total area of system is not defined, i.e., the flow chart may be seen either as representing only its core, or include much of its periphery.

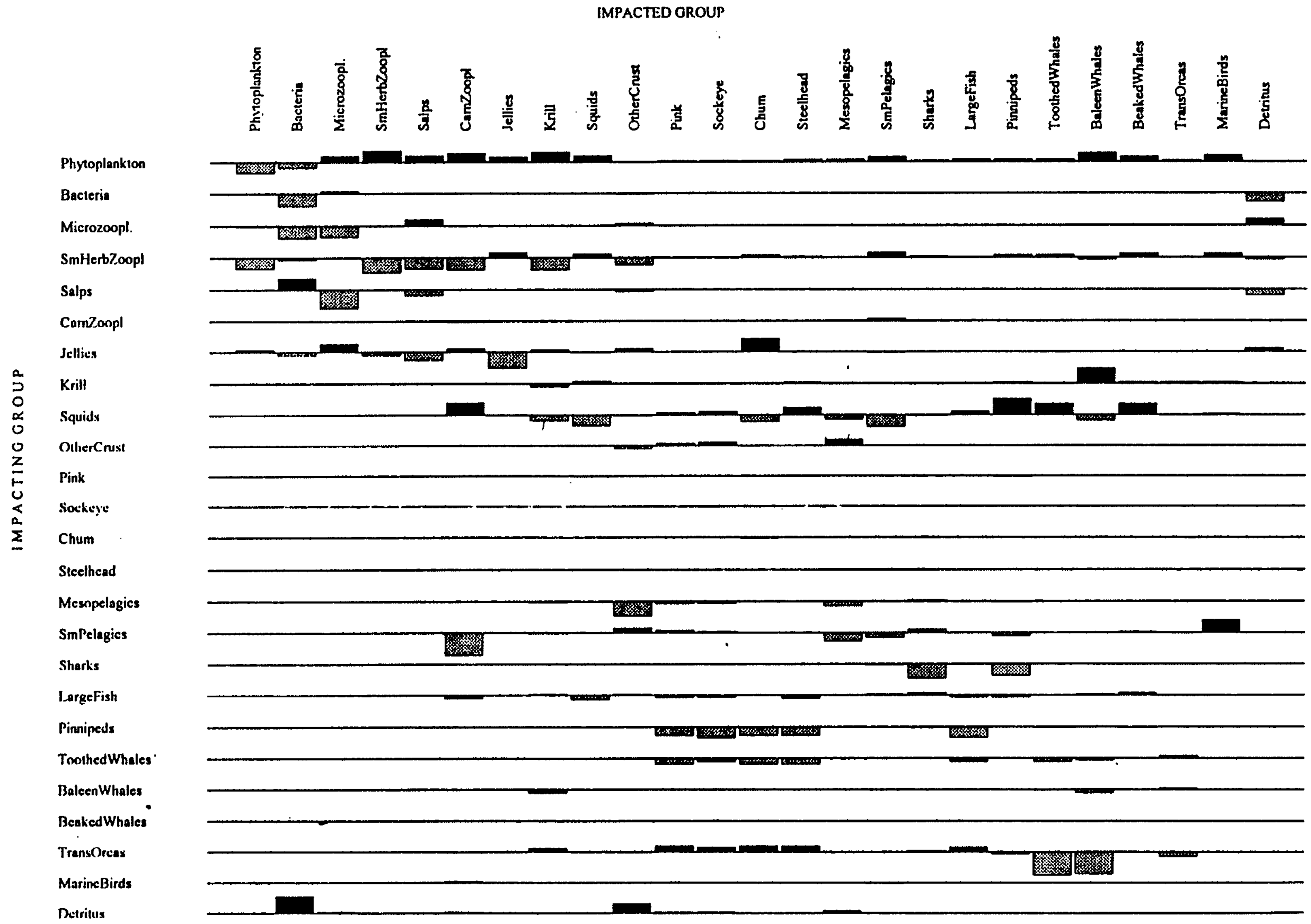

Figure 2 Mixed trophic impacts in the Alaska gyre ecosystem, generated by Ecopath, and illustrating how an infinitesimal increase in one of the groups would affect the other groups. (The scale is relative, but may be used for comparisons among groups). Note indirect effects, indicative of trophic cascades.

The model was easily balanced at the lower trophic levels, and the balance thus obtained seems very plausible. It is interesting though that the EE of phytoplankton is very close to 1, indicating a full utilization of the phytoplankton within the system. On the other hand, the EE of small herbivorous zooplankton is only 0.22, so that less than a quarter of the small zooplankton production is utilized. It is not clear if this is an artefact [shifting a larger proportion of the zooplankton feeding to large zooplankton (chaetognaths) would have increased the biomass of these, which in turn would have lead to a demand for, and hence higher utilization of the small zooplankton]. However, artificially shifting a major part of zooplankton feeding toward the larger zooplankton is not enough to strongly increase the utilization of small herbivorous zooplankton. Their concentration and production is simply too high.

Interestingly, a major purpose of the SUPER project mentioned above earlier was to seek an explanation for the continuous absence of phytoplankton blooms in the offshore regions of the subarctic Pacific (Miller 1993). The absence of blooms is well in line with the present finding that the zooplankton is very productive, and capable of constraining the phytoplankton.

The above considerations are only meant to illustrate the kind of results that can be obtained from Ecopath modelling By placing the data in a rigid network, information is obtained. Some parameter combinations are simply not possible, and the present approach is indeed good for identifying inconsistencies. Much more could be done using tools for analysis built into the software (see, e.g., Figure 2).; we abstain, however, from presenting more here, until a winter model has been constructed for the area. Indeed, we expect that much would be gained by explicitly considering seasonal oscillations of mass-balance models, e.g., in the framework presented by Walters (this vol.).

SOUTHERN B.C. SHELF MODEL

The area covered

(D. Pauly)

The southern coast of British Columbia as defined here ranges from nearshore waters (about 10 m) to the shelf slope (300m), from the southern tip of the Queen Charlotte Islands in the North, along the Pacific Ocean coast of Vancouver Island to the Juan de Fuca Strait in the South, and thus excludes the Hecate, Charlotte, Johnstone, and Georgia Straits.

The system thus defined covers approximately 30,000 km^2, and is, in fact, so open to adjacent water bodies that it cannot legitimately be considered a distinct ecosystem. However, recurrent groups of interacting species of fish and invertebrates do occur in the area thus defined, and various biomass and flux estimates have been published by authors who (at least implicitly) must have assumed some degree of integration among these groups. Thus, for pragmatic reasons, we shall treat the above-defined area as if it identified the boundaries of a mass-balanced ecosystem, but return later to the open nature of the "ecosystem" defined here.

Primary production in the area has been estimated as 345 gCm^{-2} $year^{-1}$ by Robinson et al (1993), who also reviewed the oceanography of the Southern B.C. shelf.

Euphausiids, Chaetognaths and Herbivores

(Jenny Purcell)

Euphausiids

A first estimate of euphausiid biomass can be obtained by averaging the entries of Table 2 in Fulton et al. (1982), and this amounts to 3.8 ± 7.3 g wet $weight{\cdot}m^{-2}$. Another rough estimate is 0.65 g dry $weight{\cdot}m^{-2}$ (Mackas et al. 1992), corresponding to about 2.8 g wet $weight{\cdot}m^{-2}$ (Sambilay 1993).

Chaetognaths

A very approximate biomass for chaetognaths of 0.3 g dry weight m^{-2} was obtained from Mackas et al. (1992), and this translates to 3 g wet weight· m^{-2} if we assume dry weight = 10% wet weight. The diet consists almost exclusively of zooplankton (mostly copepods).

Salps

Biomass is 0.5 ± 0.5 $g{\cdot}m^{-2}$ dry weight (from Mackas et al. 1992); if we assume dry weight equal to 10% of wet weight, then biomass is about 5 g m^{-2} (wet weight).

The diet probably consists predominantly of phytoplankton, with a minor microzooplankton contribution.

Copepods

Biomass was estimated as 1.825 ± 0.9 g dw m^{-2} by Mackas et al. (1992, Figure 9). If we assume dw = 10.9% wet weight (Sambilay 1993), then biomass = 16.7 g wet weight m^{-2}.

The diet (in the Gulf of Alaska) is a mix of phyto- and microzooplankton, viz. 91.5% phytoplankton and 8.5% microzooplankton.

Invertebrate Benthos

(Astrid Jarre-Teichmann and Silvie Guénette)

A survey in the mid-1980s (Brinkhurst 1991) revealed that the benthic fauna of the southern B.C. Shelf is complex, with all major groups present (c.f. with Kozloff 1987). Thus, species composition in any one area depends on the substrate as well as on the oxygen condition. Polychaetes are dominant, bivalves are less widespread, but still common. Ostracods, harpacticoids, cumaceans, tanaids and amphipods dominate the small benthic crustaceans. Brittle stars, a heart urchin and a holothurian were also present.

In the absence of local estimates, Brey's (1995) database on macrobenthic productivity was used to obtain rough estimates of P/B and related statistics for the major benthic groups. Sea stars, sea urchins and sea cucumbers, benthic cnidarians and sponges were not considered, because their role as prey items to fish appears to be very limited. Table 11 lists the most abundant benthic groups and their P/B estimates.

Table 11 Benthic groups and their P/B ratios, southern shelf of B.C.

Functional group	**Abundant species on the southern B.C. shelf**[a]	**Species for which P/B estimates exist in a similar temperature range (point estimate, or range; year^{-1})**[b]	**P/B adopted (year^{-1})**
Polychaetes	*Mediomastus ambiseta, Galathowenia oculata, Prionospio steenstrupi, Aricidia ramosa, A. lopezi, Levinsenia gracilis, Cosssura soyeri, C.* sp., *Spiophanes berkleyorum, Glycera capitata, Sphaerosyllis brandhosti, Tharyx seconds, Nototmastus lineatus, Chaetozone* spp.	*Euzonus mucona* (1.8), *Pectinaria californiensis* (3.2-5.4), *Paraprionospio* sp. (1.2-2.0), *Aricidia* spp. (1.3-2.6), *Spiophanes bombyx* (1.5-4.7), *Glycera alba (*1.0), *Chaeozone setosa* (1.3)	2.0
Bivalves	*Axinopsida serricata, Adontorhina cyclia, Yoldia scissurata, Y. thraciaeformis, Macoma elimata, M. carlottensis, Huxleya minuta, A. cyclica*	*Yoldia thraciaeformis* (0.8) *Y. notabilis* (0.4-0.8) *Macoma balthica* (0.8) *Tegula funebralis* (0.4)	0.7
Small crustaceans	Cumacea: *Eudorella pacifica, Leucon nasica, Lamphrops serrata* Tanaidacea: *Cryptocope* spp. Amphipoda: *Harpiniopsis* spp., *Heterophoxus oculatus, Amphelisca* spp.	Cumacea: *Diastylis rathkei* (2.0-2.7) Amphipoda: *Harpinia propinqua* (3.8) *Ampelisca* spp. (0.9-5.2)	2.5
Brittle stars	*Amphioplus macraspis, A. strongyloplax, O. sarsi*	*Ophiura* spp. (0.3-1.3)	0.6

[a]from Binkhurst (1991)
[b]from Brey (1995) and references therein

Table 12 Suggested production:biomass ratio (P/B; year^{-1}), gross conversion efficiency (GE), and ecotrophic efficiency (EE) for major benthic groups of the Southern B.C. shelf.

Group	P/B	GE	EE
Polychaetes	3.0	0.09	0.95
Bivalves	0.5	0.09	0.80
Amphipods	2.4	0.20	0.95
Brittle Stars	1.8	0.20	0.80
Sea urchins	0.4	0.09	0.60
Sea stars	0.4	0.09	0.60
Shrimps	0.7	0.15	n.a.
Crabs	1.8	0.25	0.95

Benthic shrimps (*Pandalus jordani*) are commercially exploited off the west coast of Canada (Boutillier 1991). Their biomass is estimated at 0.3 g m^{-2} , and their production at 0.7 g·m^{-2}·year^{-1}. Their diet composition, based on Dahlstrom (1970) was assumed at 30% polychaetes, 25% amphipods, and 35% detritus.

Table 13 Diet composition used for the benthic groups in the model of the southern B.C. shelf (from Brey, 1995).

Group in model	Diet composition (% weight or volume)
Polychaetes	100 detritus
Bivalves	100 detritus
Small benth. crust.	90 detritus, 10 zooplankton
Benthic shrimps	35 detritus, 35 amphipods, 30 polychates.
Benthic crabs	60 detritus, 20 bivalves, 15 benthic shrimps, 3 benthic crabs, 2 other demersals
Sea stars	30 detritus, 40 molluscs, 30 polychaetes
Brittle stars	80 detritus, 18 small benth. crust., 2 polych.

Dungeness crabs (*Cancer magister*) are also exploited off British Columbia. Their total mortality was estimated at 0.7 year^{-1}, and their diet composition as 17% shrimps, 20% bivalves, 3% cannibalism, 2% fish and 58% detritus (based on Stevens 1982).

As Q/B estimates were available for neither of the benthic groups, they were estimated (Table11) based on a range of mean gross efficiencies of 9% for herbivores/ detritivores, and 30% for carnivores (Brey 1995).

With the exception of shrimps, no benthic biomass figures were available. As a guide to balancing the model, we suggest: B (polychaetes) > B (medusae) > B (amphipods). Table 12 presents our estimated Production: Biomass ratio (P/B), Gross conversion Efficiency (GE), and Ecotrophic Efficiency (EE) for major benthic groupings.

The assumed diet composition of benthic invertebrates in the Southern B.C. shelf region is summarized in Table 13.

Carnivorous Jellies

(Mary Arai)

Summer dry weights for ctenophores, hydromedusae and siphonophores on inner shelf banks and off southwestern Vancouver Island were estimated as 2.6 g dry weight·m^{-2} (Mackas 1992). Dry weight was assumed to be 4.2% of wet weight (Larson 1986), leading to a biomass for the carnivorous jelly group of 6.19 g wet weight·m^{-2}. This is probably an underestimate, as scyphozoa, which are not well sampled by Bongo and other zooplankton nets, are not included. [Dense swarms of scyphozoan occur in late summer in the neritic zone off Oregon and southern Washington, and contain at least 80% as much carbon as the corresponding copepod concentrations].

P/B estimates range from 7 to 30 year^{-1} (Larson 1986), while the minimum estimate, based on a generation time, is 6 year^{-1} + mortality rate. For these and other gelatinous animals, the "degrowth" known to occur under low food conditions, is not considered here.

An approximate diet composition for the group as a whole was derived from data in Hirota (1974), and Purcell (1990), viz

Small herbivorous zooplankton	62%
Eggs of large zooplankton	28%
Carnivorous zooplankton	5%
Fish eggs	3%
Other items	2%

In winter, hydromedusae are very scarce on the B.C. shelf, while ctenophores are virtually absent; Scyphozoa would also disappear in early fall (see also Mills 1981). The occurrence of *Valella valella* along the B.C. coast is briefly discussed in Arai (this vol.).

Krill

(Astrid Jarre-Teichmann)

Thysanoessa spinifera and *Euphausia pacifica* are the dominant krill species of the southern British Columbian shelf. Their population biology has been studied on La Pérouse Bank off Vancouver Island (Tanasichuk 1995). *T. spinifera* is more productive than *E. pacifica*, with estimated P/B ratios ranging from 1.6 to 3.7 year^{-1}. The energy balance of the krill box, described above for the Alaska gyre model was used in the absence of more detailed information.

Adult krill biomass was estimated at 3.8 t·nm^{-2}, corresponding to 1.1 g m^{-2} during an echoacoustic survey in Jervis Inlet on the British Columbia coast (Romaine et al. 1995). This estimate may be used as the initial biomass value for the model, although it is not clear how representative it is for the whole of the area considered here.

Small pelagics

(Rik Buckworth)

Herring

Pacific herring *Clupea harengus pallasi* is the subject of important roe, spawn on kelp and bait fisheries in British Columbia. It has been overfished in the past, and is also subject to considerable natural variation in stock size and recruitment.

The Summer feeding grounds are on the continental shelf (i.e., our reference area), but in early Fall, herring migrate inshore, where they are subject to intense fishing and predation (Hay and Fulton 1983). The survivors then return offshore, where they stay from February to May. The adults are pelagic planktivores, feeding mainly on euphausiids, copepods and decapod larvae. The biomasses used here refer to 1985-1989, were taken from Stocker (1993, Figure 10), and were estimated from historical catches for the inshore spawning areas. (DFO stock assessment regions Northern West Coast Vancouver Island and Southern West Coast Vancouver Island). Natural mortality was estimated as M=0.6 year^{-1}. The stock are managed under a constant (20%) harvest rate policy. The Production:Biomass ratio of 2.2 year^{-1} was obtained from $Z = F + M = P/B$.

Diet items mentioned by Stocker (1993) are euphausiids, copepods and decapods. Curiously, for such an important commercial species, no information was found on the relative composition of the diet.

Sardines

Pacific sardine, *Sardinops sagax* was historically the subject of a fishery (around 20,000 t year^{-1} in the late 1920s) in British Columbia (Hart 1973), but there has not been a fishery since the 1940s. Schweigert (1988) suggests that *S. sagax* was "a transient visitor" to Canadian waters, from the northern Californian stock, which appears to be rebuilding. Villavicencio and Muck (1983) provide some information on ration and growth efficiency in this species.

Anchovies

Northern anchovy *Engraulis mordax* is not sufficiently abundant to provide the basis of a fishery in B.C., though it was abundant during the 1940s (Hart 1973). A literature search produced no information on this species in Canadian waters.

Sandlance

Although there are large sandlance fisheries in the north Atlantic and west Pacific, Pacific sandlance (*Ammodytes hexapterus*) is not fished in the northeast Pacific and no biomass estimates for the species were found. The species is an important food item for a suite of species, for example rhinoceros auklet (*Cerorhinca monocerata*; Bertram and Kaiser 1993), Pacific halibut (*Hippoglossus stenolepsis*; Best and St-Pierre 1986, and see Venier, this vol.), salmon, lingcod and marine mammals (Hart 1973). Hart (1973) records the species as "abundant through B.C. in a wide range of habitats". No information was found that described the species distribution by depth. The diet consists mainly of copepods (Hart 1973).

Pacific Cod and Sablefish

(Patricia Livingston)

Pacific cod (Gadus macrocephalus)

Pacific cod is widely distributed on both sides of the Pacific Ocean (see Tokranov and Vinnikov 1991), though it is near the southern limit of its distribution off the west coast of the British Columbia shelf (Ketchen 1961). The main concentrations of cod in British Columbia waters south of 52° N are found in Queen Charlotte Sound and on La Pérouse Bank. Spawning occurs in winter (January to March) and the main feeding areas are occupied during April through September. Preferred temperatures in this area range from 6.4° C to 7.9° C (Westrheim and Tagart 1984). Large fluctuations in recruitment produce a great variability in annual landings (Tyler and Foucher 1990). In the 1980s, the fishery was closed during winter and the bulk of the landings occurred during April-September (Tyler and Foucher 1990).

Stock assessment of cod indicates an average catch of 1,695 t from 1985 to 1992 in DFO areas 3C-3D, i.e., west of Vancouver Island (Stocker 1994). Mean total mortality during this same period was $Z = 1.2$ year^{-1}. With $M = 0.65$ year^{-1}, F is about 0.55 year^{-1}. Average biomass for 1993 was 8,500 t. Ration ranges from 0.9-1.3% body weight daily (Paul et al. 1990), and Q/B may thus range from 3.3 to 4.7 year^{-1}.

Diet analysis from Hecate Strait (Tyler and Crawford, 1991) shows that cod consume mostly herring (60-75% by weight), demersal fish (10-40%), and sandlance (2-15%). Diet samples of cod taken from 1950 to 1980 by Westrheim and Harling (1983) show highest occurrences of sandlance in the stomachs of cod from Queen Charlotte Sound and west of Vancouver Island (frequency of occurrence: 59-83%). Herring (39-43%), euphausiids and shrimp (15-19%), and sablefish (1-5%) were also consumed by cod in those two areas. Off Vancouver Island, there are indications that herring might be the more important prey of cod during summer and fall, while sandlance might be more important during winter and spring (Westrheim and Harling 1983).

Sablefish **(Anoplopoma fimbria)**

Exploitable concentrations of sablefish normally occur between 150-1,000 m depth (Low 1976). These are long-lived fish (up to 35 years), with rapid growth until maturity. Adults, aged 3 and greater, are found in slope waters of the continental shelf. Juveniles up to 2 years of age inhabit surface and inshore waters down to a depth of 150 m. Most catch in Canadian waters in recent years was at depths of 450 m to 990 m. Therefore, for the purposes of the model, catches should be set equal to zero. Biomass, as estimated during surveys conducted in 1992 in the shallowest depth stratum (270-448 m) off the West coast and Queen Charlotte Sound areas were 7,167 t and 9,885 t, respectively (Stocker 1994).

Assuming sablefish are evenly distributed within this depth zone, and given that the model below only includes depths to 300 m, adult sablefish biomass in the model area is about 17% of the total biomass in the shallow depth zone of the survey, or 2,865 t. Many of the juveniles that inhabit inshore waters of British Columbia migrate north to Alaskan waters, and are recruited to the U.S. fishery there (McFarlane and Beamish 1983a). Estimates of juvenile biomass from the large 1977 year class range from 30,000 to 60,000 t in inshore waters, including the shelf waters of Queen Charlotte Sound and the La Pérouse Bank area (McFarlane and Beamish 1983).

Estimated natural mortality rate for adults is 0.08 $year^{-1}$ (Stocker 1994) and the average natural mortality rate for juveniles between age 0 and age 4 is about 0.6 $year^{-1}$ (McFarlane and Beamish, 1983a).

A Q/B value for adults of 3.73 $year^{-1}$ was estimated using the equation of Pauly et al. (1993), assuming an asymptotic weight of 4,392 g (Stocker 1994) and an annual habitat temperature of 9^{o} C. Q/B for juveniles was estimated to be 6.6 $year^{-1}$, based on the ration estimates for juveniles presented by McFarlane and Beamish (1983a).

Juvenile sablefish diet by weight in Queen Charlotte Sound and Hecate Strait consisted of 41% herring, 25% euphausiids, 20% unidentified fish and a total of 14% of crab, shrimp, jellyfish, and squid (McFarlane and Beamish, 1983a). Juveniles are consumed by halibut, adult sablefish, cod, lingcod, and spiny dogfish. Adult sablefish diet consists mainly of fish (50% by weight) and squid (39%). Herring was the main fish species consumed in summer. Rockfish and myctophids were also identified in the stomach contents of adults from Canadian waters. Jellyfish, shrimp, crab, euphausiids, and amphipods make up the remainder of the diet (McFarlane and Beamish 1983b).

Pacific Halibut

(Judson Venier)

Introduction

Pacific halibut is an extremely important resource of the Northeast Pacific - so important, indeed that the fishery is regulated by its own International Halibut Fisheries Commission (IHFC), created in 1923.

The species is found over the continental shelf of North America from Santa Barbara, California to Nome, Alaska (IPHC 1987). Peak abundance occurs in the central Gulf of Alaska (Deriso et al. 1985) from the Alaska Peninsula in the north to Cape Fairweather in the south (Trumble et al. 1993). Abundance declines as one moves away from this area and becomes limited south of southern British Columbia (Trumble et al. 1993). The species is demersal and is often associated with bottom features such as banks and channels, with water temperatures close to 5° C (Trumble et al. 1993). In summer, halibut are found in waters greater than 90m in depth and in winter they move into the deeper waters (300-600m) of the upper continental slope (Trumble et al. 1993).

Seasonal migrations do occur for commercially sized fish (≥81.3 cm) (Trumble et al. 1993). Fish move from summer feeding grounds inshore to winter spawning grounds offshore (Trumble et al. 1993). These movements are usually within the IPHC's statistical areas (Deriso and Quinn 1983; Quinn et al. 1985).

Reproduction and growth

Spawning is an annual event and occurs in late fall and winter (Trumble et al. 1993). Halibut congregate to spawn and two major spawning areas are located on the British Columbian shelf: one at the northwestern tip of the Queen Charlotte Islands and one at their southern tip (Trumble et al. 1993). The length at 50% maturity for females is approximately 120 cm (Trumble et al. 1993).

Fertilized eggs become part of the plankton where they hatch and turn into juveniles. The planktonic phase lasts for about 6-7 months (Trumble et al. 1993). Juveniles settle in shallow water in late spring and early summer (St-Pierre 1989). They undertake long migrations to the east and south, and at 2-3 years, move offshore (Trumble et al. 1993). These are believed to be countermigrations, which may balance the dispersal of eggs and larvae (Trumble et al. 1993). Net migratory movements of adults, as a result, are small (Trumble et al. 1993).

Pacific halibut can attain lengths of over 3 m and weigh up to 300 kg (Trumble et al. 1993). Sexual dimorphism occurs, with the females growing larger than the males (Trumble et al. 1993). The oldest halibut on record are a 42 year old female and a 27 year old male (IPHC 1987). Fish in the Pacific commercial setline fishery average 10-14 years of age (Trumble et al. 1993). Growth of both males and females is continuous throughout their lives and shows little decrease at older ages (Trumble et al. 1993). Both sexes grow at roughly the same rate up to about 5-9 years after which females tend to grow faster (Trumble et al. 1993).

Predators and preys

Pacific halibut are rarely preyed upon by other fish and cannibalism is very low (≤7%), even in nursery areas (Best and St-

Pierre 1986). Some marine mammals, such as Steller sea lion (*Eumetopias jubata*), are known to take halibut off of setline gear, but predation in more natural settings is probably low (Best and St-Pierre 1986).

Juvenile halibut tend to consume a majority of invertebrate prey but undergo a transition to piscivory as they grow (Trumble et al. 1993). When they reach about 70 cm standard length (SL), their diet consists almost exclusively of fish (Trumble et al. 1993). The diversity of prey taken is large but Pacific sand lance (*Ammodytes hexapterus*) and Pacific herring (*Clupea pallasii*) made up 60% and 23% of the diet in terms of biomass in British Columbia waters, respectively (Best and St-Pierre 1986).

Q/B was estimated at 1.73 year^{-1} using an empirical equation in Christensen and Pauly (1992b, p. 14), with W_∞ set at 300 kg (Trumble et al. 1993).

Best and St-Pierre (1986) estimated the diet composition (in numbers) of Pacific halibut, based on analysis of stomach contents for 70 fish from Hecate Strait and Dixon Entrance. Here, data on 40 of their fish from Hecate Strait were used, along with estimates of the weight of prey items, also from Best and St-Pierre (1986), to re-express the diet composition in terms of weights. This led to the following approximate values: sandlance 50%, herring 20%, miscellaneous demersals 18 %, crabs 10%, and octopus 2%.

Catches and mortality rates

Pacific halibut was an important target species even before Europeans arrived on the west coast, as the First Nations used halibut for both subsistence and barter (Bell 1981). Commercial fishing began around 1888 in the Washington-Oregon area and expanded northward in the early 1900s (Trumble et al. 1993). Commercial catches now average more than 30,000 t per year and are highest in the Gulf of Alaska, where the greatest concentration of halibut occurs (Trumble et al. 1993). In addition to the commercial harvest, halibut became a popular sport fish in the 1980s (Trumble et al. 1993). The recreational catch constituted about 5% of the total directed halibut harvest or 3600 t in 1990 (Trumble et al. 1990). Again, the majority of the recreational catch (75%) occurs in the Gulf of Alaska.

The International Pacific Halibut Commission (IPHC) was formed as a result of petitions from fishers and processors, whose resource was declining, to the governments of Canada and the US (Trumble et al. 1993). Currently, halibut can only be kept if caught on hook and line gear during open seasons. Set nets were outlawed in 1938 for halibut fishing (Bell 1981) since they were seen as targeting large spawners (Trumble et al. 1993). Trawling for halibut was banned in 1944 (Bell 1981), on the basis that it tended to catch halibut under the legal size, and to decrease yield per recruit (Trumble et al. 1993).

Trumble et al (1993) estimated an exploitable biomass estimate of 141,000 t for the entire distribution area of Pacific halibut, from Santa Barbara, California, to Nome. Alaska. Thus, total biomass for the coast of southern B.C. was obtained by assuming proportionality between biomass and catch, of which 10% is taken off southern B.C. This, given our reference area of 30,000 km^2, corresponds to a biomass/unit area of 0.473 t·km^{-2}.

A catch of 0.113 $\text{t·km}^{-2}\cdot\text{year}^{-1}$ was derived from the B.C. landing data presented in

Table 4 of the 1990 IPHC Annual Report, following division by 3 to account for the fact that our reference area represents about 1/3 of the B.C. shelf. These landing data, expressed in pounds for dressed head-off halibut, were converted to round weight by multiplication with 1.33

A natural mortality (M) value of 0.2 year^{-1} was given by Trumble et al. (1993), which seems high, given that these are large, long-lived fish (see Pauly 1980). Fishing mortality (F) was estimated at 0.24 year^{-1}, using F = catch in weight / biomass. The definitions

$$F + M = Z = P/B$$

were then used to estimate P/B = 0.44 year^{-1} (Allen 1971).

Spiny Dogfish

(Jeffrey Polovina)

Spiny dogfish (*Squalus acanthias*) is a coastal species ranging from Alaska to California. The coastal biomass is estimated at 280,000 t (Saunders 1988), with about 150,000 - 200,000 t residing along the Canadian coast (Stocker 1994). Using an estimate of the area of the Canadian shelf of 100,000 km^{-2} gives a density estimate of 1.5 - 2 t·km^{-2} . The P/B ratio is estimated at 0.1 year^{-1}, and consist mainly of natural mortality (Wood et al. 1979).

Stomach contents from a large age and seasonally averaged sample of dogfish off the British Columbia coast indicate a wide range of prey consisting of herring (22%), euphausiids (14%), flatfish (6%), smelt (6%), octopus (3%), combjelly (2%), sandlance (2%), and squid (2%). The remaining 11% is composed of many benthic organisms, none comprising more than 2% of the diet (Jones and Geen 1977). Dogfish appear to consume twice as much food in summer as in winter, with annual average consumption of 5 times body weight for small, and 2.5 times body weight for large animals (Jones and Geen 1977). Thus average (annualized) summer and winter food consumption rates for this group would be 5.0 and 2.5 times body weight, respectively.

Hake

(Tony Pitcher)

Introduction

One of 12 important species of hake world-wide, *Merluccius productus,* the Pacific hake or "whiting", is the most abundant commercial fish species along the Pacific coast of North America between 25° N and 51° N (Alheit and Pitcher 1993) Living principally offshore in 200–500 m depths over the continental shelf and its edge, the adult hake stock extends from California northwards through British Columbia in the summer, sometimes as far as the Alaskan border. It is considered that most hake in Canada migrate south to US waters in the winter (Stauffer 1985; Smith et al. 1992). Spawning and juvenile hake are generally confined to waters south of latitude 44° N, although in warm years there are reports of eggs in Canadian waters (Beamish and MacFarlane 1985). The extent of the northwards extension of 3+ hake depends on the warm water associated with ENSO, so the proportion of the stock biomass found in Canadian waters varies considerably from year to year. These coastal Pacific hake exhibit hundred-fold differences in year class strength which appear to be uncorrelated with spawning biomass. Longevity, of up to 15+ years buffers the stock against large fluctuations in total biomass, but hake scales preserved in anaerobic sediments off California reveal a history of large variations in biomass over hundreds of years (Soutar and Isaacs 1974).

In the USA some 250,000 tonnes of hake are landed annually, while the Canada takes about 100,000 t, with catches following a generally increasing trend over the past 10 years. The fishery, which is considered fully exploited, has recently been reviewed by Methot and Dorn (1995); earlier work is summarized in Dark (1975). Advances in technology now allow production of frozen fillets, blocks and surimi from a fish that traditionally spoilt rapidly due to proteolytic myxosporidian parasites in the flesh. The principal issues in assessing and managing the fishery are the influence of ENSO on the northwards extension of the stock; allocation between US and Canada; allocation between onshore and offshore processing; and a by-catch of salmon, rockfish and herring, that composes a small proportion of the hake catch but may be large in absolute amount.

There are three stocks of Pacific hake in Canadian waters. In addition to the large offshore hake stock that migrates from the south to summer in Canadian waters, there is a small resident offshore stock that spawns in Canada and whose eggs and juveniles have been found by surveys in the Barkley Sound area (Beamish and MacFarlane 1985). Isolated from the offshore hakes, an inshore, relatively under-exploited stock of hake inhabits the Straight of Georgia and Puget Sound, is distinguished by its otolith structure and lack of flesh parasites (Beamish 1979; Venier and Kelson, this vol.).

The diet of the offshore hake consists principally of krill (= Euphausiidae), but although fish and shrimp usually make up a smaller percentage of the diet, hake are opportunistic ambush predators (Pitcher and Alheit 1995) and at certain seasons and locations, larger Pacific hake may consume substantial quantities of fish, such as herring or smelts. Pacific hake generally feed nocturnally, and, surprisingly, compared to other species of hake world-wide (Alheit and Pitcher 1995), where hake diet consists of up to 40% hake, there are no reports of cannibalism by *M. productus*. Methot and Dorn (1995) consider that this is because larger hake migrate out of nursery areas.

On account of the importance of the fishery, the ecology of Pacific hake is relatively well documented, with at least 33 papers having been published since 1980. This brief account is confined to an evaluation of the literature in order to derive estimates of stock biomass (B, for 3+ adults), total mortality rate (Z = P/B ratio; Allen 1971), and diet, in summer and winter, for input to an Ecopath model of the southern B.C. shelf.

Biomass estimation

For stock assessment purposes, Pacific hake biomass is estimated using two complementary techniques: stock surveys are conducted every three years (these have been more frequent in some areas), and a sophisticated catch-at-age model analysis is run every year.

First, every three years, acoustic surveys are conducted along the shelf in both countries, supported with suitable trawl verification of species identities. Not surprisingly for an ambush predator, most hake aggregations contain few other species. Acoustic surveys have been conducted every year in the Canadian zone since 1990. The three principal uncertainties in these acoustic estimates are the geographical extent of the surveys, which can miss hake offshore and to the north of Vancouver Island, the identification of sparse hake aggregations in the weak scattering layer, and the low target strengths of juvenile hake.

Secondly, a rather complex catch at age analysis, tuned by survey biomass and age composition, is performed. Ages are based on otolith readings (Beamish 1979), and subsamples raised to a catch-at-age matrix using an age-length key and total catch data in the usual way (Kimura 1989). The current algorithms are based on a stock synthesis model (Methot 1990), in which age specific mortality is assumed separable into age-specific selectivity and fishing mortality for each year (an approach derived from the "separable VPA" of Pope and Shepherd 1982). The analysis is said to be "integrated" because of the large number of factors taken in consideration when tuning. Tuning is carried out using "emphasis factors" that determine how closely the expected values from the model approach the observed catch figures, goodness-of-fit being measured with a log-likelihood function. The fitted components of the model, each of which has an attached emphasis factor, include four equally weighted estimates of age composition, eight acoustic survey measures from NMFS in the US, two acoustic measures from DFO in Canada (given very low weighting), and four measures from US and Canadian trawl surveys, also given low emphasis. An age-specific migration model partitions the stock into Canadian and US components and separate gear selectivity curves are employed for the two countries. The model is used to project hake biomass forward under a range of management options. Risk is evaluated using Monte Carlo simulation.

Methot and Dorn (1995, Figure 7) noted an encouragingly close agreement between estimates of Pacific hake biomass from the catch-at-age analysis and survey results from 1983 - 1989. However, later analyses appear to have eroded this confidence that stock was accurately assessed, and, for later years, considerable inconsistencies and uncertainties have become apparent. Much of the information from Canada is in PSARC (Pacific Stock Assessment Review Council) reports, which are labeled as unciteable. My evaluation here is a digest and evaluation that inevitably considers this unciteable material.

It is clear that acoustic surveys in the 1990s have demonstrated hake much further offshore on the shelf break than had been previously realized, and in warm years the distribution extends further north than expected. Also, the introduction of new acoustic gear in the US has compounded calibration uncertainties.

As a consequence, biomass estimates in former years have been retrospectively revised upwards to compensate for the areas previously not covered by surveys: for example the 1986 biomass appears at 2.25 million tonnes in Methot and Dorn (1995), but has been revised (by M.W. Dorn) upwards to 3.95 million tonnes in an PSARC document dated 1995. This revision makes a large difference to estimates of fishing mortality. Moreover, in 1995 PSARC documents, we find different figures to those issued in earlier years. A further complication is that in most PSARC reports,

Table 14 Summer Pacific hake biomass ($t \cdot 10^3$) and related statistics in Canadian coastal waters from the US border to Queen Charlotte Sound.

Year	Biomass[a)]	Catch[b)]	F[c)]	M[d)]
1983	450	41824	0.10	0.22
1986	500	55653	0.12	0.22
1989	225	99532	0.58	0.23
1990	316	76680	0.28	0.24
1991	402	104522	0.30	0.24
1992	1101	86370	0.08	0.25
1993	750	58783	0.08	0.25
1994	225	106172	0.64	0.26

a) Biomasses for 1983-90 are average of survey and catch-at-age model estimates from Methot and Dorn (1995); biomass for 1991-94 are derived from an unciteable PSARC document dated 1995, and is based on acoustic data, revised upwards within the catch at age model's range for years where the unsurveyed area problem (see text) is explicitly acknowledged; b) Catch (t), from official statistics, excludes some discards and does not include estimates of unreported catch; c) from F = ln(1-exp(catch/biomass)); in year^{-1}; d) from Dorn (1992); year^{-1}.

there is a "Table 10" showing the "utilization percent" (for US and Canada) that derives from the model. This represents the portion of the estimated adult (3+) stock biomass that has been caught in each year (equivalent F values are not given). Clearly, reported catch divided by this proportion back-calculates the value of the adult stock biomass that must have been output by the model. Unfortunately, these values bear little relation to biomass figures published in earlier years, or to biomass values cited elsewhere in the same document. To compound these difficulties, acoustic survey results are now said to have consistently underestimated hake biomass because hake also occur in unsurveyed areas.

Therefore, the confident message conveyed by Methot and Dorn (1995) has been eroded, and, despite the sophistication of the modelling, the impression from this material is of worrying uncertainties entering the hake assessments. Some of the methods employed are so complex and incompletely documented that only a complete reconstruction of the modelling exercise could enable an outside reviewer to evaluate it confidently. It may be noted that alternative models of the Pacific hake stock that include environmental drivers have been published (e.g. Swartzman et al. 1987), but appear not to have been considered in assessment. Nor have simpler models with fewer parameters, such as are used to effectively manage hake stocks elsewhere in the world (e.g. Payne and Punt 1995), been compared with the heavily parametrized stock synthesis approach.

Consequently, the estimates of Canadian hake biomass that I have listed in Table 14 are not identical to those appearing elsewhere. I have calculated them by a variety of means from the published material (see table footnotes) taking into account many comments made in the most recent documents. My values have, therefore, likely wide confidence limits, at least ± 50%.

Some trawl survey biomass estimates that are independent of the stock assessment work have been published for the La Pérouse Bank area, a small part of the area covered here (48.5° to 49° N, 125.5° to 126° W). These range from 179,000 to 439,000 t (average 262,000 t; CV = 60% since 1983), depending on temperature (Ware and MacFarlane 1995). Divided by the area of La Pérouse Bank, these correspond to approximately 30 to 74 t of hake km^{-2} (average 44 $t \cdot km^{-2}$) and are said to average 61% of the pelagic fish biomass. The values correlate significantly, but with high variance, with biomass in this area calculated from the stock assessment model.

Unfortunately, there are no published estimates of the size of this resident stock, which is not fished in winter. The only relevant data are from USSR vessels in 1968, the only year in which year-round fishing was recorded (Beamish and MacFarlane 1985, Table 2). Catch from October through March is recorded as 2.6% of the 40,280 t recorded from April through September. Some of this catch would have been from the migratory stock which is still present during October (0.35% of the winter catch from the 1971 and 1972 USSR catch), so the figure adjusts downward to 1.7%. On the other hand, USSR effort was likely not as high during the winter months, and so I suggest using a figure of 2% of the average migratory stock biomass for the resident offshore Canadian Pacific hake population, i.e., a biomass of about 5000 t.

Fishing and natural mortality

Fishing mortality was estimated for the Canadian fishery as ln(1 - catch/biomass) in Table 14, and will differ from values that could be estimated using the entire international catch and the corresponding biomass. This perhaps should be done when revising the model presented below. The winter F on the resident offshore hake stock in Canada is effectively zero.

Natural mortality rate (M) between ages 3 to 12 was estimated as 0.24 year^{-1} by Dorn (1992), who used the relative strengths of "boom" cohorts between successive acoustic surveys. M is considered to be rising as result of increasing abundance of marine mammals, which are the principal hake predators in the northern part of its range (see Trites and Heise, this vol.) Over the Pacific hake's entire range, the annual consumption by marine mammals is about 250,000 tonnes of hake, roughly equal to the human harvest of hake (Livingston and Bailey 1985).

It is interesting that the F estimates in Table 14 for years when Canadian hake biomass is low are higher than in years when it is high, suggesting that management does not adjust catch to match the climate-driven northward extension of this stock. But, since in this stock, on average, F is approximately equal to M, and in a cooler year more of the stock remains in US waters, this should not compromise sustainability in this long-lived fish. Catches have expanded recently as the industry and the managers' response to the recent "discovery" of previously unreported hake concentrations.

Total mortality, here considered equivalent to a P/B ratio (Allen 1971) can be obtained by adding the F and M values in Table 14; the most recent figure is Z = 0.91 year^{--1}. Although preceding years suggest lower figures, several factors argue for a higher value. The hake stock in both US and Canada is declining, natural mortality is increasing, the catch data do not include all discards, and no allowance has been made for unreported catches. Hence my best estimate of current Z for Pacific hake in Canadian waters is 0.95 year^{-1}. If uncertainties are taken account of in Ecopath analysis (see Walters, this vol.), then I suggest using the range 0.4 to 1.1 year^{-1}.

Diet composition and food consumption

There have been 6 published studies on the diet of Pacific hake in Canada since that of Outram and Haegele (1972). The most thorough is that of Tanasichuk et al. (1991), while the most helpful for our purposes is that based on La Pérouse Bank, southwest of

Table 15 Summer diet of Pacific hake, by size (% weight) based on 466 stomachs sampled in August 1983 off the Washington and Oregon coast (from Rextstad and Pikitch 1986, Table 2).

Hake size[a]	40	45	50	55	>55	DC[b]
Euphausiids[c]	93.6	90.9	21.9	20.7	7.9	74.3
Decapods	3.1	4.5	13.7	26.5	5.3	5.9
Herring	-	3.8	34.7	28.4	-	7.4
Myctophids	1.5	-	-	-	-	0.3
Eulachon / other smelt	-	0.6	23	2.9	-	3.2
Anchovy	-	-	1.5	2.7	-	0.4
Flatfish	-	-	0.1	14.5	3.4	1.5
Gadoids	-	-	1.2	2.4	83.6	5.8
Other fish	1.8	0.3	3.6	1.8	0.1	1.1

a) Upper class limit, in cm;
b) Diet over all size classes, assuming a total mortality rate of 0.36 year^{-1} for 1983 (see Table 14);
c) this group contributes 100% of the diet in hake < 35 cm.

Vancouver Island (Ware and MacFarlane 1995). There do not appear to be published data on the diet of Pacific hake in winter.

In six years of research surveys on La Pérouse bank, from August 1983, and 1985 to 1989, 12430 hake stomachs containing food were analyzed (Tanasichuk et al. 1991). Diet by weight consisted of 64% euphausiids (CV: 24%), and 30% herring (CV: 55%).

But in the same study in August 1988, samples from commercial fishing vessels on La Pérouse, presumably catching larger hake and fish on the shelf break, gave only 9% herring and 82% euphausiids at the same time as that year's research survey gave 36% herring and 62% euphausiids. Moreover, Outram and Haegeke (1972) recorded 26% of 1196 hake stomachs as containing sandlance (*Ammodytes hexapterus*), 5% with eulachon (*Thaleichthys pacificus*), 3% lantern fish (Myctophidae), and 3% pink shrimp (*Pandalus* spp). Although the principal krill species consumed is *Thysannoessa spinifera,* Livingston (1983) showed that *Euphausia pacifica* increases in hake diet offshore. Furthermore, Rextstad and Pikitch (1986) demonstrated that diet of Pacific hake may shift dramatically away from krill to fish with size (Table 15).

Despite the large sample sizes in the La Pérouse study, the diet data discussed above raises some problems. The field data suggests that the foraging strategy of hake, an opportunistic ambush predator, may lead to great variation in the diet from location to location and from year to year (see also Dill 1983). Depending upon availability and size, hake may switch from feeding upon euphausiids to decapods to smelt to herring. The area of study of the model below is much larger than La Pérouse Bank, and so it may be unwise to use the diet data from that location without modification. I have therefore adjusted the published figures as follows.

Table 16 Summer diet composition (%, by weight) of hake, west coast of Vancouver Island.

Group	DC
Euphausids	69.1
Decapods	2.9
Herring	18.5
Gadoids	2.9
Eulachon / other smelt	1.6
Myctophids	0.2
Flatfish	0.8
Anchovy	0.2
Other fish	0.5

If the Rextstad and Pikitch diet composition figures are adjusted for the total mortality rate estimated for that year ($Z = 0.32\ \text{year}^{-1}$), the overall percentage of the diet by item will be as given in the rightmost column of Table 15: 74% krill, 5.9% shrimp, 7.4% herring, 5.8% gadoids and 3.2.% smelts (including eulachon) for the hake population studied by Rextstad and Pikitch. Although their study was based further to the south than our area of interest, many of the same species are known from commercial catches to be abundant in Canadian waters. My suggestion therefore is to combine these values with those of the La Pérouse study (Table 16). The result is about 70% krill and about 15% herring with significant amounts of other fish and shrimps.

A second problem arises from the variable diet of hake: when we incorporate the estimated diet composition into an Ecopath model, small changes in hake diet can have a high leverage on the balance of the model, because the optional preys have very different trophic roles in the ecosystem. When searching for values that balance the model, a mean diet composition may not express the actual shifts in diet that would result.

Using mean stomach fullness data related to time of day, Tanasichuk et al. (1991) estimate that hake on La Pérouse Bank in summer consume about 1.6% of their body weight per day (i.e., $Q/B = 5.84$ year^{-1}). Similar values were calculated using several alternative models for estimating daily ration size, and differential digestion rates for crustaceans and fish were not thought to be important. Hake on the shelf edge consuming more euphausiids had slightly lower daily rations. There are no published winter values.

Marine Mammals

(Andrew Trites and Kathy Heise)

The 13 species of marine mammals that feed on the British Columbia shelf during summer and winter were grouped into four categories: pinnipeds, baleen whales, toothed whales, and killer whales (resident and transient). Estimates of mean body weight for males and females of each species were obtained from Trites and Pauly (in prep.). Population estimates were obtained from published sources or represent educated guesses based on the best available information, such as Northridge's (1991) global population estimates, scaled down to our reference area. Unless otherwise stated, mean body weights, food consumption and diet composition were estimated, for each species, as described above for the marine mammal of the Alaska Gyre.

Diet composition for each of the four groups equaled the mean diet of the species within the group, weighted by the relative population abundance and ration. Summer and winter data for the marine mammal species considered here are summarized in Appendix 1, Tables F to I.

Additional information on the assumptions and estimates used for each species of marine mammal in the B.C. shelf are as follows.

Pinnipeds

Harbour seals, Steller sea lions, northern fur seals and northern elephant seals occur in the B.C. shelf in both summer and winter. A fifth species, the California sea lion, feeds in B.C. waters only during winter. The maximum rate of population growth for northern fur seals and other pinnipeds is generally believed to be about 12% (Small and DeMaster 1995). The P/B ratio was therefore set at 6%.

Northern fur seals (*Callorhinus ursinus*) from the Pribilof Islands numbered 1,019,192 animals in 1994 (Small and DeMaster 1995). This population breeds in the Bering sea and migrates annually through B.C. waters from January to June on their return trip from California to the Pribilof Islands (Bigg 1990). Between 3 and 14% of the population feed over the B.C. shelf (14% January, 6% February, 12.5% March, 20% April, 12.5% May, and 3.3% June, calculated from the number of fur seals sighted in all areas of the north Pacific during pelagic surveys, as given in Figure 8 of Bigg 1990). This represents an average of 5% of the total population over the 6 winter months (51,000 fur seals per month) and 6% over the 6 summer months (61,000 per month). The ratio of males to females was assumed to be 0.2:0.8 in both seasons. Mean body weights were for males (30.2 kg) and females (25.3 kg).

Dietary information is based on stomach contents from fur seals shot at sea from 1956 to 1972 (Perez and Bigg 1981, 1986). The British Columbia shelf corresponds to Area 9 of the fur seal pelagic survey (Table 11, Perez and Bigg 1981) where, in the winter (Jan-Mar.), the animals predominantly eat herring (36%), squid (21%), rockfish (12%), salmon (11%), smelts (7%), sablefish (6%), miscellaneous clupeids (5%), hake (1%), and sandlance (1%). In summer (April to June), the animals consume mainly herring (52%), salmon (12%), squid (14%), rockfish (7%), sablefish (4%), hake (3%), sandlance (3%), smelts (1%), miscellaneous clupeids (2%) and large pelagic fish such as pollock (2%).

Northern elephant seals (*Mirounga angustirostris*) make biannual migrations from the breeding beaches in California to deep waters of the Gulf of Alaska (DeLong et al. 1992; LeBoeuf 1994; Stewart and DeLong 1994, 1995). Males travel further north than females and are often sighted onshore along the west coast of Vancouver Island. It was assumed that 20% of the male population spent up to one month in B.C. waters in the summer, and another month feeding here in winter. Given the current population estimate of 127,000 elephant seals (Stewart et al. 1994) and an assumed sex ratio of 50%, approximately 2,000 animals should be present in each of the 6 months of summer and winter. As there is no dietary information specific to the B.C. shelf, diet composition estimates were taken from elephant seals sampled in California (Antonellis et al. 1984), i.e., 40% small squid, 20% dogfish, 10% rockfish, 10% sablefish, 10% hake and 10% miscellaneous demersal fish.

Steller sea lions (*Eumetopias jubatus*) breed on offshore rocks and islands along the B.C. coast. They generally feed within 20 km of the shore during summer, but may venture several hundred kilometers away from it during winter. The current B.C. estimate is 9,400 sea lions (P. Olesiuk, pers. comm.). Summer and winter diets were based on scat samples collected at Forrester Island in Southeast Alaska, an area similar to the B.C. shelf (Trites and Calkins, unpubl. data). Summer diet consists predominately of salmon (17%), herring (16%), pollock (12%), cod (12%), rockfish (11%) flatfish (11%), sandlance (8%), skates (3%), octopus 2%), squid (1%), smelt (1%) and hake (1%) and other fishes (4%). Winter diet consists of pollock (22%), cod (22%), herring (13%), salmon (11%), flatfish (8%), rockfish (5%), skates (5%), sandlance (4%), octopus (4%), squid (2%), smelt (2%), sculpins (1%) and other fishes (2%).

Harbour seals (*Phoca vitulina*) are the most abundant resident pinnipeds in British Columbia. Approximately 40,000 of the 135,000 B.C. population inhabit the outer shelf regions (Olesiuk et al. 1990b). Diet is not known in this region and was assumed to be similar to the non-estuary waters of Georgia Strait (from Olesiuk et al. 1990c). Thus, the summer diet comprised 65% gadoids (mostly hake), 15% herring, 4% midshipmen, 3% salmon, 2% smelts, 2 % sandlance, 2% squid, 1% hexagrammids, and 6% other fishes. The winter diet was comprised of 60% herring, 20% gadoids, 6% hexagrammids, 4% plainfin midshipmen, 3% salmon, 2% squid, 1% smelts and 4% other fish (based on Figure 22 in Olesiuk et al. 1990c).

California sea lions (*Zalophus californianus*) breed along the coasts of (Alta) California, US, and Baja California, Mexico. Each winter (from November to May) approximately 3,500 males enter B.C. waters. About half feed in Georgia Strait and half on the outer coast of Vancouver Island. The diet is not known, but was assumed to be intermediate between that of harbour seals and that of Steller sea lions.

Baleen Whales

Gray, humpback and minke whales occur off the west coast of Vancouver Island in summer and winter. With the exception of minke whales, most of the baleen whales are migratory and do not feed extensively while transiting the area. However, a few individuals do remain year round in the area. Their production was estimated to be half of the 4% maximum rate of population increase for cetaceans (from Reilly and Barlow 1986).

Gray whales (*Eschristius robustus*) migrate off the west coast of Vancouver Island *en route* to feeding grounds in the Bering Sea (Small and DeMaster 1995). It was assumed that one in three animals remains in the area to feed for 1 month. Given a total population of 21,000 whales, a summer population of 1167 animals was estimated (range 1000-1500). In winter, animals returning from the feeding grounds in the Bering Sea have thick blubber layers (Tomilin 1957) and are less likely to feed. It was therefore assumed that only half of the summer population stops to feed off the Vancouver Islands shelf in winter (585 animals, range 200-1000).

Gray whales were assumed to consume 4% of their body weight per day based on summer feeding rates for other species (Lockyer 1981b), while the winter consumption rate was based on Innes et al. (1987). Based on Wolman (1985), the summer and winter diet of gray whales was assumed to comprise 90% amphipods, 5% polychaetes and 5% molluscs.

Humpback whales (*Megaptera novaeangliae*) migrate seasonally between the warm water breeding grounds in winter and rich feeding grounds further north in summer. British Columbia appears to be an approximate geographic boundary between feeding from Alaska and California (Small and DeMaster 1995). Green et al. (1992) estimated that 67 humpbacks were present year round off the coast of Washington and Oregon. For modelling purposes, it was assumed that 100 whales were present year round off the west coast of Vancouver Island (allowing for a range between 50 and 200 animals). While this may appear to be an overestimate, it accounts for animals that migrate through the area and feed while passing by.

Humpback whales were assumed to consume 4% of their body weight per day, based on summer feeding rates for other species (Lockyer 1981b). Diet was estimated from 30 historical whaling records compiled from animals harvested off the west coast of Vancouver Island (Nichol and Heise 1992). Humpbacks feed primarily on euphausiids (80%), herring (10%) and copepods (10%).

Minke whale (*Balaenoptera acutorostrata*) abundance is poorly understood in the nearshore waters of British Columbia. Minimal stomach content data is available as the species was not commercially harvested. Based on Stewart and Leatherwood (1985), and the observations of Hoelzel et al. (1989), it was estimated that minke whales consumed a mix of euphausiids (30%), copepods (30%), herring (20%) and sandlance (20%). There is little evidence to suggest seasonal movements of minke whales.

The number of minke whales on the shelf was set at 100, with a range from 50 to 300, and was assumed to be constant year-round. This is a best guess in the absence of abundance estimates to extrapolate from. Minke whale sightings were rare in aerial surveys off the Washington and Oregon coast (Green et al. 1992).

Toothed Whales, Dolphins and Porpoises

Dall's and harbour porpoises are found in the shelf area during all months of the year. Pacific white-sided dolphins and northern right-whale dolphins are not generally seen in nearshore areas, but are found 15-20 km offshore and beyond. Resident and offshore killer whales are present year round. The maximum rate of population growth for all cetaceans is believed to be 4% (Reilly and Barlow 1986) and so the P/B ratio was estimated to be 2% (half of r_{max}).

Dall's porpoises (*Phocoenoides dalli*) have not been reliably censused off the west coast of Vancouver Island. However, Green et al. (1992) estimated 2,100 off the coast of California and Washington, with no significant difference in densities between winter and summer. For modeling purposes the year round population of Dall's porpoises was assumed to be 1,000 (range: 300-3,000) for the shelf. The year round diet consists of herring (40%), sandlance (30%), and small squid (30%) (from Stroud et al. 1981; Jefferson 1990).

Harbour porpoise (*Phocoena phocoena*) population estimates along the shelf of Vancouver Island were not available, although surveys have been conducted off the coasts of Washington and Oregon (Green et al. 1992). For modelling purposes, the number of harbour porpoises along the shelf of Vancouver Island was estimated at 1,000 (range 150-1500), based on sighting data in Green et al. (1992), and Osborne et al. (1988). The diet is similar to that of Dall's porpoises and includes herring (40%), sandlance (30%), small squid (20%) and miscellaneous demersals (10%) (Treacy 1985, Gerrin and Johnson 1990).

Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) have not been censused off the coast of Vancouver Island. In Washington and Oregon, these dolphins can be seen in nearshore areas (Green et al. 1992). Off the west coast of Vancouver Island, they are most frequently seen in July through September at distances of greater than 10 miles offshore. Total population was estimated at 2,000 (range 1,000-3,000). Based on stomach content data in Stroud et al. (1981) and Walker et al. (1984) diet composition was estimated at herring (40%), sandlance (30%), transient salmon (10%), rockfish (10%) and squid (10%).

Northern right whale dolphins (*Lissodelphis borealis*) are relatively rare on the shelf, but have been observed occasionally off La Pérouse Bank. Recent sightings (Rod Palm, Strawberry Research, pers. comm.) suggest that 100 animals (range 50-300) can be found off the west coast year round, often in association with Pacific white-sided dolphins. The diet consists of herring (50%), sandlance (40%) and small squid (10%), based on stomach content analyses of animals caught in the squid drift-net fishery (Walker and Jones 1993).

Resident and offshore killer whales (*Orcinus orca*) can be found along the Vancouver Island shelf, but they have been studied most thoroughly in the waters of the Inside Passage and in the Queen Charlotte Islands, respectively (Bigg et al. 1990, Ford et al. 1994). 290 resident whales and 200 offshore whales have been identified to date (Ford et al. 1994). Given that not all animals are on the west coast of Vancouver Island at one time, a year-round population of 100 residents and 100 offshores was assumed. Olesiuk et al. (1990a) estimated a production rate of 2.9% for resident killer whales in British Columbia. Small and DeMaster (1995) use r_{max} = 4%, a value that is considered conservative for most cetaceans (Reilly and Barlow 1986. A P/B ratio of 2% of resident killer whales was assumed for modelling purposes. Mean body weights were 2587 kg for males and 1973 kg for females (Trites and Pauly in prep.). Barrett-Lennard et al. (1995) calculated the sex ratio of female to males to be 0.64:0.36, based on data in Bigg et al. (1990).

Based on the age structure of the resident killer whale population and the calorific value of prey, Barrett-Lennard et al. (1995) estimated that male and female killer whales consume 84-85 kg per day, which is slightly higher than the consumption rate predicted by the equation of Innes et al. (1987). The diet estimates for resident and offshore whales were pooled from stomach content analyses in Barrett-Lennard et al. (1995). It was assumed that fish-eating killer whales consume 65% resident salmon, 15% shark, 15% transient salmon and 5% herring.

Transient Killer Whales

The total transient killer whales population in British Columbia is estimated at 170 (Barrett-Lennard et al. 1995). As the study area comprises about 1/5 of the known range of transients, a year round population of 34 animals was assumed. Production and sex ratio estimates were assumed to be the same as for resident killer whales.

Barrett-Lennard et al. (1995) adjusted killer whale consumption rates for transients by incorporating the higher calorific value of marine mammal prey. Transient killer whales consume 73 kg of marine mammals per day, and the difference between male and female consumption rates was not significant. The diet was assumed to be 75% pinnipeds, 20% porpoises and 5% baleen whales, based on stomach contents collected off British Columbia and Alaska (Barrett-Lennard et al. 1995). The diet was assumed to remain constant year round.

Seabirds of the southern B.C. shelf

(Yoshihiko Wada and John Kelson)

The complex coastal physiography of British Columbia creates highly diversified coastal habitats, with a rich marine avifauna, but changes in water temperatures during ENSO events affect seabirds in the southern portion of this area, due to shifts in prey abundances and distribution. Here, the estuarine and primarily nearshore species of seabirds and waterfowl (listed in Palmer's Handbook of North American Birds (1962 - 1988) are not included, as the reference area does not include shallow waters (see above). Thus, diet components originating from nearshore habitats must be treated here as "imports" to the ecosystem represented by the model below.

Summer values, (April to September) were taken from Vermeer et al. (1983). Sooty shearwaters, which were present in large numbers only in May, were included at 1/6 of their May abundance (Vermeer et al. 1983). For winter values, average population values from Pacific Rim National Park of October to March were extrapolated to the entire area (Hatler et al. 1978).

Diet composition and consumption were assumed to be the same in summer and winter for the species present in both seasons. Body weight values were obtained mainly from Campbell et al. (1990), and Palmer (1962). Diet composition were taken from Nilsson and Nilsson (1976). Group averages were used for the body weights and diet composition of mergansers, and gulls.

Table 17 summarizes the population and food consumption estimates, while Table 18 summarizes the diet composition of seabirds on the southern B.C. shelf.

Overall, these tables lead to an estimated summer biomass of 276 t, a Q/B value of 112 year^{-1}, and a winter biomass of 38.5, with Q/B = 94.8 year^{-1}. Winter population numbers were estimated to be 5% of summer populations. Biomass in winter is 14% of that in summer, because it is the bigger birds which tend to remain in the summer areas. Due to the inverse relationship between Q/B and body weight, this leads to total food consumption being, in winter, only 12% of the summer value.

The P/B ratio for "seabirds" as a whole may be set at 0.1 year^{-1}, based on data in Muck and Pauly (1987).

Table 17 Summer and winter population and food consumption of seabirds, southern B.C.

	W	Q	Summer pop.	Summer Cons.	Winter Pop.	Winter Cons.
	(kg)	(kg/year)	(N)	(kg/year)	(N)	(kg/year)
gulls	1.16	109.61	17,786	1,949,398	4,373	479,272
Cassin's auklet	0.15	19.26	738,476	14,225,196	23,822	458,877
Rhinocerous auklet	0.5	53.60	41,621	2,230,894	245	13,123
Tufted puffin	0.6	62.59	56,743	3,551,289	-	-
Common murre	0.8	79.92	8,139	650,522	897	71,690
Marbled murrelet	0.4	44.34	8,000	354,720	203	8,980
Pigeon guillemot	0.4	44.34	2,721	120,670	473	20,961
Merganser	1.2	112.81	4,000	451,241	3,525	397,704
Pelagic cormorants	2	174.15	2,801	487,824	71	12,350
Leach's storm petrel	0.05	7.57	38,333	290,230	551	4,172
F.-tailed storm petrel	0.05	7.57	1,765	13,365	-	-
Northern fulmar	0.78	78.22	200	15,644	92	7,220
Sooty shearwater	0.68	69.61	83,333	5,800,907	5,263	366,373
Db.-crest cormorant	1.9	166.72	4,000	666,876	10,167	1,694,977
Common loon	3.3	266.55	600	159,931	314	83,709
grebes	1.24	116.00	300	34,800	300	34,800
Sum			1,008,818	31,003,506	50,295	3,654,208

Table 18 Summer and winter diet composition of seabirds, southern B.C.

Predator\ Prey	Benthic org.[a]	Small pelagics	Carn zoopl.	S. herb. zoopl.	L. herb zoopl.	Small squids	*Velella velella*	Small salmon
Gulls	50	30	10					10
Cassin's auklet		10	35	35	15	5		
Rhinocerous auklet		83				15		2
Tufted puffin		83				15		2
Common murrelet		60			40			
Marbled murrelet		80			15			5
Pigeon guillemot	30	70						
Merganser		35						65
Pelagic cormorants	26	74						
Leach's storm petrel	6	25	55	5		4	5	
Fork-tailed storm petrel	6	25	55	5		4	5	
Northern fulmar						100		
Sooty shearwater		73				27		
Double-crest cormorant	10	90						
Common loon	30	70						
Grebes	10	90						
Summer diet (%)[b]	**4.1**	**42.4**	**17.2**	**16.1**	**7.9**	**10.2**	**~0.1**	**2.0**
Winter diet (%)[b]	**12.2**	**62.9**	**5.8**	**4.4**	**2.7**	**3.6**	**~0.0**	**8.4**

a) Consisting of crabs and other invertebrate organisms, and imports from the intertidal;
b) Weighted average for all birds combined. Based on diet composition from this table, and Q/B and other statistics from Table 17.

Fisheries catches

(Eny A. Buchary)

Commercial landings are useful when constructing ecosystem models, as they tend to be estimated more accurately than are other fluxes. However, some knowledge of the biology of the fishes generating the landings is important for these to be correctly interpreted, as is a knowledge of discarding practices. Exclusion of some salmonid species to avoid overestimation of export from the system is a good example. The fact that DFO statistical areas are open offshore, while the model area is defined vertically by the 300 m bathymetric contour (see above) is another related problem, here assumed to be to be negligible, as the bulk of the landings stem from shallower waters.

Data Sources and Methods

The data covers the nine year period from 1985 to 1993 and were extracted from the B.C. Commercial Catch Statistics Database of the Department of Fisheries and Oceans (DFO, Vancouver Office). Data categories include year, type of gear, species and weight (kg), by species. These categories are important when corrections have to be made from dressed (with the head either on, or off) to round weight. A QuickBasic programs was used to assemble and extract data from the diskette kindly provided by DFO.

For DFO's purposes, British Columbia waters are divided into northern and southern halves, further divided into Statistical Areas whose boundaries are often defined by a headland or island (Capt. G. Nelson, pers. comm.), and which have open seaward boundaries. The reference area for a model of southern B.C., as defined above, thus consist of DFO Statistical Areas 11 (111), and 21 (121) to 27 (127).

All landings are presented for two six-month periods ("Summer", from April to September and "Winter", from October to March), and are reported as "round weight", i.e., the weight of the whole fish as it comes from the water before any treatment or dressing (Anon 1992). A conversion factor of 1.18 was used to convert salmonids caught by troll and troll freezer from dressed weight head-on to round weight. A conversion factor of 1.33 was used to convert halibut from dressed head-off to round weight. All other catches are reported as round weight. Salmonid landings from the southern B.C. Shelf include red and white chinook, coho, chum, pink and sockeye, but only chinook and coho are permanent residents. Chum, pink and sockeye, on the other hand swim through the area, without feeding, on their spawning migration. Hence, they are not considered to belong to the ecosystem. DFO data also record salmon roe, which was not considered here as it stems mainly from chum salmon.

Hake are problematic because the DFO data do not include the apparently high volumes that are traded at sea (T. Pitcher, pers. comm.). Discarded by-catches are discussed below.

Results and Discussion

Overall, an average of about 75 000 t of fish and invertebrates are reported to be landed annually from our 30,000 km^2 reference area, or 2.5 t·km^{-2}. A breakdown by functional groups and season is presented in Table 14, while Appendix 1, Table I gives a breakdown by species, i.e., identifies the species included in each functional group .

As might be seen, landings vary very strongly between summer and winter, with catches of salmon, sablefish, hake and halibut being higher in summer, while urchins and miscellaneous catches, especially of roe herring, are higher in winter. The landings in Table 19 underestimate true catches, as they do almost anywhere (Alverson et al. 1994). Table 20 suggests that in British Columbia, discards represent on the average, *in target species*, 22.3% of landings.

Regarding *non-target* species, Alverson et al (1994, Table 10) indicate a ratio of discarded by-catch to landed catch of 2.21 for "British Columbia Cod Trawl", and this figure may be used for the demersal group in the model.

Table 19 Mean landings (kg year^{-1}·km^{-2}) from the southern shelf of B.C., by functional group and season (based on DFO data for the years 1985 to 1993).

Functional group	Summer	Winter
Bivalves	71.8	72.7
Miscellaneous benthos	1.3	0.6
Sea cucumber/urchins	8.7	33.8
Octopus	0.6	0.5
Squids	4.8	0.2
Planktons	0	0.03
Cods/black cods	346.6	142.1
Prawns/shrimps/crabs	118.7	33.4
Large pelagics	1303.4	143.8
Small pelagics	1.9	0.3
Miscellaneous demersal	177.4	87.1
Ocean perches/rockfishes	377.3	401.1
Sharks	71.5	68.4
Transient salmon	419.4	252.7
Resident salmon	454.7	4.3
Other	8.0	408.6
All landings	3366.2	1649.6

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Balancing the Southern B.C. Shelf Model

(Judson Venier)

The following is a brief account of the actions taken to balance the Ecopath model of the self of southern B.C., by functional group (See also Table 20 and Appendix 1, Table J).).

Marine Mammals

The data from these groups were considered to be the most reliable and thus all estimates remained unchanged.

Table 20 Details on trawl catches in B.C. waters, allowing estimation of observer bias (ratio of at sea / offload weight), and of discarding (ratio discarded / kept weight). Based on hauls performed by 84 trawlers from February 16 to May 17, 1996 (Source: Archipelago Marine Research, Victoria, B.C.).

Functional groups	Retained		Ratio at sea / offload weight	Discarded at Sea			Ratio discarded/ kept weight
	At sea estimate	Offload weight		Marketable Dead	Marketable Live	Not marketable	
Yellowtail	3,641,512	3,758,515	0.97	1,192	0	18,139	0.005
Widow	991,371	1,214,935	0.82	6,126	0	215	0.006
Canary	253,931	216,295	1.17	419	0	415	0.003
Silvergrey	619,926	659,023	0.94	567	0	2,846	0.006
Yellowmouth	2,342,587	2,169,677	1.08	809	0	51,725	0.022
Rougheye	721,359	654,578	1.10	1,560	0	2,462	0.006
Shortraker	104,441	71,574	1.46	4	0	158	0.002
Redstripe	973,000	986,627	0.99	1,458	0	176,614	0.183
Sharpchin	193,745	284,903	0.68	667	0	122,452	0.635
Sablefish	83,849	82,657	1.01	9,767	38,281	99,184	1.756
Pacific cod	294,190	284,489	1.03	282	507	15,123	0.054
Dover	1,730,936	1,814,032	0.95	1,490	9,535	103,155	0.066
Rock	528,371	499,200	1.06	25	225	87,821	0.167
Lemon	228,110	185,672	1.23	794	2,331	89,415	0.406
Petrale Sole	278,317	266,094	1.05	70	445	9,363	0.035
Lingcod	394,876	556,715	0.71	408	3,669	11,795	0.040
Pollock	993,280	1,084,001	0.92	0	0	91,140	0.092
Hake	7,429	4,618	1.61	4	0	77,758	10.467
Dogfish	140,379	136,645	1.03	0	0	1,205,445	8.587
Turbot	2,030,668	1,709,479	1.19	0	100	1,440,253	0.709
Skate	148,610	257,584	0.58	0	0	246,501	1.659
All Species *	**21,385,504**	**21,125,047**	**1.01**	**32,175**	**55,795**	**4,676,474**	**0.223**

* = Including species other than those listed in this table

Birds

Only one change was made to the input parameters for this group as all other estimates were deemed reliable. The DC was reduced from 0.041 on decapods to 0.040 and the remaining 0.1% was put into sea stars. This was done to reduce predation pressure on the decapod group and also to account for some sea birds predation on sea stars (pers. obs.).

Spiny Dogfish

This box includes salmon (both resident and transient) and miscellaneous pelagic fish such as walleye pollock. P/B was increased from 0.1 (Polovina, this vol.) to 0.75 year^{-1} to account for other pelagics incorporated into the box. Biomass was decreased, for the same reason, from 1.75 (Polovina, this vol.) to 5 t·km^{-2}.

Pacific Halibut

All input parameters remained the same.

Pacific Hake

This group proved to be a major problem when balancing the model, for its biomass is very high. The amount of predation pressure it exerts on anything it eats, no matter how trivial a percentage of the diet, was large and posed the greatest difficulties. Since many hake inhabit the system, and the Southern British Columbia Shelf is so open, it was necessary to reduce DC of hake on all components of its diet by half and to assume that 50% of its diet is an import. Still, it was necessary to lower the diet composition on the Pacific cod group to reduce pressure on it, and to switch a small percentage to their own group. The same was true for the herring/small pelagic group, whose biomass could not support the pressure exerted on it.

Salps

Inputs remained unchanged.

Copepods

Same as for chaetognaths (see below).

Phytoplankton

Biomass was estimated by dividing the primary production of the southern British Columbia shelf area (Pauly, this vol.) by the P/B of primary producers from the Strait of Georgia model (Mackinson, this vol.). Detritus biomass was estimated using the empirical equation in Pauly et al (1993b; see also Venier, this vol.).

Pacific cod / miscellaneous fishes

I reduced predation of this group from sablefish to hake. The DC of cod was also changed, from a highly specialized diet of small pelagic fish, to a mix of benthic organisms, both to reduce pressure on the herring/pelagic fish group and to reflect the diversity of feeding strategies of the various demersal fishes included along with the cod.

Juvenile and Adult Sablefish

Estimates for these two groups remained the same.

Table 21 Basic parameters of southern B.C. shelf model. (Biomass in t·km^{-2}; P/B and Q/B in year^{-1}.)

Group	B	P/B	Q/B	EE
Transient orcas	0.002	0.20	12.13	0.00
Odoncetae	0.020	0.40	15.59	0.61
Pinnipeds	0.180	0.40	15.33	0.25
Mysticetae	0.750	0.02	13.02	0.08
Seabirds	0.009	0.10	112.00	0.00
Spiny dogfish	5.000	0.75	5.00	0.85
Pacific halibut	0.473	0.44	1.73	0.54
Pacific hake	44.000	0.75	5.84	0.24
Pacific cod	7.000	1.20	4.00	0.78
Juv. sablefish	1.500	0.60	6.60	0.39
Adult sablefish	0.100	0.08	3.73	0.00
Herring/sm. pel.	17.269	2.20	11.00	0.95
Carn. jellies	6.190	7.00	23.33	0.20
Decapods	10.000	1.80	7.20	0.54
Shrimps	5.000	1.20	8.00	0.75
Polychaetes	20.000	3.00	33.33	0.48
Sea stars	5.000	0.40	4.44	0.56
Sea urchins	5.000	0.40	4.44	0.70
Brittle stars	5.000	1.80	9.00	0.80
Bivalves	5.000	0.70	7.78	0.88
Amphipods	5.000	2.40	12.00	0.96
Euphausiids	29.586	3.70	15.00	0.95
Chaetognaths	3.000	12.00	40.00	0.46
Salps	5.000	3.00	12.00	0.58
Copepods	16.700	55.00	183.33	0.93
Phytoplankton	26.000	135.00	0.00	0.80
Detritus	7.000	-	-	0.64

Herring / small pelagic fish

In addition to Pacific herring, Pacific sandlance, anchovies and sardines are included in this group. To obtain a reasonable biomass estimate, an EE of 0.95 and a GE of 0.2 were entered (Christensen, pers. comm.) and Q/B was left unknown. In addition, the DC values for this group were altered to reflect a more planktonic diet instead of one which concentrated on euphausiids. This is believed to be correct as herring and the other pelagic fishes in the box are too small to feed heavily on such large prey (V. Christensen, pers. comm.).

Carnivorous Jellies

Input parameters remained unchanged.

All Macrobenthos Groups

The data for all of these groups were scarce, especially regarding diet compositions, but were used when available. Missing parameter estimates were derived that were deemed compatible with the model. Note that here, the "shrimps" group includes cephalopods.

Euphausiids

Krill are heavily fed upon within this ecosystem and as a result, their biomass was estimated to be very high. The original biomass estimate from Jarre-Teichmann (this vol.) had to be disregarded as it was not high enough to support the predation pressure upon this group. An EE value of 0.95 was entered and the biomass was left unknown.

Chaetognaths

Since Q/B was unknown for this group, a GE of 0.3 was entered; the other parameters were not changed

Results

Figure 3 presents the flowchart of the model based on the basic inputs in Table 21, and the diet matrix in Appendix Table J.

I abstain from presenting a detailed analysis of this model, given its very tentative nature, itself due to the openness of the ecosystem the model is meant to describe.

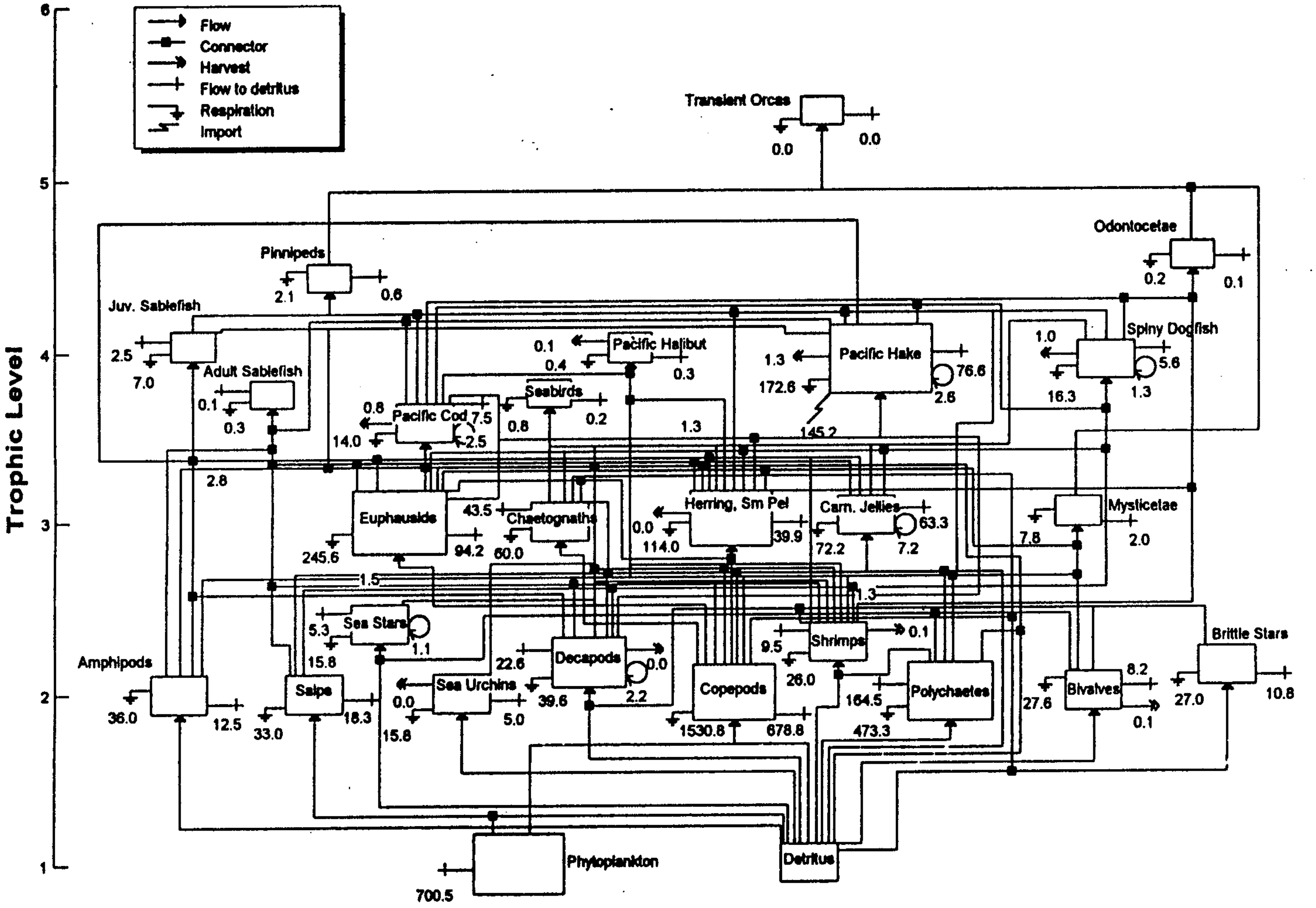

Figure 3 Flow chart of trophic interactions in the shelf system off southern British Columbia. All flows are expressed in $t \cdot km^{-2} \cdot year^{-1}$ and all biomasses in $t \cdot km^{-2}$; minor flows are omitted, as are all backflows to the detritus.

STRAIT OF GEORGIA MODEL

System definition and primary production

(Steve Mackinson)

System definition and oceanographic conditions

The Strait of Georgia is a partly enclosed basin on the west coast of Canada lying between the mountainous coast range of mainland British Columbia and the southern half of Vancouver Island. Essentially, the Strait is a narrow basin intensely mixed at both ends, with a major point source of freshwater in the southern half. The Strait of Georgia is a valuable fishing and nursery area for the young of several major stocks of Pacific salmon and for large stocks of herring. It also provides a lesser fishery for cod, groundfish, shellfish, shrimp and crab.

The Strait of Georgia is 200 km long with a mean width of 30 km, a total area of 6,900 km^{-2}, and a mean depth of 156 m; it is open to the Pacific Ocean through the Juan de Fuca Strait to the south and through Johnstone Strait to the north (Harrison et al. 1983). Mean summer temperature is 10.9° C (annual range 5° C). Prevailing winds are SW in winter and NW in summer. Precipitation ranges from 90 - 200 $cm{\cdot}year^{-1}$. Water circulation in the southern half of the Strait of Georgia is strongly affected by the large discharge of the Fraser River, which contributes to 80% of total land runoff and causes most salinity variation in surface waters. The passages to the Pacific Ocean are generally narrow and restrict tidal flows, resulting in strong tidal current. Tides are mixed, semi-diurnal with a maximum daily range of 0.5 m (Harrison et al. 1983). Extinction coefficient (k) and Secchi disc depth (m) range from 0.16 to 0.95, (mean = 0.37) and from 2.69 to 9.78 (mean = 5.9 m), respectively (Stockner et al. 1979).

The Fraser River flows into the southern end and creates a large brackish-water surface plume (Légaré 1957) which extends far out from the river mouth. The system can thus be viewed as a "narrow basin intensely mixed at both ends, with a major point source of freshwater in the southern half" (Harrison et al. 1983).

The Strait is an economically important area (Harrison et al. 1983) and has been the object of many ecological and oceanographic investigations (Arai and Mason 1982). As a result, there is much literature pertaining specifically to the Strait of Georgia. However, many of these studies have been done on single species in isolated inlets, bays, and/or fjords and the estimates of life history parameters which have resulted only apply to a small area of the entire Strait. This makes integration of data for various species groups difficult. In addition, many studies covered only a limited part of the year.

One characteristics of well-defined ecosystems are strong interactions within themselves and modest, controlled interactions with the outside. The Strait of Georgia ecosystem is very complex, but it fulfills the criterion of being reasonably well defined as an ecosystem. Some fish (herring, salmon) use the Strait only for migration to spawning grounds and feed minimally while in the Strait. Thus, although they might comprise a large percentage of the total fish biomass, they impact the system very little.

biomass, they impact the system very little. This is discussed in more detail further below.

Phytoplankton Production

The phytoplankton community is dominated by diatoms. Advection, turbulence, zooplankton grazing and summer nitrate depletion collectively impart a heterogeneous distribution to phytoplankton in surface waters. Three estimates of annual Primary Production (PP) were found:

- Parsons et al. (1970): 120 g Cm^{-2} year^{-1};
- Stockner et al. (1979): 345 gCm^{-2} year^{-1}; and
- Harrison et al. (1970): 280 g Cm^{-2} year^{-1}.

Assuming 0.1 gC = 0.2 g dry weight ≈ 1g wet weight (Mathews and Heimdal 1980), the estimates convert to:

- 1200 t wet weight km^{-2} year^{-1};
- 3450 t wet weight km^{-2} year^{-1}; and
- 2800 t wet weight km^{-2} year^{-1}.

The mean of these values is 2483 t wet weight km^{-2} year^{-1}, and this may be used as input.

Several, highly variable estimates of Production:Biomass (P/B) ratio were found in Stockner et al. (1979), expressed in terms of photosynthesis/chlorophyll *a*. For our purpose, a P/B ratio expressed on a wet weight basis is required, and a value of 200 year^{-1}, pertaining to diatoms (dominant in the Strait), and based on Olivieri et al (1993, Table 1) may be suggested. Allochthonous input to the Georgia Strait is estimated to be as great as total primary production, i.e., about $2 \cdot 10^6$t year^{-1} (Seki et al. 1969), possibly leading to an eutrophic state (Parsons 1980).

Macroalgae (kelp) production

No data on kelp production in the Strait of Georgia were found in the literature, and hence data from similar areas were used (Table 22).

Table 22 Standing crop (biomass; t km^{-2}) estimates of *Laminaria* spp.

Location	Biomass	References
Helgoland, Germany	12,700	Lüning (1969)
Nova Scotia, Canada	16,000	Mann (1972)
Lagoon Pt., Alaska	14,500	Calvin & Ellis (1978)
N.W. Atlantic	3,685$^{b)}$	Brady-Campbell et al. (1984)
Mean of all locations	11,720	this study

a) Converted from dry weight, assuming dry weight = 21% of wet weight; b) Brady-Campbell et al. (1984) also estimated an average P/B ratio of 4.43 year^{-1}, used here.

Assuming that kelp grow on rocky shores to depths of about 20 m would suggest, given the bathymetry of the Strait of Georgia (Guénette, this vol.), that kelp cover about 2 % of its surface area, which may be used as a raising factor for the contribution of kelp to total primary production (Table 23).

Table 23 Summary statistics on primary production (wet weight) in the Strait of Georgia.

Producer	PP (t·km^{-2}·year^{-1})	P/B (year^{-1})	Area (%)
Phytoplankton	2483	200	98
Macroalgae	52700	4.43	2

Zooplankton (incl. Jellies)

(Judson Venier and Claudia Octeau)

Table 24 summarizes key information on zooplankton and jellies in the Strait of Georgia.

Our suggested diet of jellies in summer is: herbivorous zooplankton (71%); carnivorous/omnivorous zooplankton (26%); and other jellies (3%) (Arai and Jacobs 1980; Larson 1987a, 1987b; Purcell 1991a, 1991b), though fish larvae are also taken (Arai and Fulton 1982; Purcell 1989).

The euphausiacean *Euphausia pacifica* is one of the most important species of zooplankton in the Strait of Georgia, representing 50% of the summer biomass (Heath 1977). Harrison et al. (1983) consider *Neocalanus plumchrus* to be the most abundant component of the zooplankton, but it occurs in surface waters (20 - 50 m) only in early spring; in early summer, *N. plumchrus* migrates downward, with maturation and spawning occurring in deep water (400 m, in the center of the Strait).

Table 24 Biomass (wet weight); P/B; Q/B; and P/Q for zooplankton, Strait of Georgia.

Group	Biomass ($t\cdot km^{-2}$)	P/B ($year^{-1}$)	Q/B ($year^{-1}$)
Herbivorous zooplankton	7.8[a)]	8.4[b)]	10.5[b)]
Carn./omniv.zoopl. (excl. jellies)	----	2-9[c)]	10.5[b)]
Misc.jellyfish and ctenophores	312[d)]	15	150[e)]

[a)] Probable summer value; yearly range is 0.05 - 1.4 $g\cdot m^{-3}$; [b)] From Harrison et al. (1983); [c)] From Heath (1977); estimate includes *Euphausia pacifica*; [d)] Annual maximum for organisms >350µm at depth to 400m: range is 0.1 - 2.0 $g\cdot m^{-3}$; [e)] Based on maximum daily intake of herring larvae in Kulleet Bay (Purcell 1989), converted to ash-free dry weight using data on *Aequorea victoria* in Larson (1986).

Macrobenthos

(Sylvie Guénette)

In the mid 1960s, Ellis (1967a, 1967b, 1968a, 1968b, 1968c) conducted an extensive study of the benthic community of the Georgia Strait, based on stations scattered all over the Strait, though at depths greater than 10 m. Stations were sampled (3 replicates) once or twice during a three year period (1965 to 1967). Since depth is a major factor in benthos distribution, these samples were here grouped into depth strata following Levings et al. (1983, Table 1). (See Table 25).

Table 25 Definition of depth strata (m) for the Strait of Georgia, with estimated areas after Levings et al. (1983).

Depth strata	Area (km^{-2})	Area (%)
20-50	800	10.8
50-100	1,560	21.1
100-200	2,130	28.8
200-300	150	21.2
300-400	1,000	13.5
>400	330	4.5
Total	7,390	100

Samples from intertidal stations in the Puget Sound (Nyblade 1979) were used to account for the intertidal zone which is important to shore birds and many invertebrates. Here, samples were stratified by sediment type (rock, gravel, sand, and mud) following Levings et al. (1983, Table 2); Table 26 shows our stratification by bottom type.

Table 26 Bottom types in the intertidal areas of the Strait of Georgia (from Levings et al. 1983).

Substrate type	Slope (^{0})	Area (km^2)
Rocky shores, steep	60	54
Rocky shores, gentle	45	266
Gravel	25	93
Sand	10	424
Mud	5	408
Total	---	1,245

For each class of organism, biomass values (in g·m^{-2}) were averaged by stratum (2-7 stations per stratum). The intertidal zone, and those of Ellis' stations located at depths <20 m, were each allocated 50% of the intertidal zone. The final biomass of specimens were averaged by weighing each stratum by its estimated area. The methodology underestimates large burrowing clams such as geoduck *Panope abrupta,* abalone *Haliotis kamtshatkana* and the crabs e.g. Dungeness crabs *Cancer magister*. Detailed results are presented in Appendix 1, Table J. These data were used to identify two functional groups: 1) small herbivorous or detritivorous benthos and 2) large carnivorous/detritivorous benthos. The latter group includes starfish and crabs.

Abalone typically eat 10-15% of their weight of seaweed per day (Mottet 1978, based on data from the Queen Charlotte Islands). Given a mean weight of 200g for legal size specimens (Breen 1980), and low recruitment, one specimen would eat 36-55 times its own weight per year. Along the California coast, at 15^{0}C, red sea urchins (*Strongylocentrotus purpuratus*) eat algae at a rate corresponding to 6.4% of their body weight per day (Mottet 1976). Since only 5.5% of the population are juveniles (Adkins et al. 1981), the mean weight of a legal size red sea urchin (*S. franciscanus*), that is 565g, was used for estimating consumption. By this reckoning, an adult would eat 23 times its body weight per year. Comparing these values with the relatively low values in Christensen (1995, Table 4), the more conservative value of 23 was chosen. The Q/B value for carnivorous benthos comes from Olivieri et al. (1993). The values of gross efficiency (P/Q) come from Christensen (1995), while a conservative value of ecotrophic efficiency (EE) was chosen following Christensen and Pauly (1993). Mortality rate estimates (Z; year^{-1}) for commercial species are: red sea urchins 0.2 (Jamieson 1984); abalone 0.23-0.91 (Breen 1980); geoducks, 0.3-0.4 (Noakes 1992); and Dungeness crabs, 2.5 (Smith and Jamieson 1991). Table 27 summarizes our suggested biomass and rate estimates for the two benthos boxes:

Table 27 Tentative estimates of biomass, P/B, Q/B, P/Q and EE for the macrobenthos of the Strait of Georgia.

Benthos group	Biomass (t·km^{-2})	P/B (year^{-1})	Q/B (year^{-1})	Gross eff. (P/Q)	EE (-)
Herb. & detritiv.	375	0.6	23	0.15	0.9
Carnivorous	---	2.5	10	0.2	0.9

Diet composition of adult crabs is 20% young crabs and 80% other benthic organisms (Stevens et al. 1982, Table 5). Fifty % of the animals eaten (cannibalism excepted) consist of carcasses and other detritus. This is similar to values used for similar benthic communities by Jarre-Teichmann et al. (in press). Table 28 gives our suggested diet composition for the macrobenthos.

Table 28 Approximate diet composition of herbivorous/ detritivorous benthos, and of adult crabs in the Strait of Georgia.

Consumer group	Macrophytes and algae	Detritus	Herbivorous benthos.	Carnivorous benthos
Herb. & detrivores	40	50	-	10
Adult crabs	-	40	40	20

The Demersal Fish "Box"

(Judson Venier and John Kelson)

No single reference was found which reviewed the status of demersal fishes in the Strait of Georgia, and Table 29, which presents key parameters for the group, was assembled from a number of disparate sources.

Overall, the estimated biomass of the demersal fish box, consisting mainly of hake, is 198,306 t, or 28.7 t·m^{-2}, while the mean (weighted by biomass) P/B and Q/B ratios for this box are estimated as 0.6 and 5.54 year^{-1}, respectively.

The diet composition of the demersal fish box was estimated, based mainly on the sources also used for Table 29, as follows: euphausiids (40% by weight), copepods (15 %); decapods (10%); shiner, sandlance and flatfish (10%); and cannibalism (25%), this high value being due mainly to over-aggregation within the box. These estimates are expected to be much modified when the model is balanced, due to the leverage effect discussed in Pitcher (this vol.).

The Pelagic "Box"

(Rik Buckworth)

The data summaries below refer to the pelagic component of the Strait of Georgia ecosystem, excluding planktonic elements and marine mammals, and concentrating upon species for which information was available. Surprisingly, although this component contains species which are subject to intensive and very valuable fisheries, the particular data types upon

Table 29 Biomass, P/B, and Q/B of demersal fish in the Strait of Georgia.

Species a)	Biomass (t·km^{-2})	P/B (year^{-1})	Q/B (year^{-1}) b)
Hake 1,2)	23.5	0.40-0.72	5.84
Walleye Pollock 3,4)	3.3	0.7-0.9	4.76
Rockfish 5,6)	0.40-1.07 c)	0.06-0.28	3.44
Lingcod 7,8)	0.30-0.51	0.40-0.76	3.30
Flatfish 9,10)	0.32-0.42 d)	0.40-1.15	3.21
Pacific Cod 11,12)	0.42	1.03-1.50	3.43
Sum (means)	28.74	(0.6)	(5.54)

a) References for biomasses and P/B ratios: 1) Saunders and McFarlane (1994); 2) Dorn et al. (1993); 3) Shaw et al. (1989); 4) Saunders et al. (1989); 5) Yamanaka and Richards (1992); 6) Hand and Richards (1991); 7) Richards and Yamanaka (1992); 8) Smith et al. (1990); 9) Fargo (1995); 10) Fargo (1991); 11) Stocker et al. (1995); 12) Westrheim and Foucher (1987); b) From Table II and empirical relationships in Pauly (1989), except for hake, taken from Pitcher (this vol.); c) Biomass estimates pertain to west coast of Vancouver Island, divided by approximate shelf area (see Pauly this vol.); d) Biomass estimates pertaining to rock and English soles in Hecate Strait, divided by rough estimate of area (~30,000 km^{-2}).

which Ecopath modeling depends were not easy to come by in the literature. There are thus several shortcomings in the data presented. However, one of the objectives of Ecopath is to identify the relative importance of different pieces of information and it is hoped these shortcomings are not major.

Some aspects of the pelagic box should be clearly emphasized. One is that some important components - herring and salmon - are not permanent occupants of Strait of Georgia. Herring enter the Strait to spawn and are subject to intense fishing and predation. Herring spawn is itself the subject of a fishery and is heavily utilized by other species and may be a very significant input into the Strait as a stimulus for secondary production (Hay and Fulton 1983). Because little of the life cycle is spent in the Strait of Georgia, probably a fair proportion of the herring and salmon biomass should be considered as an import to the system.

Herring and salmon abundance fluctuate considerably interannually. Current abundance also reflects overfishing. Herring biomass estimates vary between about 100,000 t for the early 1980s down to about 30,000 t (Hay and Fulton 1983; Stocker 1993; Environment Canada 1994). Annual spawning stock biomass in the late 1980s for the Strait of Georgia was between about 30,000 and 60,000t, depending on year and estimation method (Schweigert and Fort 1994). Northcote and Larkin (1989) estimated the numbers of salmonids produced by the Fraser River system at about 14 million fish annually. The historical abundance of pink salmon (*O. gorbuscha*) alone was around 48 million fish (Ricker 1989), but has been as low as 2 million in 1961.

The dominant pelagic species in the Strait of Georgia ecosystem are herring *Clupea pallasi;* spiny dogfish (*Squalus acanthias*); sockeye salmon *Oncorhynchus nerka;* coho *Oncorhynchus kisutch;* chum *Oncorhynchus keta;* pink *Oncorhynchus gorbuscha;* chinook *Oncorhynchus tshawytscha;* steelhead *Oncorhynchus mykiss;* lampreys *Lampetra ayresi;* and eulachon *Thaleicthys pacificus.* Other pelagics of the Strait of Georgia are, in deeper waters, the bathypelagids and the myctophids, not considered here (but see Keiser 1922).

Table 30 Ecological parameters of key pelagic component of the Strait of Georgia.

Groups[a)]	Residence time	Biomass $(t\cdot km^{-2})$	Ration $(\%W\ day^{-1})$	P/B $(year^{-1})$
Herring [1,2,3,b)]	Nov-April, 20 weeks	6.67		0.60
Dogfish[4,c)]	Resident	1.45	3	0.20
Salmon[5, 6,7,d,e)]	Aug.-Oct., 10 weeks	5.80	5	0.75
Lamprey[8,f, g)]	Apr.-Sep. ≈ 90days.	1.04	-	4.60

a) References: 1) Environment Canada (1994); 2) Hay and Fulton (1983); 3) Stocker (1993); 4) Thompson (1994); 5) Northcote and Larkin (1989); 6) Tutubalin and Chuchukalo (1992); 7) Walters et al. (1978); 8) Beamish and Youson (1987); b) Biomass based on mean of 1985-1989 estimates in Stocker (1993); c) Low risk yield (2,000 t), multiplied by 5 to get biomass: F is low, mean 1985-1990 was 948 t (Thomson 1994); d) Biomass based on annual yield of 30,000 t, raised by exploitation rate of 75%; e) Ration estimates were 3-10% of body weight daily (Tutubalin and Chuchukalo 1992); f) Total biomass declines from 13,000 t to 1,300 during residence (5); g) Life cycle is about 1 year; lampreys each attack 0.8 fish/day, with average size 54g (Beamish and Youson (1987).

Table 31 Approximate diet composition of key components of the pelagic box of the Strait of Georgia ecosystem.

Predators[a)]	Preys (in % volume)		
Herring [1,2,3,4)]	zooplankton (90)	benthos (10)	--
Dogfish[5,6,7,8)]	zooplankton (56)	hake (14)	herring, shrimp, salmon (15)
Salmon[9)]	macro(zoo)plankton, squids,	herring,	myctophids, other fishes
Lampreys[14)]	Herring (84)	Salmon (16)	--

a) References: 1) Arrhenius and Hansson (1993); 2) Environment Canada (1994); 3) Hay and Fulton (1983); 4) Stocker (1993); 5) Beamish et al. (1992); 6) Jones and Green (1977); 7) Tanasichuk et al. (1991); 8) Thomson (1994); 9)Tutubalin and Chuchukalo (1992).

Table 30 summarizes the biological data for the different groups. I have included the group "other" to emphasize that the information presented cannot include all species in the pelagic component, but only those for which significant information is available. Table 31 lists the prey of the different groups, and Table 32 provides numerical catches of salmon by species.

The herring biomass estimate was based on data presented by Stocker (1993; mean of total biomass estimates in Figure 10, p. 280). Numerical abundance and exploitation estimates for salmon species were from Northcote and Larkin (1986). Landings were from Anon. (1987, 1988). Walters et al. (1978) provided a detailed model of passage of juvenile salmonids through the Strait of Georgia.

Catches for salmon for the Strait of Georgia are around 30,000 t·year^{-1}, but vary a lot among years, e.g. 1986: 25,000; 1987: 39,000 t.

Marine Mammals and Birds

(Yoshihiko Wada)

Introduction

The purpose of this exercise being to construct a complete model of the flow of biomass between different trophic levels within the Strait of Georgia in the summer months (June 23 - September 22) of the 1980s, this contribution provides the information on food consumption and food composition required for including the marine mammals and birds which occur in the Strait of Georgia during the summer months.

Marine mammals

The marine mammals found in the Strait of Georgia in the summer are killer whales,

Table 32. Estimates of Salmon Abundance, and catches, in numbers (Northcote and Larkin 1989).

Species	Abundance	Catch	Remarks
Pink	5,000,000[a)]	3,000,000	Georgia, Juan de Fuca & Johnstone Straits
Chum	776,000	140,000	Fraser & Juan de Fuca
Coho	441,000	303,000	Mean of 1973-82
Sockeye	7,400,000	5,400,000	---
Chinook	104,000	646,000	---

a) May reach 9,000,000+ in odd years.

Dall's porpoises, harbour porpoises, and harbour seals (see Osborne et al. 1988). There are two different groups of killer whales: 1) "residents", which generally stay within the strait, and which eat fish, and 2) "transients", which travel along the west coast of British Columbia, and which eat marine mammals, such as seals and dolphins (Ford et al. 1994).

Estimates of killer whale population size were obtained from a series of interviews with marine mammal specialists in B.C, i.e., Andrew Trites, Graeme Ellis, Kathy Heise, and Lance Barrett-Lennard. The compromise numbers of 80 for resident and 11 for transient killer whales were derived by averaging the figures provided by these specialists.

Similarly, in the absence of any systematic or comprehensive study, the abundance of Dall's and harbour porpoises is based on interviews with John Ford, Kathy Heise, Lance Barrett-Lennard, Ron Bates, and Tamara Guenther.

Estimates for Dall's porpoises range between 150 - 300 (Lance Barrett-Lennard, Department of Zoology, UBC, pers. comm.) and 2,000 - 4,000 (Tamara Guenther, Victoria Marine Mammal Research Group, and Dave Duffus, Geography Department of the University of Victoria, pers. comm.), [The high estimate of T. Guenther is based on the high number of animals that wash up dead each year]. The estimates for harbour porpoises ranged from 50 - 150 (Lance Barrett-Lennard) to 2,000 - 4,000 (Dave Duffus, pers. comm., with Tamara Guenther in agreement). The general consensus is that there are more Dall's porpoises than harbour porpoise in the Straits of Georgia and Juan de Fuca (T. Guenther, pers. comm.). This is consistent with Barrett-Lennard who also thinks that Dall's porpoises are more plentiful in the Strait of Georgia.

Thus, midranges of 1,125 and 500 were retained as best estimates for Dall's and harbour porpoises, respectively,

The harbour seal population of 14,326 was determined from the data in Olesiuk et al (1990, Figure 21), based on field data were collected in 1988, a year assumed to be representative of the 1980s.

Mean body weights were obtained from Trites and Pauly (in prep.) for all species except transient killer whales, whose average body weight of 3,550 kg was taken from Barrett-Lennard et al. (1995).

The daily ration of harbour seals in the Strait was from Olesiuk et al. (1990); for all other species, ration and Q/B were estimated as for marine mammals in the Alaska Gyre (Trites and Heise, this vol.).

Diet compositions for resident killer Whales, Dall's and harbour porpoises were obtained from Pauly et al. (1995), from Barrett-Lennard et al. (1995) for transient killer whales and from Olesiuk et al. (1990c) for harbour seals, for which the data were also broken down into estuary and non-estuary, and by month, then re-aggregated. Diet composition on a species basis are presented in Appendix 1, Table L.

Table 33 summarizes our overall results.

Marine birds

Here, marine birds are defined as birds that feed extensively in the waters of the Strait of Georgia, i.e., all shorebirds except great blue heron have been omitted. Most of the omitted birds, such as dabbling ducks,

Table 33 Statistics of marine mammals in the Strait of Georgia.

Species	Mean weight	Daily ration	Q/B	Pop. no	Pop. biomass	Food cons.
(Units)	(kg)	(kg·day^{-1})	(year^{-1})	(N)	(t·km^{-2})	(t·km^{-2}·year^{-1})
Orca (resident)						
female	1,974	43.28	8.0	40.2	0.011	0.09
male	2,587	53.73	7.6	40.2	0.015	0.11
Orca (transient)						
female	2,761	56.62	7.5	5.5	0.002	0.09
male	3,068	61.59	7.3	5.5	0.002	0.11
Dall's porpoises						
female	61.4	2.69	16.0	563	0.005	0.08
male	63.1	2.75	15.9	563	0.005	0.08
Harbour porpoises						
female	29.5	1.50	18.6	250	0.001	0.02
male	32.6	1.63	18.2	250	0.001	0.02
Harbour seals						
female	56.4	1.78	11.5	7,163	0.059	0.67
male	63.9	2.02	11.5	7,163	0.066	0.76
All mammals	--	--	11.2	16,041	0.168	1.88

geese, and swans, feed only to a very limited extent in the marine realm proper (Vermeer and Ydenberg 1989, p. 62).

Mean body weight figures were obtained mostly from Palmer (1962, 1976a, 1976b, 1988) and Nilsson and Nilsson (1976), while population size estimates were taken mainly from Vermeer (1981, p. 115) and Vermeer and Ydenberg (1989).

Bird rations were derived from:

$$\log R = -0.293 + 0.85 \log W$$

where R is the daily ration in g, and W is body weight, also in g (Nilsson and Nilsson 1976). The results are consistent with a graph in Muck and Pauly (1987, Figure 4) illustrating the relationship between body weight of fish-eating Peruvian guano birds and their daily food consumption.

The mean body weight and population figures for glaucous-winged gull, double-crested cormorant, and pelagic cormorant were taken from Vermeer and Ydenberg (1989, p. 67). The original data covered the period between May 1 and August 31 (year not specified).

The mean body weight of Brandt's cormorant was taken from Palmer (1962, p. 345). Vermeer's estimate of the population in March-April, 1977 was used for the summer population (Vermeer, 1981, p.115). Vermeer also included a November value, but this was considered less relevant, since the March-April environment is more similar to the summer environment.

The mean body weight of Arctic and other loons is represented by the value for Arctic loons provided by Palmer (1962, p.43), as Arctic loons have been reported to represent 90% of all loons in the Strait. The population value in this study is the mean for March-April, 1977 (Vermeer 1981, p. 115).

Western brebes represent approximately 90% of all the grebes in this study area

(Vermeer 1981, p. 115). Thus, the mean body weight of grebes can be represented by an the average value for Western grebes (Nuechterlein and Storer (1989, p. 40). The population value for grebes is the mean for March-April, 1977 (Vermeer, 1981, p. 115).

The mean body weight of surf scoters is from Vermeer (1981, p. 114), as is the population estimate; the latter, however, was multiplied by 0.5 to eliminate seasonal bias. The mean body weight of white-winged scoters is from Palmer (1976b, p. 284). The population value is the average of March-April, 1977 Vermeer (1981, p. 115). Other diving ducks include oldsquaws, Barrow's golden eye, greater and lesser scaup, and other unidentified species. Mean body weights were assumed similar to that of oldsquaw (Palmer 1976a, p. 354), and values for May were averaged. The population estimate is the average for March-April, 1977 (Vermeer 1981, p. 115).

The mean body weight and population values for pigeon guillemot are from Vermeer and Ydenberg (1989, p. 67). The data were for the period between May 1 and August 31 (year not specified). Other auks are common murre and marbled murrelet. The mean body weight of these auks was assumed similar to the value for pigeon guillemot. The population is the average of March-April, 1977 (Vermeer 1981, p. 115).

The mean body weight of great blue herons is from Palmer (1962, p. 393). The population value is the average of the years 1980, 1981 and 1987 (Butler 1989, p. 114).

Food composition data for glaucous-winged gull, double-crested cormorant, and pelagic cormorant are from Vermeer and Ydenberg (1989, p. 63). The data are for the nesting season. Food composition data for Brandt's cormorant are from Palmer (1962, p. 349). The original data were collected from the west coast of Vancouver Island and Oregon and are not specific to the Strait of Georgia.

Vermeer (1981, p. 115) reports that Arctic loons represent 90% of all the loons in the Strait of Georgia. (Palmer (1962, p. 49) reported that Arctic loons feed on herring. Pacific loon stomachs obtained from Active Pass also contained Pacific herring (Robertson 1973).

Western grebe is the most common species of grebe to visit the Strait (Vermeer et al. 1983). Robertson (1973) reported only the winter and March data, from which summer food composition has been inferred. Herring is an important food of Western grebes in the Strait (Vermeer and Ydenberg 1989, p. 64).

Surf scoters have been reported to be the most common diving ducks in the Strait (Vermeer, 1981, p. 115). They feed mostly on blue mussels, but also on snails, errant polychaetes and barnacles (Vermeer and Ydenberg 1989, p. 65). White-winged scoters consume mainly clams, but, like scoters, they also feed on snails, errant polychaetes, and barnacles (Vermeer and Ydenberg 1989, p. 65). Oldsquaw eat mostly bivalves and snails in the summer (Vermeer and Levings 1977, p. 58). The diet composition of other diving ducks was assumed similar to that of oldsquaw.

The diet composition of pigeon guillemot was taken from Vermeer and Ydenberg (1989, p. 63). Pigeon guillemot feed mainly on benthic fish. The diet composition of other auks, such as common murre and marbled murrelet, was assumed similar to that of pigeon guillemot (Vermeer and Ydenberg 1989, p. 63).

Table 34 Body weights and related statistics of marine birds in the Strait of Georgia.

Species	Mean weight	Daily ration	Q/B	Pop. No	Pop. biomass	Food cons.
(Unit)	(kg)	(kg·day^{-1})	(year^{-1})	(N)	(t·km^{-2})	(t·km^{-2}·year^{-1})
Glaucous-winged gull	1.16	0.30	94.49	26,000	0.0044	0.41
Db.-crested cormorant	2.00	0.48	87.07	4,000	0.0012	0.10
Pelagic cormorant	1.80	0.44	88.46	4,800	0.0013	0.11
Brandt's cormorants	2.43	0.56	84.59	1,661	0.0006	0.05
Loons (Arctic & other)	1.95	0.47	87.41	2,768	0.0008	0.07
Grebes (west. & other)	1.24	0.32	93.56	17,159	0.0031	0.29
Surf scoters	1.10	0.29	95.24	10,793	0.0017	0.16
White-winged scoters	1.35	0.34	92.36	1,384	0.0003	0.03
other diving ducks	0.91	0.24	98.01	24,354	0.0032	0.31
Pigeon guillemot	0.45	0.13	108.91	1,000	0.0001	0.01
other auks	0.45	0.13	108.91	3,875	0.0003	0.03
Great blue heron	2.95	0.66	82.15	812	0.0003	0.03
All birds	--	--	91.77	98,604	0.017	1.57

Food composition data for great blue Herons were taken from Verbeek and Butler (1989, p. 75). Gunnels represent almost 50% of their food.

Diet compositions are presented on a per species basis in Appendix 1, Tables L. Table 34 gives a summary of the population estimates.

Fisheries harvest in the Strait of Georgia

(Eny A. Buchary)

Data Sources and Methods

Fisheries catch data were extracted from the B.C. Commercial Catch Statistics Database of the Department of Fisheries and Oceans (DFO). Data from July, August and September were chosen to represent "summer". The years covered were 1982 to 1989 (no computerized data were available for the years prior to 1982). Information on life history, used for grouping species were obtained from Hart (1973).

The DFO statistical areas corresponding to the Strait of Georgia as defined by Mackinson (*vide supra*), are 14 to 18, 28 and 29. Because of their importance for the salmon fishery, DFO treats the lower Fraser River and estuary (areas 28 and 29, further divided as subareas 29-A to 29-F) separately from the Strait of Georgia. However, they are included in our definition of the Strait of Georgia (see Mackinson, this vol.)

The same factors were used for conversion to round weight as for the catches on the B.C. shelf (see above)

Based on their life history (Hart 1973), the various species caught in the Strait were combined into functional groups such as demersal fish, shellfish, pelagic fish, eggs, non-food biota and zooplankton.

The demersal fish box includes halibut, lingcod, Pacific (grey) cod, sablefish (i.e., black cod), brill sole, Dover sole, lemon

Table 35 Commercial fisheries harvest ($kg \cdot km^{-2} \cdot year^{-1}$), Strait of Georgia. (Summer values only; based on DFO data for the years 1982 to 1989).

Functional Groups	Areas 28 & 29	Areas 14 - 18	Whole Strait
Bivalves	7.1	405.04	412.2
Sea cucumber/urchins	4.02	25.6	29.6
Octopus	0.07	1.47	1.54
Squids	0.006	0.09	0.1
Plankton	0.9	0	0.9
Cods/black cods	6.9	22.95	29.8
Prawns/shrimps/crabs	176.2	48.1	224.3
Large pelagics	0.02	13.2	13.2
Small pelagics	0.7	18.9	19.6
Misc. demersals	3.6	6.6	10.2
Ocean perches/rockfishes	2.8	19.8	22.5
Sharks	0.95	34.5	35.4
Transient salmon	2065.1	327.4	2392.5
Resident salmon	99.4	176.8	276.2
Others	0.2	0.04	0.2
Sum	2367.9	1100.34	3468.24

sole, rock sole, Pacific Ocean perch, greenies (i.e., yellow tail), rockfish, red snapper (i.e., yellow eye), hagfish, flounder, skate, (silver perch), turbot, pollock and hake.

DFO use "shellfish" as a catchall term for all invertebrates. Major components include benthic organisms such as red sea urchin, prawn, shrimp, razor clam, butter clam, Manila clam, native littleneck clam, Dungeness crab, red rock crab, geoduck (Harbo et al. 1992), horse clam, scallop, crayfish and sea cucumber, but also includes non-benthic organisms such as squid.

Salmonids, (recorded as red and white chinook, sockeye, coho, pink, chum and steelhead) are the dominant pelagic species. Aside from salmonids, other species, i.e. eulachon, sturgeon, tuna, smelt, dogfish, shark and herring also contribute to the pelagic box. (See also Buckworth, this vol.).

Another component is "eggs" which includes both salmon roe and herring roe, while "non-food biota" consist of organisms used for "mink feed, scrap and reduction"; the "zooplankton" group consists solely of euphausiids.

Table 35 presents estimates of summer catches for these and other functional groups, by sets of subareas of the Strait of Georgia.

Balancing the Strait of Georgia Model

(Judson Venier)

Ten functional groups ("boxes") were originally identified for inclusion in the Strait of Georgia model, but problems arose during the process of parameter estimation and more boxes had to be incorporated. For example, demersal fish were split into two boxes (hake and demersal fish) because of excessive cannibalism within the original box. After a meeting with the parties involved in input estimation, initial guesses of B, P/B, Q/B, catches and of diet compositions (DCs) were identified which were questionable, and thus provided leeway for balancing the model. The changes thus effected were as follows:

Mammals and Birds

The top predators (birds, resident mammals, transient orcas) were believed to have the best data and few of the inputs (in Wada, this vol.) needed to be modified. The P/B value of resident mammals was too low to accommodate the predation pressure exerted by the transient killer whales and was increased by 0.2 $year^{-1}$. We believe this change to be justified because the bulk of the biomass of resident mammals is made up of harbor seals, which have a fairly high reproductive rate, and hence a high P/B ratio.

Also, part of the DC's of Resident Mammals and Birds was changed to reduce predation pressure on Miscellaneous Demersals. Resident Mammals were changed to feed more heavily on salmon and Birds were changed to feed more strongly on krill (Carnivorous Zooplankton).

Salmon

Salmon were incorporated as an individual box. In this model, salmon catch was 0.743 $t \cdot km^{-2} year^{-1}$, B was 3.8 $t \cdot km^{-2}$, their P/B was 0.75 $year^{-1}$, and Q/B was 0, i.e., they do not act as predators in the system. Large pelagic harvest was lowered to include only dogfish. The outputs were generally similar, but EE of large pelagic fish was reduced by ~0.5 because of decreased fishing pressure and a shift of predation by resident mammals from large pelagics to salmon. This model is more representative of the system, as it includes the B of salmon and the influence, although minimal, that they exert on the other components.

Large Pelagics

Biomass was estimated to be ~15$t \cdot km^{-2}$ which is 1.5 $t \cdot km^{-2}$ lower than the estimate in Buckworth (this vol.). P/B was reduced from 3.5 $year^{-1}$ to 1 $year^{-1}$, the latter being a more realistic value for larger fish. DC was adjusted to reduce predation on Miscellaneous Demersals and increase that on krill.

Small Pelagics

P/B was assumed to be higher (by 1 $year^{-1}$) than the value for Large Pelagics. The Q/B value was set at a high 18 $year^{-1}$, meant to reflect the high feeding activity of small pelagic fish. An EE value of 0.95 was input to obtain a reasonable biomass estimate, and to reflect our assumption that most of the small fish production is consumed within the ecosystem.

Hake

The biomass estimate input into the model was increased by 1$t \cdot km^{-2}$ over its value in Venier and Kelson (this vol.), and the P/B value slightly increased, from 0.72 $year^{-1}$ to 1 $year^{-1}$, to accommodate the high predation pressure to which this group is subjected. The Q/B value was reduced by 0.84 $year^{-1}$ from that in Pitcher (this vol.) to decrease the predation by hake on the Miscellaneous Demersals, whose biomass would otherwise shoot up. The DC was shifted to increase predation on krill and decrease that on Miscellaneous Demersals, for the same reason.

Miscellaneous Demersals

The biomass estimate of 13 $t \cdot km^{-2}$ used in the model is more than twice as large as the value in Venier and Kelson (this vol.). However, the original estimate was based on the large, commercially important species for which catch statistics are available, and did not include the many smaller species also found in the ecosystem. Thus the increase seems justified. For the same reason, the P/B value used here is 1 $year^{-1}$, which is higher than the mean in Venier and Kelson (this vol.). The EE value estimated from the model is very high, indicating that this group is heavily fed upon within the system.

Jellies

The high biomass estimate of 312 t·km^{-2} in Venier and Octeau (this vol.) pertained to an annual maximum from an specific area of the Strait, which cannot be considered representative of the entire system and period considered here. The abundance of gelatinous organisms within the Strait is very habitat specific and numbers can be very high on a local scale within some of the fjords and bays. Here, the biomass for the Strait as a whole was set at 15t·km^{-2}, pending a comprehensive study. The original values of P/B and Q/B values in Venier and Octeau (this vol.) were also adjusted downward, another reflection of our difficulties with the conversion of site-specific, dry weight-based estimates.

Large Macrobenthos

The biomass value of 140 t·km^{-2} is based on the work of Ellis (1967-1968), cited by Guénette (this vol.) A P/B value of 2 year^{-1} was used, which is slightly less than that estimated value for carnivorous macrobenthos (in Guénette, this vol.) because the group contains omnivores as well. The Q/B value in Table 27 was lowered slightly to reduce predation on Small Macrobenthos.

Small Macrobenthos

The original B estimate of 375t/km^2 in Guénette (this vol.) had to be increased to 400 t·km^{-2} to accommodate predation. P/B also needed to be raised for the same reason and also because the P/B value of 0.6 year^{-1} estimated from the literature is probably too low for such small organisms.

Carnivorous Zooplankton

The biomass estimate was obtained from the model by entering an EE value of 95%. This value is reasonable as most of the production from this group can be assumed to be consumed within the system. P/B is higher than the maximum estimated in Venier and Octeau (this vol.) but lower than that estimated for other models (e.g. Christensen 1995). The Q/B value was raised to yield a positive estimate of respiration.

Herbivorous Zooplankton

The biomass used for this group is twice that one estimated in Venier and Octeau (this vol.); similarly, a P/B value of 55 year^{-1} was used instead of the value in Table 24, to accommodate predation. Christensen (1995) used a similar value for planktonic groups in the North Sea ecosystem. The value of Q/B in Table 24 was raised for the same reason as for Carnivorous Zooplankton. These changes imply that the original parameters may not have been realistic.

Primary Producers

Biomass was estimated by the model after entering an EE value of 0.40 and a P/B value of 125 year^{-1}. This EE value reflects our assumption that the bulk of primary production is not directly consumed within the system, but instead cycled to the detritus. The P/B value is intermediate between an upper estimate, pertaining to phytoplankton and a lower estimate, pertaining to the macroalgae.

Detritus

The biomass of this group was estimated using the empirical formula:

$$\log_{10}D = -2.41 + 0.954 \log_{10}PP + 0.863 \log_{10}E$$

where D is the detritus standing stock in $gC \cdot m^{-2}$, PP is the primary production in $gC \cdot m^{-2} \cdot year^{-1}$, and E is the euphotic depth in m (Pauly et al. 1993b).

Results and Discussion

The basic parameters for the strait ecosystem are presented in Table 36, while Appendix Table O shows the corresponding diet matrix.

As can be seen, both zooplankton types, small macrobenthos, hake, and small demersal fish were all consumed heavily in the system. Large pelagic fish, salmon, jellies and detritus were not used much as sources of food: their EE values are low.

Table 36. Basic parameters for the Strait of Georgia model. Biomasses are given in $t \cdot km^{-2} \cdot year^{-1}$, while production/biomass (P/B) and consumption/biomass (Q/B) both are annual rates. EE is the ecotrophic efficiency expressing the proportion of the production that is lost to exports or predation mortality.

Group	Biomass	P/B	Q/B	EE
Mammals (Res.)	0.153	0.400	11.540	0.605
Lg. pelagics	15.000	1.000	5.000	0.821
Sm. pelagics	24.160	2.000	18.000	0.950
Hake	24.500	0.900	5.000	0.879
Misc. demersals	13.000	1.000	4.240	0.985
Jellies	15.000	3.000	12.000	0.137
Lg. macrobenthos	140.000	2.000	8.750	0.260
Sm. macrobenthos	400.000	3.500	23.000	0.631
Carn. zooplankton	16.577	12.000	40.000	0.950
Herb. zooplankton	16.269	55.000	183.333	0.950
Prim. producers	250.100	15.000	0.000	0.760
Birds	0.017	0.100	91.770	0.000
Trans. Orcas	0.005	0.200	7.400	0.000
Salmon	3.800	0.750	0.000	0.403
Detritus	7.000	-	-	0.967

During the summer, large increases in zooplankton biomass arise following the large blooms of phytoplankton in the late spring. This increased production of plankton in early summer supports the system throughout the rest of the summer months.

The Strait of Georgia ecosystem is a complex one with many trophic energy flows (Figure 4). Many components in the ecosystem appear to be generalists, feeding on a high diversity of prey. For example, the resident mammals' omnivory index (the heterogeneity of the DC values) is extremely high. They feed at several separate trophic levels, and their own trophic level is comparatively low compared with that of some of their prey items. One of their prey species, hake, indeed has a trophic level higher than theirs. The varied nature of many groups' diets and the high variety of trophic levels present in the system may makes successful single-species management of the specific components of the ecosystem rather difficult given their interactions (Figure 5). Thus the use of ecosystem models, such as Ecopath, as tools in the formation of management decisions are important for proper management. The more one understands the system as a whole, the more one can understand its components, and better management decisions can result from these ecosystem analyses.

The food consumption of birds is very high, due to their fast metabolism. They consume as much food as both groups of marine mammals combined even though their biomass is much smaller. Marine birds are also feeding at a wide range of trophic level.

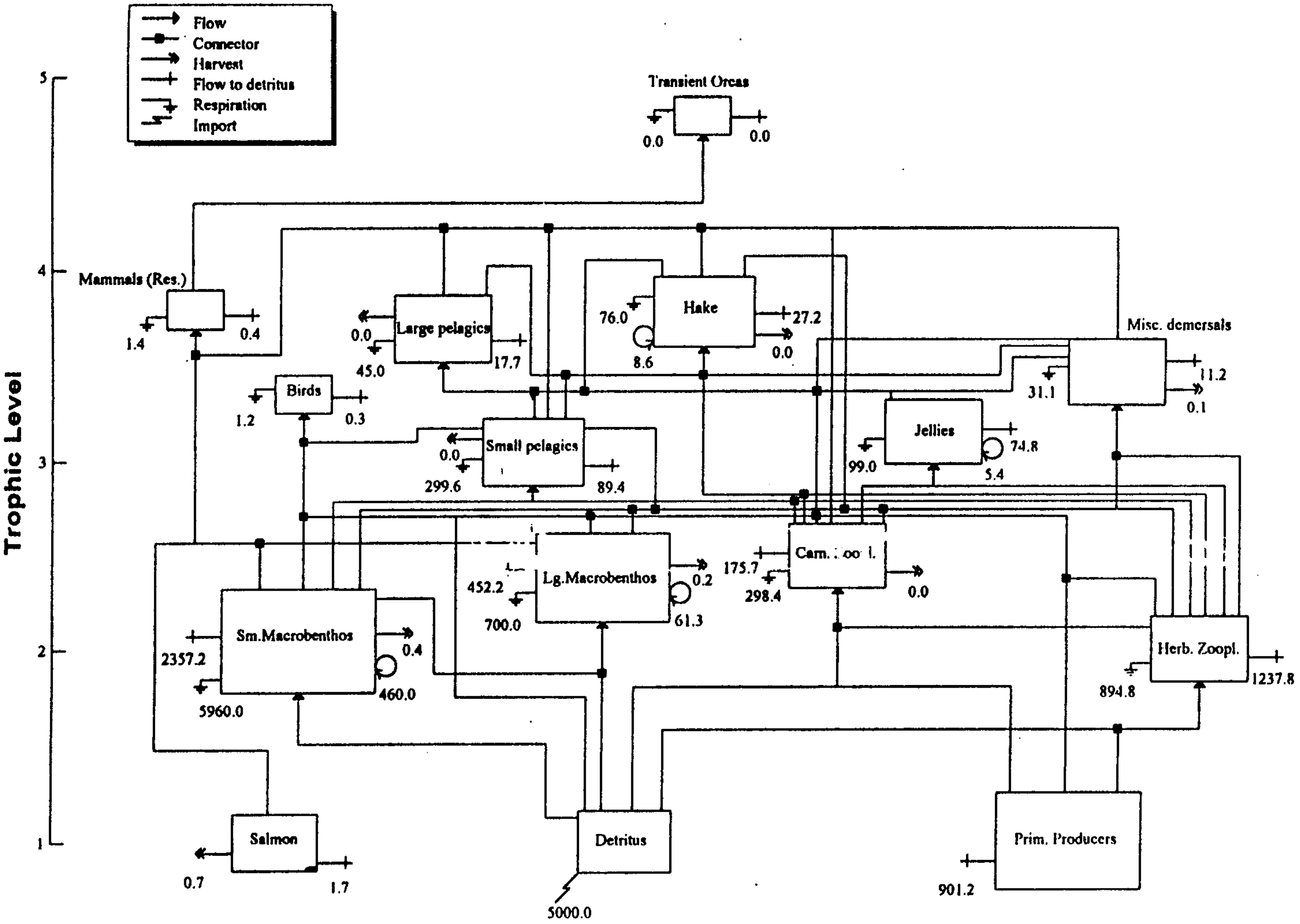

Figure 4 Flow chart of trophic interactions in the Strait of Georgia. All flows are expressed in $t{\cdot}km^{-2}{\cdot}year^{-1}$ and all biomasses in $t{\cdot}km^{-2}$; minor flows are omitted, as are all backflows to the detritus.

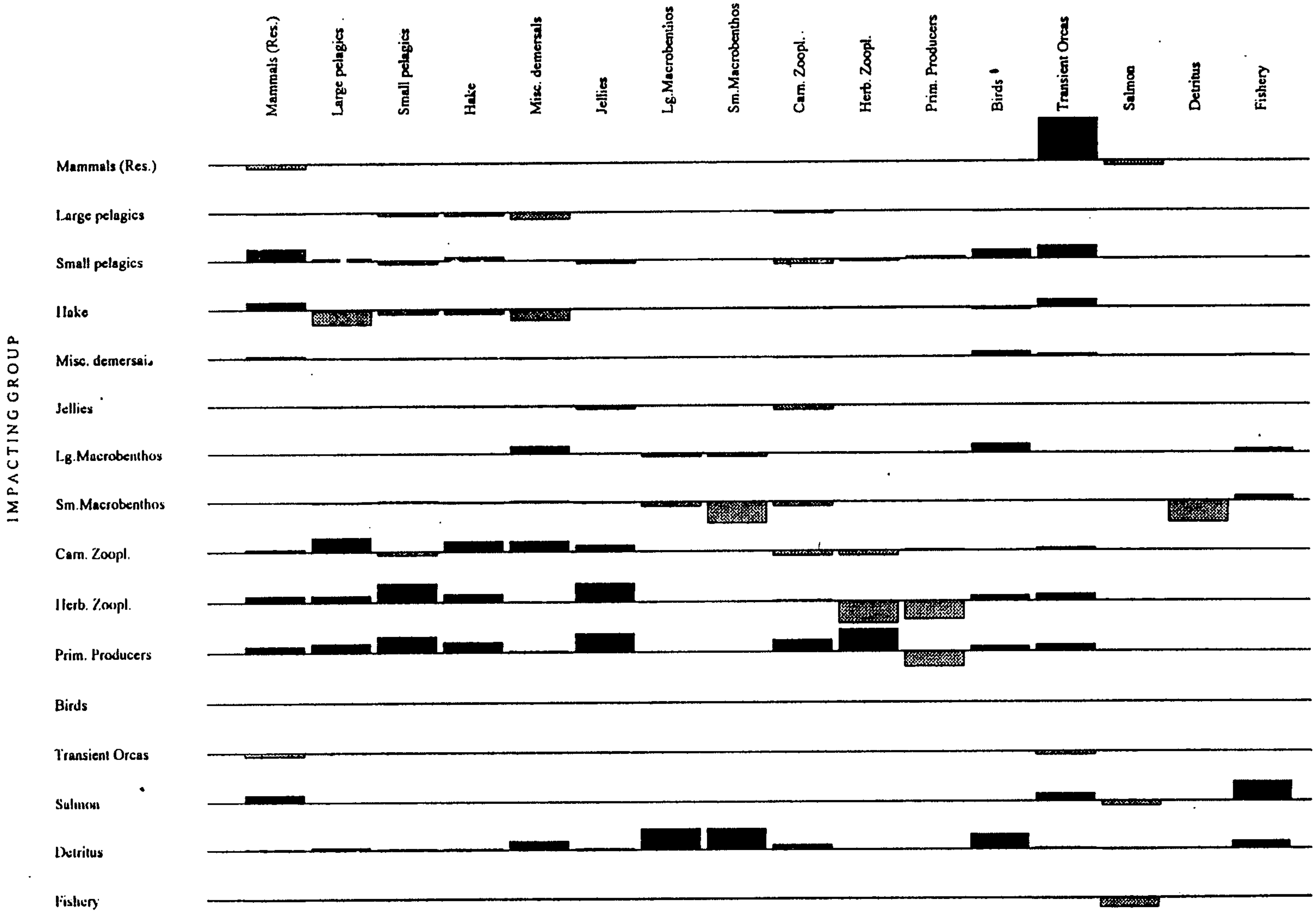

Figure 5 Mixed trophic impacts in the Strait of Georgia ecosystem.

A few problems were identified in the balancing of the model which warrant discussion. Migrations into the strait of large quantities of salmon had to be accounted for. These fish enter the strait in mid to late summer, spend little time there, then enter the rivers to spawn and die. They are consumed by resident mammals, especially orcas, and in turn, consume almost nothing while migrating. They contribute to the detritus as their carcasses are carried down the Fraser and other rivers and into the Strait of Georgia. Although they do not affect the ecosystem as a whole very significantly, they are nevertheless one of its components. The resident mammals depend on them for a food source and there are large fisheries for them throughout the Strait. Their contribution to the detritus, although small in comparison with other components of the system, is an important source of nutrient influx in late summer when other nutrients have been depleted.

Further studies need to be conducted in order to get a clearer picture of the ecosystem functions in the Strait. A problem when collecting data for input into the model was their heterogeneity. The Strait of Georgia has a very varied coastline consisting of bays, inlets, fjords, muddy shores, estuaries, rocky shores, as well as a vast open pelagic zone, each harboring localized fauna. Integrating data boxes was often difficult because many estimates were obtained from specific sites with species not found in other sites. Therefore, finding common input values for aggregated groups of organisms that could be used to run the model was a difficult task (this was particularly evident for the zooplankton box, whose parametrization appears quite problematic). This resulted in the drastic modifications of some P/B and Q/B values when the model was balanced.

Conclusion

Through this run of Ecopath, a clearer picture of the highly complex ecosystem of the Strait of Georgia was presented. The steady-state representation of a naturally dynamic system and the identification of shortcomings in the data should provide good reference points for future studies concerning the strait. Models such as Ecopath have implications in the proper management of resources which are intricate components of the ecosystems in which they live. Understanding the processes and interactions within the systems, and that impacting one group will cause changes in another, can aid in the formation of long-term management policy.

GENERAL DISCUSSION

A Road Test of Ecopath

(Rik Buckworth)

A *road test*, you might ask? Why report the construction of a mass balance model as "a road test"? A new car model is reported to the motoring public on the basis of some characteristics with which they are reasonably in tune, usually by a motoring writer who is not otherwise familiar with the vehicle - and need not be an especially good driver - but who has a wide range of experience with different cars. This note uses the analogy of a road test as a framework for reporting the experience of a group of graduate students in using the Ecopath system to model the Strait of Georgia ecosystem.

The scene of the road test

The Strait of Georgia separates southern British Columbia from Vancouver Island. It is a long, narrow and relatively sheltered basin with a total area of around 7000 km^2 and mean depth of 156 m. Constrictions at each end by narrow straits, a fjord coast and the presence of several islands create strong tidal flows. The environment of the southern half is strongly influenced by the Fraser River (Mackinson, this vol.). The Strait and its tributaries thus provide a diversity of habitats, including those for several commercial and recreational fish species, including Pacific salmon, as well as a suite of marine mammals and birds (Wada, this vol.).

Power

The real power of a model is not so much in the result, as in the process, in the learning that it engenders - it's not your destination that matters, but the fun you have on the way there! Students reported that learning to drive Ecopath forced them to think about a whole system, emphasizing both the amount of appropriate information available, and the data gaps. As this information - biomass, diet composition, etc., had not previously been combined in such a way, Ecopath allows users to evaluate the importance of gaps. The system thus has two important attributes of a useful model - it predicts, and it has the capacity to surprise, as shown by the total fish consumption by mammals and birds in Georgia Strait (see Wada, this vol.).

Handling

An attractive, almost seductive, attribute of Ecopath is its simple data requirements. Estimates of biomasses, consumption rates, diet, etc. are often easy to come by. However, it is important to emphasize that the requirements are not simplistic. Immense amounts of work may be represented by a few numbers, and conversion of information between different units or currencies can make the derivation of those numbers problematic. But there is a danger, too. Sins of omission can occur through plain ignorance: an important component of an ecosystem may be unrepresented in the literature, or lack of knowledge about functioning of an ecosystem (such as the timing and degree of movements of animals) may mean that a model represents reality very poorly.

Fuel economy and Price

At first glance, Ecopath can appear deceptively fuel hungry. It requires simple data inputs that may really have been rendered down from a vast amount of information - there can be lots of legwork needed, lots of searching for information that just may not be there. We estimated that the development of inputs for the Strait of Georgia model cost around 300 person hours. Balancing the model and reporting can probably be accomplished in something less. But is this really expensive?

Fuel quality is important to Ecopath: it will go further if good fuel is available. Expertise on trophic groups in the area being modeled substantially reduces the amount of legwork. It thus took a mere 200 person hours to assemble the information for the more complex Alaska Gyre model.

Market

Who might use Eopath? I see fisheries applications of the system as a means of testing understanding of, for example, the bounds on biomass or exploitation rates of a fished species, or generating hypotheses about the impact of fishing on different ecosystem components. But the application should be broader - wherever there is need to understand a system or guess at its behavior, Ecopath has potential application.

Conclusions

Yes, the Ecopath system is powerful - but drive carefully!

Suggested Improvements for Ecopath Modeling

(Carl Walters)

Moving to Dynamic Predictions Using Mass Action (Volterra) Assumptions[1]

Ecopath could be extended to either (1) estimate the rates of effective search a_{ij} from the flow and biomass estimates (a_{ij}=flow/[B_iB_j]), or (2) constrain and possibly improve the flow estimates given independent estimates of a_{ij}. Given the a_{ij} estimates, Ecopath could be used to make transient, non-equilibrium predictions for at least modest perturbations in the flow rate structure (all that is needed here is a simple differential equation solver).

For non-equilibrium modeling, trophic flows between the biomass pools representing consumers and their food have generally been modeled as the product of a functional response representing the consumption rate per consumer, times the consumer biomass.

$$\text{flow}_{ij}=f(B_i)B_j \qquad \text{where}$$

i = resource species, j = consumer

Usually we use a nonlinear, saturating functional response of the form

$$f(B)=aB_i/(1+aB_i/c_{max}) \quad \text{where}$$

c_{max} = maximum consumption per consumer.

But when we run such models, and when rates of effective search "a" (volume per time) are calculated from field data on

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[1] Since the workshop was held, a dynamic simulation model (Ecosim for Ecopath), including the ideas presented below, has been developed and described (Walters et al., in press).

search efficiencies, and when stomach contents of consumers are examined to see if consumption rates are near c_{max}, it is usually found that f(B) is small compared to c_{max}. That is, consumers in nature most often act as though f(B)=aB, with only modest effects from handling times/satiation. There is in fact an evolutionary argument due to Crowley (1975) that "optimal" consumption rate parameters in nature should generally reduce "a" enough to make consumption rates be well below c_{max} (working hard enough at feeding to approach c_{max} is often not a wise evolutionary strategy).

Thus data and evolutionary arguments support the use of simplified mass action (Volterra) models for the flows, of the form:

$$flow_{ij}=a_{ij}B_iB_j$$

For independent estimation of the a_{ij} it is useful to note that the units of these parameters are area or volume "swept" for prey per unit of time per unit of consumer biomass (units are area/time biomass in aerial units, volume/time for biomass in per volume units). Variation in a_{ij} among prey types i represents "preference" by consumer j created by either variation among prey in the consumer's willingness to take them when it encounters them, or variation among prey in habits/behaviors/morphological characteristics that affect vulnerability to the consumer.

The simplest possible estimate of a_{ij} is reaction field width (or area for volumetric prey biomass units) times the sum of average swimming speeds of the predator plus the prey, divided by the average weight of a predator individual. Generally the a's are much smaller than this estimate would indicate, due to relatively low probabilities of reacting to prey that enter the swept volume. For zooplankton, there are lots of a_{ij} estimates (called "filtering rates" in the literature). There are some estimates for planktivores, and a few for piscivores.

Labeling the probability distributions for output (derived) variables[2]

Ecopath computes values of some "output" flow/biomass variables needed to provide mass balance (equilibrium in flows and biomasses) given "input" values for other variables. The Ecoranger routine (Christensen and Pauly 1995) allows Ecopath users to specify probability distributions for the input variables, and uses a Monte Carlo procedure to sample from these input distributions so as to generate probability distributions of the output variables. Such Monte Carlo simulation procedures are perfectly acceptable (and indeed probably most efficient) as a method for numerical assessment of probability distributions that are complicated functions of probabilistic inputs. During the workshop, a question has arisen about whether the Ecoranger output distributions can properly be labeled "Bayes posterior" distributions.

Strictly speaking, the Bayes posterior distribution for a parameter is the conditional distribution for the parameter given the data, and thus, the first answer to this question is no. The Bayes posterior probability assigned to parameter value b given a data set Y is the ratio $p(b|Y) = p(Y|b)p_o(b)/p(Y)$, where p_o is a prior probability assigned to b and p(Y) is the total probability of obtaining Y (integrated

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[2] Since the workshop was held, Ecopath was modified to incorporate the semi-Bayesian approach described below.

over all possible values of the parameters, i.e. the integral of $p(Y|b)\ p_o(b)$ over all b values). If one thinks of the Ecopath inputs as Y and the Ecoranger probability specifications for Y as $p(Y|b)$, there is an apparent resemblance to the Bayes posterior distribution since the Ecoranger simulation procedure also maps $p(b|Y)$ from $p(Y|b)$. But the mapping is not as simple as Bayes formula above.

The Ecopath model structure provides a unique value of b for each input combination Y that is biologically (and thermodynamically) feasible, and also defines combinations Y that would imply biologically impossible b values. Thus, what Ecoranger does is to generate the probability distribution for a *transformation* or *function* (b) of the input variables Y. That is, it is finding the marginal distributions p(b) of functions b(Y), given the distributions p(Y) from which the functions b(Y) are calculated. This is a perfectly valid probabilistic calculation [the textbook case is: "find p(u) given p(y) and assuming $u = f(y)$"] whether or not a Bayesian interpretation is given to the p(b) by viewing the p(Y) as "priors". If the p(Y) are viewed as Bayes prior credibility measures, then strictly speaking the p(b) distributions generated by Ecoranger should be termed "derived Bayes Prior Distributions for output parameters b". In this phrase, "derived" means that p(b) is derived from p(Y) by using the fact that each Y value implies a unique b value, which has a non-zero probability only if it is biologically and thermodynamically feasible. [Among other things, all Ecopath "boxes" in an model must have parameter values within acceptable ranges, and their consumers cannot consume more than the boxes produce.]

This is a bit more than haggling over terminology. Suppose a prior distribution is provided for the b, $p_o(b)$, which is then compared to the "tighter" distribution p(b) that is produced by Monte Carlo routine in Ecoranger. Clearly, *information* about b has been gained. But this information came not from gathering "data" in the classical statistical sense, but rather from the structural relationship $b = f(Y)$, defined by the Ecopath model. Combining this structural information with prior probabilities p(Y) to generate p(b) is similar to combining data with priors to generate posteriors in Bayesian statistics. But there are those who would argue that combining structural knowledge with prior probabilities is not the same as combining data with priors.

To be safe, and to avoid silly arguments about Bayesian analysis and what data "really" are, Bayesian terminology should be avoided unless one is indeed predicting b values for which there are (1) particular observed values, and (2) likelihood functions for these observed values, derived by analysis of the sampling process leading to the observed values. At least some Ecopath assessments and their corresponding field estimates may be treated this way in the future. Here, it is necessary to be careful about the form and parameters of the distributions specified in Ecoranger for such b values, since these distributions have to be regarded as likelihood functions $p(b_{measured}|b_{true})$ rather than as specifications of prior belief about the true value.

Another development that would move Ecopath more directly into the traditional Bayesian approach would be the inclusion in Ecopath models of derived quantities not required for the mass balance solutions, but for which there are observed data or "likelihood" expectations. For example, Ecopath could be used to predict rates of effective search for predators j on prey types i, as a_{ij}=$flow_{ij}/B_iB_j$. If likelihood functions are specified for the observed input values of such derived quantities, then the product of such likelihood, for any specific Ecopath input parameter combination Y, is an additional measure of the credibility of that combination Y (beyond the p(Y) measures included using Ecoranger).

To include likelihood functions for some b and derived quantities in the Ecoranger calculations, the Monte Carlo sampling procedure must be modified slightly, so as to perform "Sampling/Importance Resampling" (SIR, see McAllister et al. 1994). This procedure is very simple and consists of the following steps: do the Monte Carlo simulations as at present, and for each of the k=1...n sampled parameter combinations $(Y,b)_k$, store the $(Y,b)_k$ value and the likelihood function value (product of probabilities of observed values b, a_{ij}, etc., *given* Y) L_k for the sampled combination. Then, instead of summarizing and plotting the results of these n sample trials, plot only the results from a subsample m of the trials, where the probability of each sample k being included in this subsample (resample) is just the sample "importance weight" w_k, i.e., simply L_k divided by the sum of the L_k values over all n samples. There are more elaborate procedures for obtaining the w_k weights, but these only apply when the Y input samples are chosen from distributions or criteria other than the Ecoranger priors for these Y.

Suppose a SIR algorithm is being set up wherein prior distributions p(b) have been specified for the Ecopath derived variables (computed from Y variables), and that the product of these p(b) values over b were treated as though it were the likelihood L_k. Then, when the (Y, b) subsample from the resampling process is examined, it will generally be found that the sample distributions p(Y) for the inputs is different than originally specified; that is, including p(b) information in the resampling process leads to the impression that one has gained some information about the inputs Y as well as the outputs b. This information arises not from data in the traditional Bayesian sense, but rather from applying the relations among Y and b implied by the Ecopath functional structure. So what is being done, technically, is finding the joint distribution for (Y, b) implied by the marginal priors p(Y) and p(b) under the relational constraints on (Y,b) implied by Ecopath structure. I do not know of a standard technical term to describe this joint distribution, but it could perhaps be called a "joint prior" or just the "joint distribution given Ecopath relations and constraints". When the sample frequency distributions for individual Y and b parameters selected by the resampling process are plotted, the resulting individual frequency patterns could be referred to as the "marginal distribution under Ecopath". However, each distribution should only be referred to as a "Bayes marginal posterior distribution" if the p(b) has been structured explicitly as a likelihood function $p(b_{observed} | b)$ for some particular observed values(s).

Incorporating Seasonality

Ecopath does not actually require equilibrium on seasonal time scales. Its balance relationship is on total *flows* over a defined time step. Biomasses (B) are assumed to be the same at the end as the start of this step, but may vary arbitrarily over the step. However, to correctly specify P/B and Q/B ratios, and consumption patterns, at least the relative pattern of B change in time (t) and these ratios must be defined by the user.

Consider production $P_i = (P/B)_i B_i$

The annual total can be calculated as a sum over t=1,…., n time steps within the year as

$P_i = \Sigma (P/B)_{it} \cdot B_{it}$

If we let P/B_{MAXi} be the maximum value of P/B_{it} over t, and B_{MAXi} be the maximum B_{MAXi} over t, then the above sum can be written as

$P_i = (P/B_{MAXi}) \cdot (B_{MAXi}) \cdot \Sigma (RP/B)_{it} \cdot (RB)_{it}$

or

$P_i = (P/B_{MAXi}) \cdot (B_{MAXi}) \cdot (GP/B)_i$

where $R \cdot P/B_{it} = (P/B_{it})/(P/B_{MAXi})$ and $(R \cdot B_{it}) = (B_{it})/(B_{MAXi})$ are relative P/B ratios and biomasses by season, respectively, and GP/B_i is the sum of products of the relative P/B ratios times relative biomass.

To use this approach, a way must exist for the user to specify seasonal patterns in the *relative* biomasses, $RB_{it} = (B_{it}/B_{MAXi})$, products $(RP/B_{it}) = (P/B_{it})/(P/B_{MAXi})$, consumptions $(Q/B_{it})/(Q/B_{MAXi})$, and in the diet composition matrix DC_{ijt}.

Operationally, this reduces to just four changes in Ecopath:

1. Warn the user to input seasonal maxima for known quantities, rather than averages;
2. Provide a graphical interface for the user to *shape* the B_{it}/B_{MAXit}, and other ratios listed above in, say, monthly steps;
3. On exit from this seasonal interface, set the model $G \cdot P/B_i$ weights by summing over the n seasonal values (with n = 12 for monthly values) of the ratios;
4. Feed the known B, P/B, etc. values into Ecopath as usual and rescale output calculations using the G functions as appropriate to provide both seasonal maxima and annual averages.

Exploring ecosystem responses to environmental variation[3]

(J.J. Polovina)

Considerable progress has been made in modelling links between ocean physics and plankton dynamics on seasonal, inter-annual, and decadal scales (Fasham 1995; Polovina et al. 1995; Sarmiento et al. 1993). However few studies have attempted to model impacts to higher trophic level. While physical parameters are not explicitly formulated in Ecopath and Ecosim, these ecosystem models can be used to explore ecosystem responses to physical variation.

Ecopath provides a tool to examine ecosystem structure and function in different climatic states. For example, it now appears that both the physical and biological regimes in the Gulf of Alaska gyre were different between 1960-76 and 1977-88. In particular,

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[3] This section was written in October 1996, and its references to "Ecosim" pertain to the software implementing the dynamic simulation approach suggested above by Walters (this vol.) and fully documented in Walters et al. (in press).

zooplankton and salmon abundance were substantially greater in the Gulf of Alaska in 1977-88 than in 1960-76. An Ecopath model constructed for each period could be used to evaluate whether the increase observed in salmon is simply a bottom-up response of the observed increase in zooplankton, or whether more complex trophic changes were involved.

Ecosim provides a tool to examine the dynamics response of ecosystems to environmental changes. One approach is to explicitly describe biological parameters currently in Ecosim as functions of physical variables and then drive Ecosim with physical time series. For example, since plankton dynamics can be describe by a system of differential equation driven by mixed layer depth, temperature, light, and nutrients, these equations could be incorporated directly into Ecosim to couple plankton dynamics with higher trophic dynamics. While this will result in an Ecosim model with physically driven plankton dynamics, modelling plankton dynamics with weekly temporal resolution as is done with these differential equations may not be particularly useful when we are interested in ecosystem dynamics on scales of years and decades. However, this same approach may prove more useful at higher trophic levels. For example, sardine survival or recruitment appears to be linked to wind speed following a dome-shaped relationship (Cury and Roy 1989). This relationship could be used to modify sardine survival or biomass in Ecosim and then Ecosim could be driven with a time series of wind speed to examine the response of an upwelling ecosystem to inter-annual changes in wind intensity.

In many cases the functional relationship between a physical and biological variables are not known or the physical time series are not available. Ecosim can still be a very useful tool to explore ecosystem responses. The approach in this case would be to drive the model directly with time series of Ecosim biological variables such as biomass, growth, mortality, etc., which represent the response to a physical change. For example, in the Northwestern Hawaiian Islands, the carrying capacity of all trophic levels appears to have dropped by about 50% over a 10 year period. One hypothesis is that this was a response to a 50% drop in primary productivity. To explore this hypothesis, Ecosim could be driven over a 10 year period with declining primary production to evaluate how the ecosystem responds to a 50% drop in primary production over 10 years. A second hypothesis is that this decline was due to increased larval advection. The ecosystem impact of this hypothesis could be evaluated by an Ecosim run simulating a 10 year period with increasing mortality (or decreasing recruitment) of all species groups in proportion to the time the spend as passive larvae.

Thus in summary just as Ecopath and Ecosim can be used to explore impacts of exploitation strategies, they can also be used, in very similar fashion, to explore impacts due to environmental variation. I am optimistic these tools will lead to new insights in ecosystem dynamics and at the very least help us to get beyond the often encountered dichotomy that all ecosystem change is either entirely due to environment variation or entirely the result of fishing.

Integration of local environmental knowledge[4]

(Nigel Haggan)

There has not so far been a great deal of crossover between Local Environmental Knowledge (LEK) and scientific knowledge. This is due not so much to a lack of respect for LEK, after all, a great many scientists rely on it during their research. The problem is more one of format. Science is precise but, partly as a result of its precision, its language is generally impenetrable at the community level. With notable exceptions such as Johannes (1981), scientists have found LEK to be too diffuse, uncertain and difficult to replicate. Also, with the exception of some countries in the South Pacific, few attempts have been made to integrate LEK into fisheries management systems.

How can Ecopath, a mathematical model living in computer circuits and feeding on quantitative data help? Would it have served to have fishing community and Aboriginal community members at the November Ecopath workshop? Probably not for the reasons of format outlined above. Yet, there are parallels between Ecopath and LEK, notably that they both are more concerned with relationships, interactions and connections within an ecosystem than with achieving a deep understanding of the isolated elements. In their own way, both Ecopath and LEK are intuitive. To be successful, fishers exploiting the resources of a given area must consider an entire constellation of factors along with the potential target species: their preys and other associated species, and the weather, current, tide, phase of the moon, to name but a few. They will also compare and balance their observations on this particular fishing day with related experience on other days in the same season. To this, they will add records and recollections of previous years and the information which has been handed down to them. Similarly, when Ecopath models are constructed by a group of experts (or based on published expert knowledge handed down through the scientific literature), a number of interrelated factors must also be accommodated simultaneously, and rendered mutually compatible.

This similarity may be deep enough for Ecopath models to provide a framework for integrating LEK, and thus strike a chord at the local community level. Indeed, this integration may lead to cross-validation as in Johannes (1981), where LEK and scientific knowledge about the target species of Palauan fishers where found to be mutually compatible, and where incompatibilities led to new insights, sometimes for the fishers, but often for the scientists as well. Two approaches are suggested to test this proposition.

The first approach is to incorporate as much LEK as possible into the existing databases used as data sources by Ecopath model builders, notably FishBase (Froese and Pauly 1996). This relational database, now available in form of a CD-ROM (see McCall and May 1995), covers the fishes of the Northeastern Pacific rather well, and its 1997 release will include detailed information on the fishes of British Columbia. This database can accommodate local knowledge that is species-specific (e.g. that in Compton et al. (1994), pertaining to the role of *Catastomus macrocheilus* in the

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[4] I am grateful to Rosemary Ommer for this term, which includes both indigenous knowledge and the knowledge of contemporary fishing communities.

Secwépemc/Shuswap culture), through a series of interrelated tables (Pauly et al 1993a, Palomares et al. 1993), thus enabling comparisons between LEK and scientific knowledge, and cross validation. Field and literature-based projects devoted to accumulating and encoding such knowledge, e.g., in the context of Cury's (1994) theory of site fidelity in spawning fishes, would seem particularly worthwhile, given that FishBase, once it incorporate this knowledge, could be used to disseminate it in schools, community centers, etc.

The second approach would consist of a workshop that would be convened to present an Ecopath model of a coastal area to a group of knowledgeable fishers from First Nations and the community-at-large. This workshop would begin the process of correlating local knowledge and intuitions with the relationships, data gaps and conflicts identified through the model. Without wanting to prejudge the results of such an exercise, there is little doubt that such cross validation would lead to new insights and directions for future collaboration to address, and perhaps resolve some data gaps and conflicts.

Updates on Ecopath development and applications

(Daniel Pauly and Villy Christensen)

The workshop reported upon in this report did not only generate three models of ecosystems important to the fisheries of

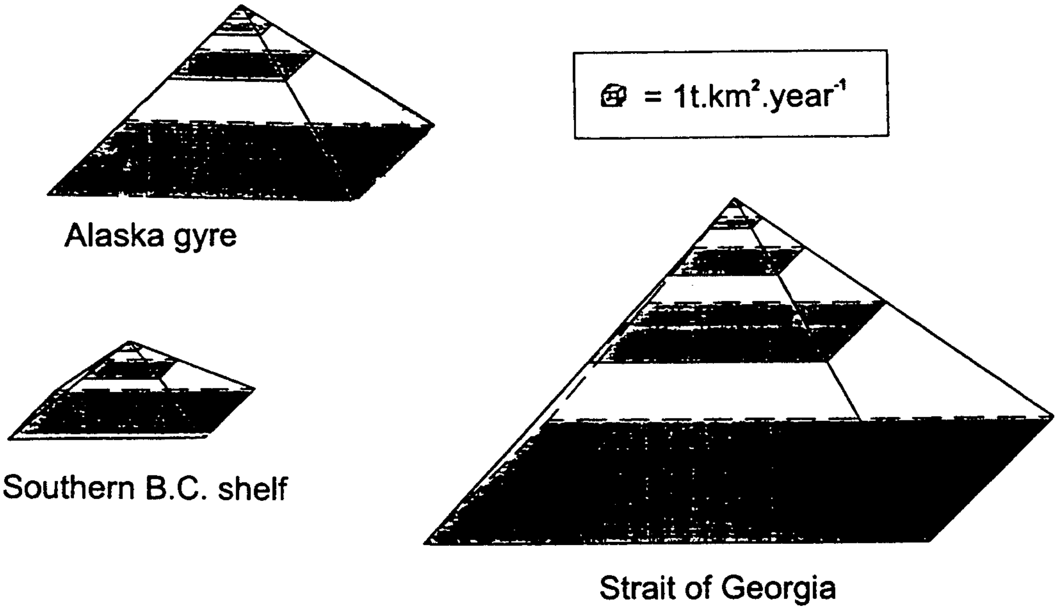

Figure 6 Trophic pyramids representing the three ecosystem models documented here. The pyramids are scaled such that the volume at each (trophic) level corresponds to the sum of all flows at that level, while the topangle is inversely related to the transfer efficiency prevailing in the system (acute angle = high efficiency). These pyramids allow direct comparisons of whole ecosystem properties.

British Columbia (see Figure 6) — though this, by itself would have been enough to meet our stated goals. Rather, the workshop became a watershed in the development of the Ecopath approach and software—and probably for the discipline of ecosystem modeling as a whole—thanks to the input of Carl Walters (see above), who contributed to:

1. re-expression of the Monte-Carlo routine built into the β-release of Ecopath 3.0 (Christensen and Pauly 1995) in form of a semi-Bayesian approach for considering uncertainties;
2. explicit incorporation of seasonal cycles of biomass and related parameters when mass-balancing a model; and
3. reexpression of the system of linear equations behind Ecopath (see Box 1) into a system of differential equations that can be integrated over time, and hence generate fully operational simulation models from Ecopath files.

Ecopath 3.0 as now distributed (free of charge, see Christensen and Pauly 1996) incorporates item (1), [in the semi-Bayesian context proposed by Walters (this vol.), i.e., the SIR approach of McAllister et al. (1994)], and hence can be used to generate, besides distributions of the *output* values, posterior distributions of the *input* values, given (uniform, triangular, or normal) distributions of the inputs.

This we hope will go a long way towards overcoming the doubts of those who feel that mass-balance models - or ecosystem models in general - do not sufficiently take account of uncertainties. However, the model in this report has been constructed before the SIR approach was incorporated into Ecopath, and hence the power of this approach will have to be demonstrated elsewhere (e.g. with the next iterations of these models).

We have developed a hybrid design for the incorporation of item (2) in Ecopath, i.e. for explicit consideration of seasonality, which we envision as driven by seasonally-varying empirical observations of biomass, catches, and diet compositions, and using a monthly cycle of temperature to force changes in P/B and Q/B, both known to be temperature-dependent (Pauly 1980, 1989).

This design is to be implemented later in 1997, and hence Ecopath users wanting to explicitly account for seasonality will continue, for a short while, to have to construct one model per month or season of a seasonal cycle, as in Jarre and Pauly (1993), and in Jarre-Teichmann (1995, respectively. The three models presented above all represent "summer" situations and colleagues interested in the ecosystems these models represent should complement these with "winter" models, for which we present much of what is required in terms of biomasses or population sizes, catches, diet compositions, etc.

Then, later the summer and winter models can provide the input for "annual" models, explicitly taking seasonal changes of biomass and fluxes when establishing mass balance.

Item (3), the use of Ecopath assessments to parametrize the system of differential equations required for simulation models has been fully conceptualized (Walters et al. in press). Also, a software module (Ecosim) has been developed whose stand-alone version (which reads unmodified Ecopath files) is presently being tested at the Fisheries Centre, while also being modified such that it can incorporated as a routine of the next (4.0) release of Ecopath (Christensen and Pauly, in press).

Ecopath has been used so far to describe nearly hundred aquatic ecosystems as well as numerous farms (see, e.g., Dalsgaard et al. 1995), a recent, and unexpected development.

However, these earlier application - successful as they were in integrating a vast amount of data, and describing the functioning of these ecosystems, remained - for some colleagues at least - under the dark clouds of assumptions of determinism (there were no procedure to explicitly account for uncertainties) and equilibrium (change was hard to express, for lack of an explicit temporal dimension). These dark clouds have now been blown away, and we anticipate a bright future for mass-balance modelling.

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Appendix 1

Table A Biological and population statistics of marine mammals, Alaska Gyre (Summer).

Species	Mean weight (kg)		Population	Sex ratio	Area	Ration	(kg/day)	Q/B
	(males)	(females)		(females)	($10^3 km^2$)	(males)	(females)	(per year)
Northern fur seals	30	25	130000	0.8	70	1.5	1.3	20.7
Steller sea lions	210	186	0	0.6	70	7.2	6.5	0.0
N. elephant seals	412	330	4000	0	70	12.4	10.4	9.2
PINNIPEDS								**16.9**
Killer whale (resid.)	2587	1973	238	0.64	70	84.6	84.1	14.0
Dall's porpoise	63	61	21200	0.5	4420	2.8	2.7	16.0
Sperm whales	27400	26938	2000	0	612	822	351	4.7
TOOTHED WHALES								**5.4**
Baird's beaked whales	3134	3833	10000	0.4	10600	62.6	73.6	7.4
Stejneger's b. whale	497	511	1000	0.5	5300	14.4	14.7	10.5
Cuvier's b. whale	961	893	1000	0.5	10000	24.3	22.9	9.3
BEAKED WHALES								**7.5**
Blue whale	95347	110126	1700	0.5	5300	3814	4405	14.6
Fin whale	51361	59819	17000	0.5	5300	2055	2393	14.6
Sei whale	16235	17387	14000	0.5	5300	649	696	14.6
BALEEN WHALES								**14.6**
KILLER W. (trans.)	2587	1974	44	0.64	70	73.0	73.0	**12.1**

Table B Biological and population statistics of marine mammals, Alaska Gyre (Winter).

Species	Mean weight (kg)		Population	Sex ratio	Area	Ration	(kg/day)	Q/B
	(males)	(females)		(females)	($10^3 km^2$)	(males)	(females)	(per year)
Northern fur seals	30	25	5000	0.8	70	1.5	1.3	20.7
Steller sea lions	210	186	5000	0.6	70	7.2	6.5	13.0
N. elephant seals	412	330	4000	0	70	12.4	10.4	9.2
PINNIPEDS								**11.1**
Killer whale (resid.)	2587	1973	238	0.64	70	84.6	84.1	14.0
Dall's porpoise	63	61	21200	0.5	4420	2.8	2.7	16.0
Sperm whales	10098	26938	0	0	612	160	351	0.0
TOOTHED WHALES								**14.1**
Baird's beaked whales	3134	3833	0	0.4	10600	62.6	73.6	`0.0
Stejneger's b. whale	497	511	1000	0.5	5300	14.4	14.7	10.5
Cuvier's b. whale	961	893	1000	0.5	10000	24.3	22.9	9.3
BEAKED WHALES								**9.9**
Blue whale	95347	110126	1700	0.5	5300	963	1080	3.6
Fin whale	51361	59819	17000	0.5	5300	587	663	4.1
Sei whale	16235	17387	14000	0.5233	5300	234	247	5.2
BALEEN WHALES								**4.2**
KILLER W. (trans.)	2587	1974	44	0.64	70	73.0	73.0	**12.1**

Table C Diet composition of marine mammals in the Alaska gyre (Summer).

	diet compositions								
Species	benthic org.	euphaus.	Cope-pods	small squids	large squids	small pel.	meso pel.	salmon	large pel.
northern fur seals	0.00	0.00	0.00	0.78	0.00	0.00	0.00	0.11	0.11
Steller sea lions	0.00	0.00	0.00	0.30	0.20	0.10	0.00	0.00	0.40
N elephant seals	0.00	0.00	0.00	0.40	0.20	0.00	0.25	0.00	0.15
pinnipeds	**0.000**	**0.000**	**0.000**	**0.713**	**0.035**	**0.000**	**0.044**	**0.091**	**0.117**
Killer whale (resid.)	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.80	0.10
Dall's porpoise	0.00	0.00	0.00	0.20	0.00	0.10	0.70	0.00	0.00
Sperm Whales	0.00	0.00	0.00	0.05	0.80	0.00	0.00	0.00	0.15
toothed whales	**0.000**	**0.000**	**0.000**	**0.041**	**0.634**	**0.021**	**0.006**	**0.159**	**0.139**
Baird's beaked whale	0.00	0.00	0.00	0.30	0.35	0.10	0.00	0.00	0.25
Stejneger's beaked w	0.00	0.00	0.00	0.50	0.45	0.00	0.00	0.00	0.05
Cuvier's beaked w	0.00	0.00	0.00	0.35	0.35	0.00	0.15	0.00	0.15
beaked whales	**0.000**	**0.000**	**0.000**	**0.309**	**0.354**	**0.093**	**0.005**	**0.000**	**0.239**
blue whale	0.00	0.95	0.05	0.00	0.00	0.00	0.00	0.00	0.00
fin whale	0.00	0.75	0.20	0.00	0.00	0.05	0.00	0.00	0.00
sei whale	0.00	0.10	0.80	0.05	0.00	0.05	0.00	0.00	0.00
baleen whales	**0.000**	**0.663**	**0.285**	**0.009**	**0.000**	**0.044**	**0.000**	**0.000**	**0.000**

Table D Diet composition of marine mammals in the Alaska gyre (Winter).

	diet compositions								
Species	benthic org.	euphaus.	Cope-pods	small squids	large squids	small pel.	meso pel.	salmon	large pel.
northern fur seals	0.00	0.00	0.00	0.15	0.15	0.25	0.15	0.00	0.30
Steller sea lions	0.00	0.00	0.00	0.15	0.00	0.20	0.00	0.00	0.65
N elephant seals	0.00	0.00	0.00	0.40	0.20	0.00	0.25	0.00	0.15
pinnipeds	**0.000**	**0.000**	**0.000**	**0.274**	**0.112**	**0.105**	**0.137**	**0.000**	**0.371**
Killer whale (resid.)	0.00	0.00	0.00	0.00	0.00	0.20	0.00	0.60	0.20
Dall's porpoise	0.00	0.00	0.00	0.20	0.00	0.10	0.70	0.00	0.00
Sperm Whales	0.00	0.00	0.00	0.15	0.60	0.05	0.05	0.00	0.15
toothed whales	**0.000**	**0.000**	**0.000**	**0.009**	**0.000**	**0.196**	**0.030**	**0.574**	**0.191**
Baird's beaked whale	0.00	0.00	0.00	0.35	0.30	0.10	0.10	0.00	0.15
Stejneger's beaked w	0.00	0.00	0.00	0.50	0.45	0.00	0.00	0.00	0.05
Cuvier's beaked w	0.00	0.00	0.00	0.35	0.35	0.00	0.15	0.00	0.15
beaked whales	**0.000**	**0.000**	**0.000**	**0.431**	**0.404**	**0.000**	**0.069**	**0.000**	**0.096**
blue whale	0.00	0.90	0.10	0.00	0.00	0.00	0.00	0.00	0.00
fin whale	0.00	0.60	0.20	0.05	0.00	0.05	0.05	0.00	0.05
sei whale	0.00	0.10	0.70	0.05	0.00	0.05	0.05	0.00	0.05
baleen whales	**0.000**	**0.526**	**0.296**	**0.044**	**0.000**	**0.044**	**0.044**	**0.000**	**0.044**

Table E Diet matrix used for Alaska gyre model.

Prey	Predator																			
	3	4	5	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1 Phytoplankton	.75	.915	.53	.85	-	.30	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2 Bacteria	.25		-	-	-	.10	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3 Microzoopl.	-		.40	-	-	.10	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4 Sm. herb.	-	-	-	.05	.63	-	-	.03	-	-	.6	.75	-	.05	-	-	.285	-	-	-
5 Salps	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6 Carn. zoopl.	-	-	-	-	-	-	-	-	-	-	-	.10	-	.05	-	-	-	-	-	-
7 Jellies	-	-	-	-	-	-	-	-	.98	-	-	-	-	-	-	-	-	-	-	-
8 Krill	-	-	-	-	.20	-	-	-	-	-	.1	.10	-	-	-	-	.662	-	-	.06
9 Squids	-	-	-	-	.05	-	.75	.75	.02	.95	-	-	-	.75	.748	.678	.009	.663	-	.45
10 Crustaceans	-	-	-	-	.05	-	.15	.20	-	.04	.3	-	-	.03	-	-	-	-	-	.01
11 Pink	-	-	-	-	-	-	-	-	-	-	-	-	.050	-	.021	.040	-	-	-	-
12 Sockeye	-	-	-	-	-	-	-	-	-	-	-	-	.050	-	.025	.030	-	-	-	-
13 Chum	-	-	-	-	-	-	-	-	-	-	-	-	.050	-	.020	.040	-	-	-	-
14 Steelhead	-	-	-	-	-	-	-	-	-	-	-	-	.050	-	.025	.046	-	-	-	-
15 Mesopelagics	-	-	-	-	.02	-	-	-	-	-	-	.05	.200	.08	.044	.006	-	.005	-	-
16 Sm. pelagics	-	-	-	-	.05	-	.10	.02	-	.01	-	-	.394	.04	-	.021	.044	.093	-	.48
17 Sharks	-	-	-	-	-	-	-	-	-	-	-	-	.001	-	-	-	-	-	-	-
18 Large fish	-	-	-	-	-	-	-	-	-	-	-	-	.200	-	.117	.139	-	.239	-	-
19 Pinnipeds	-	-	-	-	-	-	-	-	-	-	-	-	.005	-	-	-	-	-	.025	-
20 Tth. whales	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	.125	-
21 Bal. whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	.100	-
22 Beak. whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
23 Orca	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
24 Mar. birds	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
25 Detritus	-	.085	.07	.10	-	.50	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Import	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	.750	-

Table F Population statistics of marine mammals, southern shelf of B.C. (Summer).

Species	**Mean body weight (kg)**		**Popu-lation**	**Sex ratio**	**Consumption (kg·day^{-1})**		**Q/B (year^{-1})**
	males	females		females	male	female	annual
Northern fur seals	30	25	61000	0.8	1.5	1.3	20.7
Steller sea lions	210	186	9400	0.6	7.2	6.5	13.0
N. elephant seals	412	3308	2000	0	12.4	10.4	9.2
California sea lions	86	585	0	0	3.5	2.6	0.0
Harbour seals	64	56	20000	0.5	2.8	2.5	16.1
Pinnipeds							**15.3**
White-sided dolphin	85	73	2000	0.5	3.5	3.1	15.2
Killer whale (resid)	2587	1974	200	0.64	85	84	14.0
Dall's porpoise	63	619	1000	0.5	2.8	2.7	16.0
Harbour porpoise	29	33	1000	0.5	1.5	1.6	18.4
N. right whale dolphin	142	682	100	0.5	5.3	2.9	14.2
Toothed whales							**15.6**
Humpback whale	28323	32493	100	0.5	365	407	4.6
Gray whale	15920	16435	1167	0.5	637	657	14.6
Minke	6121	7011	100	0.5	107	119	6.3
Baleen whales							**13.0**
Killer whales (trans)	2587	1974	34	0.64	73	73	**12.1**

Table G Population statistics of marine mammals, southern shelf of B.C. (Winter).

Species	**Mean body weight. (kg)**		**Popu-lation**	**Sex ratio**	**Consumption (kg·day^{-1})**		**Q/B (year^{-1})**
	males	females		females	male	female	annual
Northern fur seals	30	25	51000	0.8	1.5	1.3	20.7
Steller sea lions	210	186	9400	0.6	7.2	6.5	13.0
N. elephant seals	412	3308	2000	0	12.4	10.4	9.2
California sea lions	86	585	3500	0	3.5	2.6	11.0
Harbour seals	64	56	20000	0.5	2.8	2.5	16.1
Pinnipeds							**14.8**
White-sided dolphin	85	73	2000	0.5	3.5	3.1	15.2
Killer whale (resid)	2587	1974	290	0.64	85	84	14.0
Dall's porpoise	63	619	1000	0.5	2.8	2.7	16.0
Harbour porpoise	29	33	1000	0.5	1.5	1.6	18.4
N. right whale dolphin	142	682	100	0.5	5.3	2.9	14.2
Toothed whales							**15.3**
Humpback whale	28323	32493	100	0.5	365	407	4.6
Gray whale	15920	16435	585	0.5	637	657	5.3
Minke	6121	7011	300	0.5	107	119	6.3
Baleen whales							**5.1**
Killer whales (trans)	2587	1974	85	0.64	73	73	**12.1**

Table H Diet composition of marine mammals, southern shelf of B.C. (Summer).

Species	octopus	krill	cope-pods	bival-ves	poly-chaetes	amphi-pods	small squids	large squids	sand-lance	smelts
Northern fur seals	-	-	-	-	-	-	.14	-	.03	.01
Steller sea lions	.02	-	-	-	-	-	.01	-	.08	.01
N. elephant seals	-	-	-	-	-	-	.40	-	-	-
Cal. sea lions	.01	-	-	-	-	-	.02	-	.05	.02
Harbour seals	-	-	-	-	-	-	.02	-	.02	.02
Pinnipeds	.007	-	-	-	-	-	.109	-	.040	.011
W.-sided dolphin	-	-	-	-	-	-	.10	-	.30	-
Killer whale (resid)	-	-	-	-	-	-	-	-	-	-
Dall's porpoise	-	-	-	-	-	-	.20	-	.30	-
Harbour porpoise	-	-	-	-	-	-	.20	-	.40	-
N. right whale dolph.	-	-	-	-	-	-	.10	-	.40	-
Toothed whales	-	-	-	-	-	-	.055	-	.127	-
Humpback whale	-	.80	.10	-	-	-	-	-	-	-
Gray whale	-	-	-	.05	.05	.90	-	-	-	-
Minke	-	.30	.30	-	-	-	-	-	.20	-
Baleen whales	-	.043	.009	.047	.047	.844	-	-	-3	-

Table H (cont.)

Species	herring	other clup.	hake	rock-fish	sable fish	cod	coho, chinook	pink, chum sockeye	pollock	var. pelagics	sharks
Northern fur seals	.52	.02	.03	.07	.04	-	.06	.06	.02	-	-
Steller sea lions	.16	-	.01	.11	-	.12	.09	.09	.26	.05	-
N. elephant seals	-	-	.10	.10	.10	-	-	-	.10	-	.20
Cal. sea lions	.16	-	.33	.06	-	.06	.05	.05	.17	.04	-
Harbour seals	.15	-	.65	-	-	-	.02	.02	.08	.03	-
Pinnipeds	.239	.006	.170	.073	.027	.040	.049	.049	.126	.023	.030
W.-sided dolphin	.40	-	-	.10	-	-	-	.10	-	-	-
Killer whale (resid)	.05	-	-	-	-	-	.65	.15	-	-	.15
Dall's porpoise	.40	-	-	-	-	-	-	-	.10	-	-
Harbour porpoise	.40	-	-	-	-	-	-	-	-	-	-
N. right whale dolp.	.50	-	-	-	-	-	-	-	-	-	-
Toothed whales	.192	-	-	.023	-	-	.389	.113	.010	-	.090
Humpback whale	.10	-	-	-	-	-	-	-	-	-	-
Gray whale	-	-	-	-	-	-	-	-	-	-	-
Minke	.20	-	-	-	-	-	-	-	-	-	-
Baleen whales	.008	-	-	-	-	-	-	-	-	-	-0

Table I Diet composition of marine mammals, southern shelf of B.C. (Winter).

Species	octopus	krill	cope-pods	bivalves	poly-chaetes	amphi-pods	small squids	large squids	sand-lance	smelts
Northern fur seals	-	-	-	-	-	-	.14	-	.03	.01
Steller sea lions	.04	-	-	-	-	-	.02	-	.04	.02
N. elephant seals	-	-	-	-	-	-	.40	-	-	-
Cal. sea lions	.02	-	-	-	-	-	.02	-	.02	.02
Harbour seals	-	-	-	-	-	-	.02	-	-	.01
Pinnipeds	014	-	-	-	-	-	.106	-	.022	.012
W.-sided dolphin	-	-	-	-	-	-	.10	-	.30	-
Killer whale (resid)	-	-	-	-	-	-	-	-	-	-
Dall's porpoise	-	-	-	-	-	-	.20	-	.30	-
Harbour porpoise	-	-	-	-	-	-	.20	-	.40	-
N. right whale dolph.	-	-	-	-	-	-	.10	-	.40	-
Toothed whales	-	-	-	-	-	-	.044	-	.100	-
Humpback whale	-	.80	.10	-	-	-	-	-	-	-
Gray whale	-	-	-	.05	.05	.90	-	-	-	-
Minke	-	.30	.30	-	-	-	-	-	.20	-
Baleen whales	-	.316	.074	.026	.026	.471	-	-	.026	-

Table I (cont.)

Species	herring	other. clup.	hake	rock-fish	sable fish	cod	coho, chinook	pink, chum sockey	pollock	var. pelagics	sharks
Northern fur seals	.52	.02	.03	.07	.04	-	.06	.06	.02	-	-
Steller sea lions	.13	-	-	.05	-	.22	.06	.06	.35	.02	-
N. elephant seals	-	-	.10	.10	.10	-	-	-	.10	-	.20
Cal. sea lions	.37	-	.10	.03	-	.11	.04	.04	.22	.04	-
Harbour seals	.60	-	.20	-	-	-	.02	.02	.09	.05	-
Pinnipeds	.321	.005	.071	0050	.025	.080	.038	.0038	.168	.020	.030
W.-sided dolphin	.40	-	-	.10	-	-	-	.10	-	-	-
Killer whale (resid)	.03	-	-	-	-	-	.76	.10	-	-	.10
Dall's porpoise	.40	-	-	-	-	-	-	-	.10	-	-
Harbour porpoise	.40	-	-	-	-	-	-	-	-	-	-
N. right whale dolph.	.50	-	-	-	-	-	-	-	-	-	-
Toothed whales	.151	-	-	.018	-0	-	.520	.089	.008	-	.070
Humpback whale	.10	-	-	-		-	-	-	-	-	-
Gray whale	-	-	-	-	-	-	-	-	-	-	-
Minke	.20	-	-	-	-	-	-	-	-	-	-
Baleen whales	.061	-	-	-	-	-	-	-	-	-	-

Table J Diet matrix used for the southern B.C. shelf model.[a)]

Prey	Predator																								
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
1 Transient orcas	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
2 Odontocetae	.20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3 Pinnipeds	.75	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4 Mysticetae	.05	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5 Seabirds	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6 Spiny dogfish	-	.602	.278	-	.016	.05	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
7 Pacific halibut	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8 Pacific hake	-	-	.170	-	-	.02	-	.010	.050	.16	.05	-	-	-	-	-	-	-	-	-	-	-	-	-	-
9 Pacific cod	-	.023	.113	-	-	.06	.18	.005	.090	-	.05	-	-	-	-	-	-	-	-	-	-	-	-	-	-
10 Juv. sablefish	-	-	.027	-	-	-	-	-	.010	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11 Adult sablefish	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12 Herring/sm. pel.	-	.320	.296	.012	.424	.40	.70	.050	.250	.41	.40	-	-	-	-	-	-	-	-	-	-	-	-	-	-
13 Carn. jellies	-	-	-	-	.005	.05	-	-	-	.04	.03	-	.050	-	-	-	-	-	-	-	-	-	-	-	-
14 Decapods	-	-	-	-	.040	.08	.10	.014	.050	.05	.02	-	-	.03	-	-	-	-	-	-	-	-	-	-	-
15 Shrimps	-	.055	.116	-	.102	.05	.02	-	.050	.04	.39	-	-	.10	-	-	-	-	-	-	-	-	-	-	-
16 Polychaetes	-	-	-	.045	-	-	-	-	.099	-	-	-	.050	-	.3	-	.29	-	-	-	-	-	-	-	-
17 Sea stars	-	-	-	-	.001	-	-	-	-	-	-	-	-	-	-	-	.05	-	-	-	-	-	-	-	-
18 Sea urchins	-	-	-	-	-	-	-	-	.050	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
19 Brittle stars	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
20 Bivalves	-	-	-	.047	-	-	-	-	-	-	-	-	-	.10	-	-	.05	-	-	-	-	-	-	-	-
21 Amphipods	-	-	-	.844	-	-	-	-	.100	.05	.02	-	-	.02	-	-	-	-	-	-	-	-	-	-	-
22 Euphausiids	-	-	-	.043	.172	.20	-	.355	.100	.25	.02	.01	-	-	-	-	-	-	-	-	-	-	-	-	-
23 Chaetognaths	-	-	-	-	.079	.03	-	-	-	-	-	.01	.080	-	-	-	-	-	.05	-	-	-	-	-	-
24 Salps	-	-	-	-	-	.06	-	-	-	-	.02	-	.050	-	-	-	-	-	-	-		1	1	-	-
25 Copepods	-	-	-	.009	.161	-	-	-	.100	-	-	.98	.670	-	-	-	-	-	.05	-	-	-	-	-	-
26 Phytoplankton	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	.9	.9
27 Detritus	-	-	-	-	-	-	-		.050	-	-	-	.099	.84	.7	1	.61	1	.90	1	1	-	-	.1	.1
Import	-	-	-	-	-	-	-	.565	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

a) due to rounding errors, the diet composition of a few groups add up to 0.999, and not to 1.000; this does not affect computations

Table K Means seasonal landing of the fisheries, southern B.C. shelf (in t·km^{-2} per 6 month season; based on DFO data for the years 1985- 1995).

FUNCTIONAL GROUP:	Species	Summer	Winter
BIVALVES:	Butter clam	0.03	2.42
	Geoduck	969.4	682.54
	Horse clam	44.04	3.08
	Manila clam	58.51	374.08
	Mixed clam	1.68	15.60
	Mussel	0	0.10
	Native littleneck clam	3.43	12.33
	Scallop	0.36	0.21
MISC. BENTHOS:	Abalone	0.48	1.00
	Gooseneck barnacle	19.4	8.31
ECHINODERMS:	Sea cucumber	72.82	139.85
	Red sea urchin	57.58	356.64
	Green sea urchin	0	9.90
	Purple sea urchin	0	0.18
OCTOPUS:	Octopus	9.64	7.08
SQUIDS:	Squid	72.38	2.87
ZOOPLANKTON:	Euphausiids	0	0.44
CODS/BLACK CODS:	Lingcod	2278.29	553.76
	Pacific cod (grey cod)	1364.01	1096.46
	Sablefish (black cod)	1557.17	481.10
SHRIMPS/CRABS:	Dungeness crab	202.81	101.53
	Red rock crab	1.98	0
	King crab	0	0.15
	Prawn	57.76	24.46
	Crayfish	0.02	0
	Shrimp	1517.76	375.32
LARGE PELAGICS:	Hake	19500	2125.79
	Tuna	50.26	30.53
SMALL PELAGICS:	Herrings	0.16	0.10
	Anchovy	23.76	4.24
	Mackerel	5.12	0.30
MISC. DEMERSALS:	Halibut:	626.25	77.22
	Brill sole	204.77	246.27
	Butter sole	0.04	0.02
	Dover sole	442.74	542.39
	Lemon sole	95.18	28.46
	Mixed sole	37.21	21.21
	Rex sole	6.64	5.56
	Rock sole	244.18	59.52
	Flounder	5.66	30.57
	Turbot	829.95	140.11
	Skate	31.72	13.74
	Hagfish	66.53	64.33
	Pollock	69.27	76.54
	Sturgeon	0.45	0.31
	Greenlings, etc.	0.08	0.01
ROCKFISHES:	Perch (silver)	0.38	0.47
	Pacific ocean perch	857.7	627.62
	Greenies (tellow tail)	842.26	1734.45
	Idiot rockfish	33.46	37.81
	Red snapper (yellow eye)	314.49	135.72
	Reedi (yellow mouth)	393.25	401.25
	Rockfish	3218.23	3079.39
SHARKS:	Dogfish:	1071.3	1025.01
	Other sharks	0.72	1.19
TRANSIENT SALM.:	Steelhead	3.45	0.29
	Chum	458.41	3773.90
	Pink	1814.98	14.91
	Sockeye	4013.71	1.79
RESIDENT SALM.:	Chinook	2431.58	20.20
	Coho	4389.53	44.13
OTHER:	Non-food catch	83.57	71.34
	Other fish	1.07	0.11
	Roe on kelp	34.43	0.63
	Roe herring	0	6056.37
	Salmon roe	0.86	0.47

Table L Standing stock of macrobenthos (t·km^{-2}) of Strait of Georgia, by depth range.

Depth range (m): Surface (km; total: 8635)	>400 330	300-400 1000	200-300 1570	100-200 2130	50-100 1560	20-50 800	<200 622.5	Intertidal 622.5
Annelids								7.3
Polychaets	11.3	15	29	9.0	222	58	144	
Amphipods	0.2			0.50	0.80	0.60	0.20	14
Copepods	1.0		0.30					
Cumaceans					0.20			
Cirripeds								306
Isopods		7.3			1.2	0.20		27
Pelecypod (bivalves)	7.0	0.30	310	118	347	177	21	942
Scaphopods	0.85	2.7	0.50		0.40			
Gastropods	1.4	0.70	1.4	1.8	2.7	3.8	3.2	76
Amphineura	0.2		2.0	0.65	0.37		0.7	186
Arthropods					17	0.20		
Ophiurids	0.70	0.85	1.2	11	12	1.4	0.10	
Echinoids	29	25	271		116		0.20	
Holothurian	36	48	156	63	56	1.5	3.2	
Nemertines	1.7				4.3	1.7	5.0	
Sipunculoids	0.30				0.5	2.0	0.60	
Echiuroidea			65		0.7			
Porifers (sponges)	0.20	4.0	8.3	0.50		1162		
Cnidaria (anthozoa)		2.3	5.4	0.30	0.64	16		58
Unidentified benthos			4.3	1.5	0.60			
Asteroida			0.30			0.20		23
Decapods				1.5	12	1.1	13	124
All macrobenthos	104	99	430	136	650	446	177	916

Table M Diet Composition of Marine Mammals in the Strait of Georgia.

Mammal species	DC, per area (%) Estuaries / non-estuaries	DC, whole Strait (%)	Food cons. (t·year^{-1})
Killer whales (resident)			
Small squid	- / -	5.0	72.4
Large squid	- / -	5.0	72.4
Small pelagics	- / -	10.0	144.7
Miscellaneous fishes	- / -	40.0	578.9
Higher invertebrates	- / -	40.0	578.9
Killer whales (transient)			
Harbour seal	- / -	56.6	134.4
Porpoise	- / -	21.5	51.1
Whale	- / -	21.5	51.1
Bird	- / -	0.3	0.7
Squid	- / -	0.04	0.1
Dall's porpoises			
Benthic invertebrates	- / -	5.0	55.9
Small squid	- / -	30.0	335.6
Large squid	- / -	10.0	111.9
Small pelagics	- / -	20.0	223.7
Mesopelagics	- / -	20.0	223.7
Miscellaneous fishes	- / -	15.0	167.8
Harbour porpoises			
Benthic invertebrates	- / -	5.0	14.3
Small squid	- / -	10.0	28.5
Large squid	- / -	10.0	28.5
Small pelagics	- / -	30.0	85.63
Miscellaneous fishes	- / -	45.0	128.3
Harbour seals (1988 data)			
Salmonids	9 / 4	4.5	448.8
Gadoids	50 / 65	63.5	6,303.6
Pacific herring	19 / 12	12.7	1,264.1
Sculpins	5 / 1	1.4	140.4
Flatfishes	5 / 1	0.5	51.4
Surfperches	4 / 3	3.1	308.3
Hexagrammids	0 / 1	0.9	89.1
Plainfin midshipman	3 / 2	2.1	209.0
Sandlance	0 / 2	1.8	178.2
Cephalopods	1 / 2	1.9	188.4
Other	3 / 5	4.8	476.2
Unidentified	1 / 3	2.8	277.5

Table N Diet Composition of Marine Birds in the Strait of Georgia.

Bird species	DC %	Food cons. (t·year^{-1})
Glaucous-winged gull		
Refuse	65.0	1852.3
Bivalves	20.0	570.0
Pacific herrings	15.0	427.5
Double-crested cormorant		
penpoint gunnel	36.0	250.8
shiner perch	21.0	146.3
crested gunnel	16.0	111.5
snake prickleback	10.0	69.7
others	17.0	118.4
Pelagic cormorant		
crescent gunnel	37.0	282.8
Pacific sandlance	19.0	145.2
Pacific staghorn sculpin	13.0	99.4
penpoint gunnel	11.0	84.1
others	20.0	152.9
Brandt's cormorants		
herring	26.0	88.5
giant marbled sculpin	26.3	89.4
lithodid crab	8.8	29.9
shrimp	39.0	133.0
Loons (Arctic & others)		
herring	100.0	471.7
Grebes (West. & other)		
herring	70.0	1398.8
shiner perch	20.0	399.7
algae	4.0	79.9
eelgrass	4.0	79.9
snail	2.0	40.0
Surf scoters		
blue mussels	85.0	961.2
snail	5.0	56.5
errant polychaetes	5.0	56.5
barnacles	5.0	56.6

Bird Species	DC %	Food cons. (t·year^{-1})
White-winged scoters		
clams	80.0	135.8
snail	8.0	13.6
errant polychaetes	4.0	6.8
barnacles	8.0	13.6
Other diving ducks (=oldsquaw)		
bivalves	64.0	1376.9
snail	3.0	64.5
crustaceans	33.0	710.0
Pigeon guillemot		
benthic fish	70.0	34.3
herring	3.3	1.6
smaltt polychaetes	3.3	1.6
lingcod	3.3	1.6
cod	3.3	1.6
sculpins	3.3	1.6
flatfish	3.3	1.6
rockfish	3.3	1.6
squid	3.3	1.6
shrimp	3.3	1.6
Other auks (=Pigeon guillemot)		
Benthic fish	70.0	132.9
herring	3.3	6.3
smalt	3.3	6.3
lingcod	3.3	6.3
cod	3.3	6.3
sculpins	3.3	6.3
flatfish	3.3	6.3
rockfish	3.3	6.3
squid	3.3	6.3
shrimp	3.3	6.3
Great blue herons		
gunnels	48.4	95.2
staghorn sculpin	24.2	47.6
shiner perch	14.1	27.7
three-spined stickleback	9.2	18.1
bay pipefish	2.3	4.5
chum salmon	1.7	3.3

Table O Diet matrix used for the Strait of Georgia model.

Prey	Predator													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14[a)]
1 Mammals (res.)	-	-	-	-	-	-	-	-	-	-	-	-	1	-
2 Large pelagics	.010	-	-	.100	-	-	-	-	-	-	-	-	-	-
3 Small pelagics	.300	.200	-	.200	.100	-	-	-	-	-	-	.220	-	-
4 Hake	.300	.100	-	.070	.050	-	-	-	-	-	-	-	-	-
5 Misc. demersals	.101	.050	-	.070	-	-	-	-	-	-	-	.150	-	-
6 Jellies	-	.010	-	-	-	.030	-	-	-	-	-	-	-	-
7 Lg. macrobenthos	.009	-	-	-	.200	-	.050	-	-	-	-	.200	-	-
8 Sm. macrobenthos	.040	-	.100	-	.200	-	.300	.050	-	-	-	.190	-	-
9 carn. zooplankton	.010	.450	.100	.350	.400	.260	-	-	-	-	-	-	-	-
10 Herb. zooplankton	-	.190	.800	.210	.050	.710	-	-	.500	-	-	.060	-	-
11 Primary producers	-	-	-	-	-	-	-	-	.250	.900	-	.010	.050	-
12 Birds	-	-	-	-	-	-	-	-	-	-	-	-	.050	-
13 Transient orcas	-	-	-	-	-	-	-	-	-	-	-	-	.050	-
14 Salmon	.230	-	-	-	-	-	-	-	-	-	-	-	-	-
15 Detritus	-	-	-	-	-		.650	.950	.250	.100	-	.170	-	-

a) Salmon is considered not to eat within the Strait of Georgia (see text).

Appendix 2

Workshop Schedule

November 6-10, 1995
Fisheries Centre, University of British Columbia

Sunday 5	Arrival, and settling into Gage Court
Monday 6	**Workshop Day 1** at Ralf Yorque Room, Fisheries Centre
0915 - 0930	Welcome.....*Tony Pitcher,* Director, Fisheries Centre
0930 - 0945	Introductory remarks.....*Peter Larkin*
0945 - 1000	About this workshop.....*Daniel Pauly*
1000 - 1045	Coffee break
1045 - 1200	**Lecture 1**
	The Ecopath Approach: Theory and Applications. *Villy Christensen*
1200 - 1400	Sandwich lunch in Ralf Yorque Room
	1400 - 1700 **Workshop Session 1:** Definition of period (seasons/years/decades) and of areas to be covered by models. Moderator: *D. Pauly.*
1700 - 1830	Refreshment in Ralf Yorque Room
Tuesday 7	**Workshop Day 2**
0900 - 1000	**Lecture 2**
	Variation of North Pacific climate and marine ecosystems. *Jeffrey Polovina*
1000 - 1045	Coffee break
	1045 - 1200 **Workshop Session 2:** Definition of functional groups ("boxes") to be included in models and assignment of boxes to participants. Moderator: *V. Christensen*
1200 - 1400	Sandwich lunch in Ralf Yorque Room
	1400 - 1700 **Workshop Session 3:** Participants assemble key parameter estimates (biomass, mortality, etc.) for their group Moderator: *D. Pauly*
Wednesday 8	**Workshop Day 3**
	0900 - 1000 **Student presentation:** A trophic model of the Strait of Georgia. Moderator: *Rik. Buckworth*
1000 - 1045	Coffee break
	1045 - 1200 **Workshop Session 4:** Assembling the diet matrix Moderator: *D. Pauly*
1200 - 1400	Sandwich lunch in Ralf Yorque Room
	1400 - 1700 **Workshop Session 5:** Data entry and balancing of a preliminary model. Moderator: *V. Christensen*
Thursday 9	**Workshop Day 4**
0900 - 1000	Group work
1000 - 1045	Coffee Break
	1045 - 1200 **Workshop Session 6:** Construction and discussion of model alternatives by participants. Moderator: *D. Pauly*

1200 - 1400	Sandwich lunch in Ralf Yorque Room
	1400 - 1700 **Workshop Session 7:** Discussion of flow networks and ancillary statistics of balanced models. Moderator: *V. Christensen*
1900	Buffet Dinner at Green College - UBC (Small Dining Room, Graham House)
Friday 10	**Workshop Day 5**
0900 - 1000	**Lecture 3**
	Comparative studies on eastern boundary current (upwelling) ecosystems. *A. Jarre-Teichmann*
1000 - 1030	Coffee Break
	1030 - 1200 **Workshop Session 8:** Wrapping up - what has been learnt from all this. Moderator: *V. Christensen*
1200	**End of Workshop** (Lunch at Trekker's Restaurant)
1400 - 1500	**Fisheries Centre Seminar at Ralf Yorque Room**
	"Why do fish stocks collapse? The case of cod in Eastern Canada" *Ransom A. Myers,* Department of Fisheries and Oceans, St. John's Newfoundland.

Appendix 3

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