Report of the BTF Workshop on Reconstruction of the Hecate Strait Ecosystem

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Abstract

Participants gathered at a workshop held in Prince Rupert, May 20 and 21 1998, to discuss changes to the Hecate Strait ecosystem (see Appendix I for list of participants). Hecate Strait is defined here as DFO statistical areas 5C and 5D and includes Dixon Entrance. A preliminary mass-balance model of Hecate Strait in the early 1900s was constructed from information provided by participants, and a preliminary mass-balance model representing the same area during the early 1990s. Changes in biomass from the previous model were based on input from workshop participants. Thus, it presents a test of whether ECOPATH can be used to develop a picture of how the ecosystem looked based almost entirely on local knowledge. Unless otherwise noted, biomass values were adjusted according to the consensus of the workshop participants. Most changes in biomass ranged from a 25% to a 100% increase, back through time. Where information was lacking, ECOPATH was allowed to calculate new biomass values. The results indicate that a coherent mass-balance model can be developed, based on the experience gained from long histories of personal association with an ecosystem.

Introduction

First Nations, fishers, scientists, managers, conservationists and the general public are concerned about the depletion and possible disappearance of entire fish populations. This was brought forcibly to the attention of Canadians by the closure of the East Coast cod fishery. Coincident with the opening day of the workshop, the Minister of Fisheries announced the most severe salmon fishery closures in BC history to preserve depleted coho salmon (*Oncorynchus kisutch*) populations. Introductory comments reflected a deep sense of loss and fear for the future. One hoped that we had not just gathered to write an epitaph. The Aboriginal and commercial fishers present represented several hundred years of experience of the Hecate Strait ecosystem and its fisheries for salmon, herring, halibut, lingcod, dogfish, rockfish, trawl, crab, and other fish and invertebrate species. The degree of overlap and exchange of information not only on 'commercial' species, but also on the rise and fall of seal, seal lion, whale and seabird populations was particularly striking.

Some participants had over 50 years personal experience - lifetimes spent on the water, some could draw on generations of experience. Aboriginal participants drew equally from their personal and family experience of commercial fishing, subsistence fishing for many species and a rich oral history (Jones, this vol.; Watkinson this vol.). Others drew on history and archaeology for insights into past abundance and previous occurrences of the shift, now apparently under way, between herring vs. sardines and anchovies as the dominant pelagic species.

The volume and diversity of information was impossible to fully absorb in the time available. This is because it reflects the complexity and diversity of the ecosystem itself. It also contains information about the processes of change, not only over the last 100 years, but reaching back through archaeological evidence to a time when Hecate Strait was a grassy plain (Fedje *et al.* 1996; Fedje and Josenhans 1998).

Box 1. The 'Back to the Future' approach

The BTF approach (BTF) is based on two beliefs. First, understanding ecosystems as they were before modern industrial fishing is a good first step to setting goals for rebuilding. Second, that all concerned have important contributions to make to reaching a broader and deeper understanding of how ecosystems work. BTF workshops use recent advances in ecosystem modelling to bring the knowledge of commercial fishers, First Nations, government scientists and managers, historians, archaeologists and others together. For additional information on BTF please see (Haggan *In press*; Pauly *et al.* 1998; Pitcher *in press*; Pitcher *et al.* 1999; Pitcher 1998a,b,c).

The greatest strength of BTF is that it enables many different actors to capture the interplay between ecological, economic, social and cultural forces in the ecosystems upon which they rely. For this reason, it has a ceremonial aspect of coming to terms with the depletion of the marine environment. With recognition that all sectors have knowledge that can contribute to good management, balanced by an acknowledgement that aquatic ecosystems are severely compromised and that all concerned – government, First Nations, fishers, scientists, managers, processors and policy-makers – share responsibility, an agreement can be forged to treat different knowledge systems with respect and work towards sharing knowledge in the interest of improved understanding (Haggan *in press*; Haggan *et al.* 1998; Haig-Brown and Archibald, 1996; Salas *et al.* 1998).

Ecosystems are still far too complex for us to grasp completely. Thus, ECOPATH (Christensen and Pauly 1992 and 1993) simplifies an ecosystem by combining species in up to 50 groups or 'boxes.' Groupings are usually made up of fish or other animals that eat, and are eaten by, the same things. For example, we have grouped lemon, rock, petrale, rex, and dover soles together in a box called 'Flatfish'. Done with care, the boxes will implicitly include all the animals and plants making up the system. This approach represents a significant advance over previous models of food webs, for instance multispecies virtual population analysis (MSVPA). The application of MSVPA is hampered by the high degree of expertise required by modellers, data needed are both difficult and expensive to obtain and the overall lack of transparency in the estimation procedure (for a more detailed citique, see Walters *et al.* 1997). Perhaps most importantly, MSVPA only includes harvested fish. In contrast, the relative ease of the application of ECOPATH has resulted in its increasing use to model aquatic ecosystems. A recent cooperative project between the UBC Fisheries Centre and University of Tennessee constructed a 47 group model of Prince William Sound for the period after the *Exxon Valdez* oil spill (Okey and Pauly, 1998). In addition, more than 100 ECOPATH models have been published world-wide describing upwelling systems, shelves, lakes, rivers, open oceans and terrestrial farming systems (http:\\www.ECOPATH.org).

ECOPATH is designed to help understand the ecological process of eating and being eaten. ECOPATH works like an accounting system. Each ECOPATH box gains or loses capital as the creatures in it feed, or are fed upon. ECOPATH tracks the flow of capital between boxes, ensuring the amount eaten does not exceed what is available. Furthermore, there must be a balance between all levels within the 'food chain'. A food chain consists of many links, each one of which represents a species, or a group of species. Each chain has a 'bottom' and a 'top'. At the base are the primary producers (plankton and kelp), which produce their food directly from sunlight. At the top are the predators, such as killer whales and of course, humans. At each level in the food chain animals are either eating prey, or are being eaten by predators.

The food chain is a very simple way of thinking about an ecosystem. In fact, ecosystems consist of many different food chains linked together like a spiderweb – a food 'web'. The figure in Appendix II shows the boxes and connections in the Hecate Strait model, giving some idea of how complex systems can be. ECOPATH requires five main types of information in order to model these food webs:

- The average weight of each group for the period covered by the model;
- The amount each group grows during a year;
- The amount each group eats during a year;
- How much of each group is caught during a year;
- The kind of food each of the groups eat.

If all of the above information is available, you have more than enough to proceed with the building of an ECOPATH model. Most often, not all of the above is available. In those cases, as long as you have any four of the above, ECOPATH can calculate the missing one.

Summary of Participant Input and Biomass Values

The following summary of the main parts of the Hecate Strait ecosystem 100 years ago is based on information provided by participants and research by graduate students at the UBC Fisheries centre. Where information is lacking, the ECOPATH software treated the value as an unknown, to be estimated from the balance of the various inputs.

Initially, it was planned that the model would reconstruct the ecosystem of 50 years ago. During discussion, however, participants pointed out that there had been fairly extensive steam trawl fisheries in the early 1900s. It was therefore agreed that reconstructing the system of 100 years ago would give a better sense of what the system was like prior to modern industrial fishing. Note that all references to the 'present day model' refer to Beattie (this vol.). As well, a detailed account and map of the study area may be found in Beattie (this vol.)

Transient killer whales, dolphins and porpoises (Odontocetae)

Information from Aboriginal and commercial fishers indicated a reduction in killer whales since their early days, but their numbers are now on the increase. There was some discussion about transient killer whales including an account of Orcas apparently trying to drown two Grey whales (*Eschrictius robustus*) by 'jumping' on top of them, thus preventing them to surface and breathe. It was agreed that a modest recovery in the population of both resident and transient killer whales is attributable to higher numbers of salmon and seals over the last 20 years. Porpoises (*Phocoenoides dalli*) were harpooned during the war as oil from a sack in the nose has a high freezing point and was valued for use on rifles and equipment in the Arctic. The meat was also used. Porpoises were previously "thick" in Juan Perez and Skincuttle inlets. Porpoises also followed eulachons (*Thaleichthys pacificus*) to the Nass. An association was made between dolphins and tuna, both being associated with warmer water. A recent coastwide increase in Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) was also noted.

Despite the recent recovery in killer whales, it was agreed their present biomass is still low. The 100-year biomass was increased by 20% based on a rationale that there was "more of everything" before industrial fishing started. More food allows for more top predators.

Seals and Sea Lions

Seals are an emotive topic these days. There was concern about the effect of Harbour seals (*Phoca vitulina*) on salmon populations, particularly the presence of large numbers of seals in river systems when juvenile salmon are out-migrating. Examples included the Skeenan River and Oweekeno Lake/Rivers Inlet. This was tempered by comments that human impacts such as fishing, pollution and habitat loss were also to blame and a realization that ecosystems are complex. Seals are highly visible taking salmon from gillnets, lying in wait in rivers for in-migrating adult salmon or hatchery releases, but seals also eat hake (*Merluccius productus*), a major predator of juvenile salmon. Some recalled the Department of Fisheries and Oceans bounty on seals in the 1970s, but no one expressed any real desire to return to those days. One Haida participant recalled a stack of fur seal (*Callorhinus ursinus*) bones on the beach at Tow Hill, near Masset and said that fur seals used to be "like the buffalo on the prairies." Steller sea lions (*Eumetopias jubatus*) were said to be up since the 1950s when they were shot for mink feed and the skins used as anti-chafe material on beam trawls. More recently, Steller sea lions have decreased sharply, but have been largely replaced by California sea lions (*Zalophus califonianus*).

For the model, Seals and Sea Lions were left the same on the assumption that any decline of the Steller sea lion population has been offset by the increase in the California sea lion and Harbour seal populations

Baleen whales (Mysticetae)

It was noted that the Haida hunted whales (Jones, this vol.). Grey whales in particular have increased over the last 15 years and cause some problems for the spawn-on-kelp fishery on Haida Gwaii due to silt stirred up by their feeding habits. Grey, Humpback and Minke whales are believed to have recovered from past industrial whaling operations. Blue and Fin whales have not. Since the former group comprises the main bulk of the biomass, the 100-year biomass was assumed to be the same as at present.

Seabirds

General comments reflected the conceptual split between how fishers and fisheries scientists regard birds. All who make their living from fisheries pay close attention to the presence, absence and behaviour of birds. Negative impacts on Ancient Murrelets (*Synthliboramphus antiquus*), Auklets (*Ptychoramphus aleuticus*) and other bird populations include logging, the introduction of rats and raccoons (*Procyon lotor*) that prey on eggs and young and overall reduction in food availability due to intensive fishing. Discards from the trawl fishery, on the other hand, provide a new food source for some species.

Participants provided a wealth of information on this area that, up to now, has not had a formal place in fisheries science. This is not to say that there is a lack of good research, just that there has been no tradition of fisheries scientists and ornithologists working together. It is thus a rich area for ecosystem research and one place where ECOPATH provides a new opportunity to link seabirds to the marine ecosystem (Bishop and Okey 1998; Esler 1998; Kelson *et al.* 1996; Okey and Pauly 1998; Ostrand and Irons 1998; Wada and Kelson 1996). Perry and Waddell (1994) also address plankton availability to seabirds in Queen Charlotte Island waters. Areas for further research therefore include correlation of past and present studies, Audubon Society Christmas counts on Haida Gwaii and Prince Rupert, interviews with birdwatchers, fishers and other observers and archaeological research now under way at pre-contact village sites around Hecate Strait. Incorporating the impact of rats and raccoons on seabirds and their prey will be a challenge.

In view of the overall negative impacts, the 100-year biomass is tentatively increased by 100%.

Spiny dogfish (*Squalus acanthias*)

There was a general impression that dogfish had recovered well from an intensive WWII era fishery. The 100-year biomass is tentatively left unchanged, on the assumption that the population has recovered from the directed fishery. More research and follow-up interviews are needed to correlate observations on the relative abundance of dogfish in halibut and other fisheries over time.

Ratfish/skates

There was a small fishery for ratfish (*Hydrolagus collei*) in order to process them for oil used for guns and on slipways, though primarily it was a bycatch species in the dogfish fishery. Skates (*Raja* sp.) were only recently the target of a directed fishery. Tentatively the 100-year biomass will be left the same as for the present day model.

Pacific halibut (*Hippoglossus stenolepsis*)

Halibut have always been very important to BC First Nations, indeed, for the Haida, halibut may have been more important than salmon. Input included 6,000 years evidence of halibut in middens and a pre-contact catch estimate of close to 1,400t per year north of Cape Caution. In fact, Tsimshian elders were unable to attend the workshop primarily because they were at camp drying halibut and picking seaweed (*Porphyra* spp.). First Nations fished from canoes, with lines made of variously twisted cedar, animal sinew/intestine, or kelp (*Macrocystis* spp.), and wooden hooks with boned barbs (Jones, this vol.). By the turn of the century, gasoline and diesel engines were used, and in 1907 the commercial halibut catch reached more than 20,000 t. After 1915 catches were declining, and the International Fisheries Commission (IFC), later renamed the International Pacific halibut Commission (IPHC) was formed in 1923 to ensure proper management.

The discarding of bycatch is a major concern; several participants referred to the number of red snapper discarded in the halibut fishery before a market developed. One comment was that the sea looked "like a pumpkin patch." Bycatch in the trawl and blackcod fisheries is an ongoing concern. There is also a belief that small 'homesteader' populations of halibut may have been depleted or fished out in a similar manner to small herring stocks. This should be the default assumption in the absence of unequivocal scientific evidence to the contrary. There was also concern that although the sport fishery catch is a fraction of the commercial take, sport fishers have a tendency to fish out the corners where commercial vessels do not necessarily go. This has a dual role of eroding populations of resident species and impacting the Aboriginal subsistence fishery that depends on the ready availability of stocks that are nearby and can be easily accessed using small boats.

Overall, the recovery of the stock appears to be a rare fishery management success. The consensus of the workshop was that there were more halibut today than before, perhaps twice as many. The available data suggest, however, that there is perhaps only as many as there were 100 years ago. For the purpose of this model, halibut are tentatively left the same as for the present day model.

Pacific cod (*Gadus macrocephalus*)

Between 1918 and the late 1950s, Pacific cod landings increased from about 400 to 8000 t. There is a spawning ground at the north end of Banks Island. Substantial amounts were landed at Bellingham. Data may be available through the University of Western Washington.

The consensus of the participants is that cod have only 10% of their historical abundance, and the 100-year biomass is tentatively set at that figure.

Walleye pollock (*Theragra chalcogramma*)

Despite mention of a winter midwater fishery at the top end of Two Peaks, the consensus was that pollock were never very common. The 100-year biomass was tentatively left as in the present day model.

Juvenile and Adult blackcod (*Anoplopoma fimbria*)

Blackcod were considered to be reduced in numbers, by as much as 33-50%. The BC blackcod fishery began sometime in the 1890s as a setline fishery, but landings were minor until 1913. The current blackcod fishery is by trap. The 100-year biomass for juveniles and adults was tentatively increased by 33%.

Herring (*Clupea harengus pallasi*), small pelagic fish

The herring reduction fishery was cited as an example of how little is known about unfished levels and the importance of herring to other ecosystem components (Jones *in press*; Newell 1993). Fishers, the Union and First Nations concerns were disregarded by DFO biologists until a crash forced a six-year closure. There was a consensus on the crucial ecosystem role of herring. Fishers also believe that the Hecate Strait area is (or was) home to a very large number of small discrete stocks as well as one (or more) large stocks of bigger herring. Skidegate Inlet, Prince Rupert Harbour and Chismore Pass were cited as areas where stocks had been virtually eradicated. Chismore Pass was also given as an example of how sport fisheries can target small stocks for bait. Concern was also felt about inconsistencies in the way herring spawn is measured and reduction in effort in this program.

Based on the critical role of herring, it was agreed that a precautionary approach that considers the ecosystem role of herring is essential (Jones *in press*). Recent examples were given of Haida and Tsimshian (Kitkatla) fishers opposing DFO openings. In the absence of information to the contrary, the default assumption should be that stocks are discrete, fishing strategies should also be very conservative. The idea of 'sanctuaries' (marine protected areas) to protect small local herring stocks as well as other species was discussed and well received.

The relative abundance of herring compared with sardines/pilchards, anchovies and mackerel was a recurrent topic. Observations tallied that the 1990s have seen a significant rise in pilchards. There was also a fishery for sardines/pilchards in the 1960s and other species

The consensus of the workshop was that herring biomass was in general down, with some areas showing more of a reduction than others. For eulachons, the general feeling was the biomass is down 25-30%. The average reduction for the entire study area for herring was estimated to be 75%. The 100-year biomass was be tentatively increased 75% above present day model levels.

Juvenile salmon (*Oncorhynchus* spp.)

Loss of spawning and nursery habitat, coupled with decades of heavy fishing has forced a decrease in the amount of salmon spawning in BC waters, and therefore the number of juvenile salmon in the Strait. Possible negative impacts include increase in seal populations and more mackerel due to El Niño. However, little information has been found on how much of a reduction has taken place. For the want of better data, the biomass will be left the same as for the present day model.

Pacific Ocean perch (POP, *Sebastes alutus*)

The general feeling was that POP were down, although no overall percentage was obtained. Until the 1950s, POP were not an important species to the BC fisheries, comprising less than a 1/4 of Pacific cod landings and about the same for total flatfish landings (Figure 1). In the 1960s and 1970s, POP were heavily targeted by foreign fisheries, including Japanese and U.S. fleets (Westrheim 1987). Little is known about actual quantities of fish removed, or how well the population has recovered. For this model, the biomass was thus left for ECOPATH to estimate.

Flatfish

Information provided indicated a reduction in Dover sole, lemon sole and Arrowtooth flounder, previously taken in large amounts and used for mink feed. The overall impression was a reduction in flatfish numbers of about 1/3. The 100-year biomass will therefore be set 1/3 higher.

Rockfish and small bottom dwelling fish

The consensus was that rockfish are at 10% of their historical abundance. In particular, it was felt that Yelloweye rockfish or red snapper, (*Sebastes ruberrimus*) were significantly reduced (see above on bycatch in the halibut fishery). Within this model, however, they are grouped with a variety of small bottom-dwelling species. It is not known whether the biomass of these has decreased, increased, or remained the same; indeed, this box was problematic for the present day model. The biomass was therefore left for ECOPATH to estimate, as was done for the present day model.

Turbot (*Atheresthes stomias*)

Although turbot has only recently been the target of directed fisheries, it was used in the past for mink food, although apparently retained principally as by-catch. Turbot is very common in the trawl catches today. For

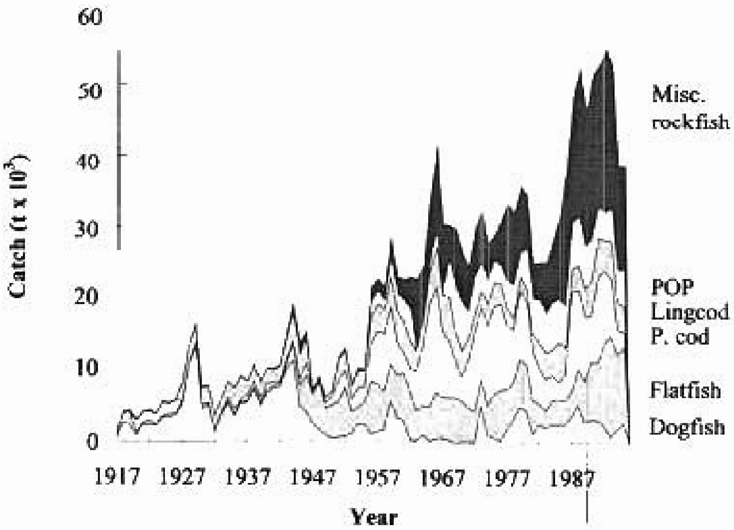

Figure 1. Catches by species for the Canadian trawl fleet for the years 1917-1994. Data from Forrester *et al.* (1978), Forrester *et al.* (1983), Westrheim *et al.* (1986) and Pauly *et al.* (*In press*).

this model, the biomass is tentatively left as for the present day model.

Lingcod (*Ophiodon elongatus*)

lingcod provoked a great deal of discussion. Input included a belief that male lingcod migrate across Hecate Strait to Haida Gwaii returning in February to spawn and guard eggs. This is based on large seasonal catchers by bottom trawlers ('draggers'). Longtime participants in the fishery spoke of severe reduction in numbers and size attributed to the introduction of longlines (including ghost fishing by lost gear), catch by draggers and cleanup of the corners by charterboat (sportfishing) operations. One longtime participant recalled that landings for a good day trolling would be 450 kg with 110 kg on a poor day. Average size jigging was 14 kg., 3.5 kg. trolling. Average weight in the sport fishery is now 3.5 kg.

Overall, lingcod are considered to be severely reduced in abundance (Martell, this vol.). Biomass for the 100-year model is tentatively set for a 95% increase, based on Martell and Wallace (1998), who estimated a 95% reduction in Georgia Strait lingcod.

Jellyfish, Zooplankton, Phytoplankton and Detritus

No consensus was reached during the workshop. For phytoplankton and zooplankton, any large increase or reduction seems unlikely as climatic conditions seem to be constant over the period. The 100-year biomasses are tentatively left the same as for the present day model.

Crustaceans, Shellfish and Echinoderms

It was felt that biomass of clams and prawns were in general down. Other groups such as sea urchins were thought to have increased. Haida participants expressed great concern about the number of traps in the crab fishery as well as ghost fishing, i.e., killing of fish by lost or discarded gear. Concern was also expressed about the depletion of abalone (*Haliotis kamtschatkana*), including an interesting observation about the role of raccoons in depleting abalone in Naden Harbour. The biomass 100 years ago was tentatively left unchanged from the present day model.

Fishery harvests

Modern commercial fishery harvest in the Hecate Strait region apparently did not begin in earnest until 1910. Thus, commercial harvest was left at zero. The Aboriginal harvest figure calculated in the Strait of Georgia BTF project was used in the absence of better information (Pauly *et al.* 1998). This is probably low as a verbal report on archaeological information by David Archer indicates that the study area had one of the highest Aboriginal population densities in North America. Boyd (1990) gives figures of approximately 14,500 for both the Haida and Tsimshian, but allows that these are probably low.

Results

Figure 2 shows the results of the trophic flows estimated by ECOPATH. Note that the diagram is virtually identical to the one obtained for the present day model, as also confirmed by the similar or identical trophic levels of the various groups (Table 1, also see Table B, Appendix II for more details).

Both models are preliminary in nature, and as such we will not attempt a detailed analysis of their structure. It is worth noting, however, that the perceptions of the people involved in the workshop as to the state of the Hecate Strait ecosystem as it was 100 years ago were found to be entirely plausible under the ECOPATH mass-balance assumption. Thus, with more study, such results (subject to further verification) may provide a solution to, or at the very least mitigate the effects of the 'shifting baseline syndrome of fisheries' (Pauly 1995).

Table 1. Comparison of the trophic levels calucualted for the present day and 100-year models. Differences are highlighted.

Group name	Trophic level	
	Present	100-year
Adult sablefish	**3.6**	**3.7**
Carnivorous jellyfish	**3.0**	**3.1**
Crustaceans	2.2	2.2
Flatfish	**3.1**	**3.5**
herring, small pelagic fish	3.1	3.1
Juvenile sablefish	**3.8**	**3.7**
Juvenile salmon	3.1	3.1
lingcod	4.0	4.0
Macrobenthos	2.1	2.1
Mysticetae	3.1	3.1
Odontocetae	4.1	4.1
P.O. perch	3.1	3.1
P. Cod	3.4	3.4
P. halibut	3.9	3.9
Pinnipeds	4.1	4.1
ratfish, skates	**3.4**	**3.5**
rockfish, small benthic fish	3.2	3.2
Seabirds	3.6	3.6
Spiny dogfish	3.2	3.2
Transient orcas	**5.0**	**5.1**
turbot	3.7	3.7
Walleye pollock	3.3	3.3
Zooplankton	2.1	2.1

Unanswered questions

There are two kinds of unanswered question. The first relates to an absence of data on individual species or groups. Earlier discussion pointed to significant uncertainty about present and past numbers of a range of species, particularly rockfish, ratfish, skate, bottom dwelling species, even adult and juvenile salmon. Mention was made of the disappearance of tomcod *Microgadus proximus* from both Prince Harbour and Skidegate Inlet. Other information requirements include:

- Pre-contact and early fisheries harvests;
- biomass of adult salmon, and changes in abundance from 100 years ago;
- the abundance or presence of squid in the ecosystem; and,
- Information on types, abundance and harvest of sharks.

The second type of question relates to the ecosystem interactions between say herring, seals, sea lions, seabird, salmon, lingcod and commercial fisheries. This bears directly on the ability of commercial species to sustain fisheries or indeed recover from previous overfishing; the slow rate of recovery of Atlantic cod, despite 7 years of closure is a case in point. Jones (*In press*) discusses the impacts of commercial herring fisheries on Haida Gwaii stocks. Bycatch is another complex area that calls for ecosystem modelling.

Another area pertains to large changes in ecosystem structure. For example, in his introductory remarks, Tsimshian President Bob Hill mentioned a kelp forest that used to stretch from Kitamaat to Dundas. It is generally believed that the disappearance of kelp is related to the rise in sea urchin populations after the demise of the sea otter (*Enhydra lutris;* Paine 1980). However, this

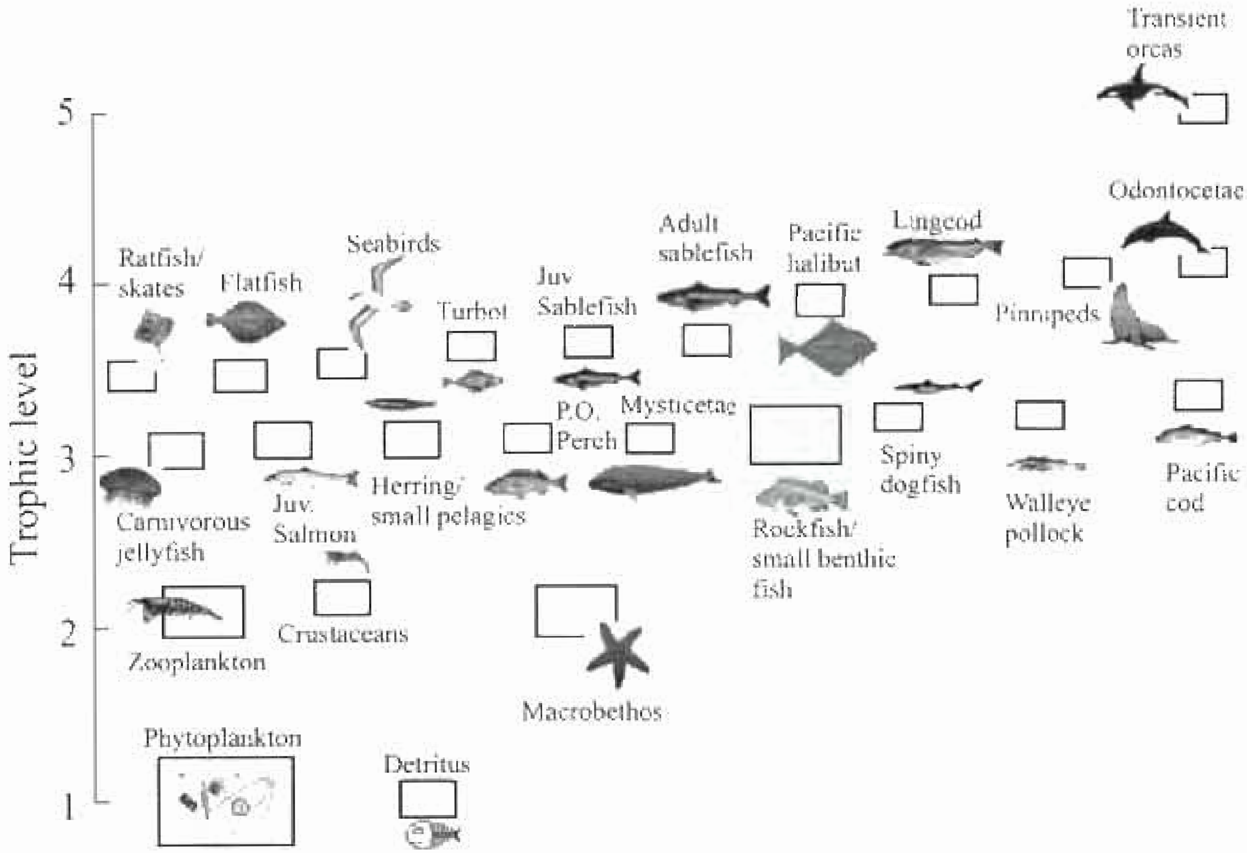

Figure 2. Pictorial representation of the elements of the Hecate Strait ecosystem, as it might have been 100 years ago. For comparison, this diagram and the diagram for the present day model are scaled to the same size, using the biomass of the phytoplankton box as reference.

large change in ecosystem structure will have profound implications for the presence, absence and relative abundance of species that depend on kelp forests for cover. Kelp is also important for herring spawn and the spawn on kelp fishery. The second example was of 'red tree' (gorgonians) in trawl fisheries. The effect of trawling on bottom structure is beginning to be documented (Auster 1998; Engel and Kvitek 1998; Watling and Norse 1998). On the credit side, ECOPATH can now accommodate the species that change actual ecosystem structure (C. Walters, UBC Fisheries Centre, pers. comm.), even if their impacts is due to effects other than predation. This should make it rewarding to revisit the models presented here.

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