MYSIS RELICTA AND KOKANEE SALMON (*ONCORHYNCHUS NERKA*) IN OKANAGAN LAKE, BRITISH COLUMBIA: FROM 1970 AND INTO THE FUTURE.

by

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Abstract

Mysis relicta and kokanee salmon (*Oncorhynchus nerka*) in Okanagan Lake: from 1970 and into the future.

Aran Kay

The opossum shrimp (*Mysis relicta*) was introduced into Okanagan Lake, British Columbia (BC), in 1966 in order to serve as an intermediate food item for kokanee salmon (*Oncorhychus nerka*). However, beginning in the early 1970s, kokanee began a sharp decline in abundance. In the search for reasons for the kokanee decline, two factors were identified: mysid competition with kokanee over zooplankton resources and reduced nutrient loads to the lake. Between 1970 and 2000, the *M. relicta* population increased 20-fold and nutrients in the lake fell to one quarter of 1970 levels.

Using the Ecopath with Ecosim (EwE) software, an Ecopath model of Okanagan Lake in 1970 was built. This model attempted to account for all biomass within Okanagan Lake and contained 16 groups and 2 fisheries. This base 1970 model was then run through the Ecosim module and biomass was predicted for all groups from 1970 to 2020. For the 1970 to 2000 period, mysid and kokanee biomass were tracked by the program with high accuracy. Two key findings for this period were that *Mysis relicta* appears to have been responsible for the original kokanee decline, but reduced nutrient loads to Okanagan Lake are currently keeping the kokanee at depressed levels.

From 2000-2020, Ecosim was used in a forecasting mode and solutions were examined which may help rehabilitating the kokanee population. The current mysid fishery does not have the capacity (30t $year^{-1}$) to catch the number of mysids required (300t $year^{-1}$) to aid kokanee populations to any great degree. Nutrient additions appear to be able to boost kokanee abundance in the lake without increasing mysid populations greatly. However, a combined approach involving nutrient additions with an intensified mysid fishery could allow kokanee abundance to approach 1970 levels.

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Introduction

1.0 – General Introduction and Project Rationale

On March 15, 1995, the Ministry of Environment Lands and Parks (MELP) closed the valuable Okanagan Lake kokanee salmon (*Oncorhychus nerka*) fishery in order to conserve the remaining stock which had dwindled to 10% of 1970 levels (Ashley *et al.*, 1998). This fishery remains closed today. To try and assess why this unfortunate event came about an Adaptive Environmental Assessment (AEA) workshop was held from June 28-30, 1995, to discuss the possible reasons for the kokanee crash (Ashley *et al.*, 1998). It was realized during this workshop that no 'quick fixes' to the kokanee salmon stock would be available and that a longer term approach to determining the cause of and solution to this crisis should be taken. The Okanagan Lake Action Plan (OLAP) was created to assist in this endeavour. This plan encompasses 20 years broken into four stages. Phase 1 (1996-2001) focuses on habitat protection, kokanee stock conservation, and collection of priority information which may aid in determining the cause of the kokanee stock depletion (Ashley *et al.*, 1998); three possibilities have been suggested.

The first is that of lake water draw down. Due to control structures placed at the outlet, water draw down adversely affects the spawning habitat and egg mortality of shore spawning kokanee in Okanagan Lake. However, Shepherd and Sebastian (1998) have shown that there is no significant correlation between drop in lake level and escapement or recruitment ratios for shore spawning

kokanee. While it is stated that lake draw down may be an aggravating factor in the decline of shore spawning kokanee, it is not proposed as a primary cause.

The second possibility is a negative role of *Mysis relicta*. The introduction of *Mysis relicta* to many temperate lakes in North America and world-wide has resulted in pelagic fish abundance decline (Morgan *et al.*, 1978; Lasenby *et* al, 1986; Langeland *et al.*, 1991; Martinez and Bergersen, 1991; Northcote, 1991). Much research has been conducted on mysid feeding habits and the possible competition with planktivorous fish for zooplankton resources (Bowers and Vanderploeg, 1982; Byron *et al.*, 1986; Koksvic *et al.,* 1991; Langeland *et al.*, 1991; Lasenby, 1991; Naesje *et al.*, 1991; Nesler and Bergersen, 1991; Northcote, 1991; Richards *et al.*, 1991; Johannson *et al.*, 1994; Smokorowski, 1998; Spencer *et al.,* 1999; Chipps and Bennett, 2000; Whall, 2000). Since the introduction of *Mysis relicta* into Okanagan Lake in 1966, it has become clear that this freshwater shrimp competes with kokanee salmon in Okanagan Lake for zooplankton resources (Whall and Lasenby, 1998). However, it is not known to what degree mysids have been responsible for depressed zooplankton resources in this lake. Therefore, while *Mysis relicta* can be implicated in the fall of kokanee salmon stocks, it is not know if correlation equals causation as of yet.

The third possibility may be related to nutrient inputs. Decreased anthropogenic nutrient loads to Okanagan Lake over the past three decades through the implementation of municipal sewer treatment systems and better farming practices is also thought to be a candidate as a cause to the depressed kokanee salmon stocks. Specifically, annual loads of nitrogen and phosphorus

to Okanagan Lake have fallen dramatically (Forty, 1996; Jensen,1999). This has led to the possibility of co-nutrient limitation in Okanagan Lake (Jensen, 1999; McEachern, 1999). The result has been an increased preponderance (compared to 1970s) of blue-green algae, especially in the spring (Jensen, 1999), and the possibility of depressed zooplankton production rates as has been seen in Lake Tahoe during periods of decreased nutrients (Byron *et al.*, 1986; Richards *et al.*, 1991).

As a result of the debate regarding the cause of the kokanee stock crash this project was designed to shed some light on the topic. Through the medium of a computer software program (Ecopath with Ecosim), a search for the factor(s) which may have been involved in the decline of the kokanee salmon in Okanagan Lake was conducted. While the BC Ministry of Fisheries and the OLAP team are looking at many ways of conserving and rehabilitating the kokanee salmon stock, the decision to attempt a large scale mysid fishery will be evaluated in light of the information gathered throughout this project.

1.1 – Biology of *Mysis relicta*

The opossum shrimp *Mysis relicta* is a freshwater shrimp of the Order Mysidacea. *Mysis relicta*'s natural distribution in North America follows the maximum extent of the Pleistocene glaciation and is therefore known as a post-glacial relict species (Lasenby *et al.*, 1986). Mysids are a reddish-orange colour when light is shone upon them (personal observation) and are known to reach

up to 3 cm in length. In Okanagan Lake, mysids adults are usually 12-18 mm long, while juveniles are 4-8 mm in length (Whall and Lasenby, 1999).

Mysids have life cycles that run from 1 to 4 years. The key to calculating time to maturity appears to be the productivity of the lake, as Morgan (1980) found an inverse relationship between lake primary productivity and mysid life cycle. In lakes of high productivity, *M. relicta* has a 1-year life cycle and in lakes of low productivity *M. relicta* has a two-year life cycle or greater. In most lakes the life cycle is two years (Langeland *et al.*, 1991).

The typical life cycle begins with the release of juveniles (usually < 20 per brood; Steve Matthews, MELP, pers. comm. March 2001) in the spring, generally around April or May. The juveniles then spend the summer feeding and growing, becoming sexually differentiated by the end of the fall (Quirt, 2000). After spending the winter as immatures, these mysids spend the spring and summer feeding and increasing size until finally reaching maturity in the October to December period. After mating, females carry their brood over winter and die upon brood release in the spring. Most males, however, die upon breeding in the fall, but some do occasionally survive over winter to die in the spring (Whall, 2000). Why some males survive over winter to die in the spring is unknown.

Mysid feeding habits and diel vertical migration bahaviour have been the focus of intense study over the last 30 years. *M. relicta* is known as a negatively phototactic animal and responds to daily light cycles by undergoing vertical migrations. Mysids diel vertical migrations involve ascending from the sediment water interface, or in very deep lakes (>100m) from 90-150 m (Levy, 1991), at

dusk and then descending at dawn (Beeton and Bowers, 1982). As omnivores, mysids are known to eat detritus, phytoplankton and zooplankton (Gossnickle, 1982). Little is known about the benthic feeding habits of mysids. Although, bottom sediments (Gossnickle, 1982) and chironomid head capsules (Lasenby and Langford, 1973) have been found in mysid guts. Much more is known about mysid pelagic feeding habits. In general, the juvenile stages of mysids depend heavily on phytoplankton for the first 3-4 months of life (Gossnickle, 1982). Once mysids begin to feed on zooplankton, a preference for certain species is developed. The cladocerans *Daphnia* and *Bosmina* seem to be the preferred prey (Bowers and Vanderploeg, 1982; Koksvic *et al.*, 1991; Langeland *et al.*, 1991; Lasenby, 1991; Richards *et al.*, 1991; Spenser *et al.*, 1999; Chipps and Bennett, 2000).

It should be noted, however, that both the mysid's vertical migration behaviour and feeding abilities are constrained by temperature. *M. relicta* tends to avoid the epilimnion when temperatures are above 14 °C (Rieman and Falter, 1981; Martinez and Bergersen, 1991, Spencer *et al.*, 1999). In laboratory test, mysids survival was high (93%) in temperatures up to 17 °C, but fell significantly at any higher temperature (Rudstam *et al.*, 1999). Peak feeding rates for adult mysids were achieved at 12 °C and fell dramatically if temperatures were any higher. Lower temperatures (to 4 °C) do not affect mysid feeding rate significantly (Rudstam *et al.*, 1999).

1.2 – *Mysis relicta*: Introductions and Effects

The Norwegian biologist Knut Dahl was the first to suggest the introduction of *Mysis relicta* into unproductive Norwegian lakes in 1910 (Northcote, 1991). Clemens *et al.* (1939) made the first documented suggestion to do the same in North America. However, Mysis *relicta* was not introduced into British Columbia (BC) until 1949 (Sparrow *et al.*, 1964) after Peter Larkin, then the Chief Fishery Biologist for the BC Game Commission, suggested the introduction a year earlier (Larkin, 1948). Approximately 25 000 mysids were transported from Waterton Lake, AB to Kootenay Lake, BC (Sparrow *et al.*, 1964). For the first decade after introduction, no *Mysis* were observed in the lake (Sparrow *et al.*, 1964). However, in the summer of 1961, *Mysis* were observed at the surface of the lake and in stomach samples of rainbow trout in the West Arm (Sparrow *et al.*, 1964). Shortly thereafter, it was noted that the population of kokanee salmon, *Onchorynchus nerka*, in the West Arm of Kootenay Lake showed an amazing increase in growth rate and size at maturity. This was attributed to heavy predation on the newly established *Mysis* shrimp (Northcote, 1991). News of the large kokanee quickly spread to anglers and soon the sport fishery for *O. nerka* mushroomed to a point where over 100 000 fish were taken annually (Northcote, 1991).

The success of the Kootenay Lake *Mysis* introduction did not go unnoticed and by the early 1980s, there were over 200 documented cases of *Mysis* introductions worldwide (Lasenby *et al.*, 1986; Martinez and Bergersen, 1989; Northcote, 1991). The three areas where *Mysis* were introduced most

extensively were Sweden (61), Colorado, (51) and BC (21 introductions). While scientists in both North America and Scandinavia recognized that *Mysis relicta* was an important component of fish diet in lakes where *Mysis relicta* occurred naturally (Larkin, 1948; Langeland *et al.*, 1991; Lasenby *et al.*, 1986), the rationale for the introductions were different for both of these areas. In Scandinavia, it was recognized that *Mysis relicta* showed benthic feeding and moderate diel vertical migration behaviour. Therefore, mysids could act as an 'energy elevator,' bringing nutrients to the upper littoral zone from the benthos where the energy was considered to be trapped in most alpine lakes (Lasenby *et al.*, 1986). In North America, most alpine lakes contain sport fish such as the rainbow trout and kokanee salmon. However, the size of these fish remained small in nutrient poor lakes and showed especially poor growth rates during their transition from planktivory to piscivory as there were no mid-sized items to eat. It was thought *M. relicta* could fill this dietary gap (i.e., provide an intermediate size food item that would allow growth rates to remain high; Lasenby *et al.*, 1986). Hopefully larger fish would result in increased angler interest and spawn a larger sport fish industry as was seen in the Kootenay Lake case.

Unfortunately, Kootenay Lake was a very inappropriate model to use as rationale for further *Mysis relicta* introductions. The West Arm of Kootenay Lake had a particular hydrology that caused significant upwelling at the entrance. This upwelling entrained mysids and swept them up into the upper water column where they became available to kokanee and rainbow trout (Martin and Northcote, 1991). In most deep lakes, however, mysids are able to avoid

predation from visual pelagic predators by undergoing significant diel vertical migrations (Beeton and Bowers, 1982; Moen and Langeland, 1989; Levy, 1991). *Mysis relicta* remain on the bottom of the lake during the day, feeding on detritus, and return to the surface under the cover of darkness to feed on zooplankton and phytoplankton at night (Gossnickle, 1982).

Due to the lack of predation pressure on mysids, this invertebrate has grown to large numbers in many lakes and has been implicated in many detrimental effects on lake communities. Competition with planktivorous fish for zooplankton, especially the cladoceran species of *Daphnia* and *Bosmina*, has been the focus of most mysid introduction impact studies (Bowers and Vanderploeg, 1982; Byron *et al.*, 1986; Koksvic *et al.,* 1991; Langeland *et al.*, 1991; Lasenby, 1991; Naesje *et al.*, 1991; Nesler and Bergersen, 1991; Richards *et al.*, 1991; Johannson *et al.*, 1994; Ashley *et al.*, 1997; Smokorowski, 1998; Spencer *et al.,* 1999; Chipps and Bennett, 2000; Whall, 2000). It is believed that mysids can out-compete species such as kokanee for the zooplankton resources in a lake and are thus responsible for the major declines in kokanee in lakes where *Mysis* were introduced. Specifically, *Mysis* and kokanee are known to prefer cladoceran prey items. *Mysis relicta* is a voracious predator that is capable of virtually extirpating species of *Daphnia* and *Bosmina* from some lakes (Koksvic *et al.*, 1991; Langeland *et al.,* 1991). Kokanee populations do not seem to be able to withstand the reduction of cladoceran prey items in their diet and a reduction in kokanee abundance results. However, the co-existence of cladoceran zooplankton and *Mysis relicta* in the same lake is not impossible. In

particular, lakes or regions of lakes that have higher trophic status (more nutrients) have been shown to be capable of sustaining both species at the same time (Byron *et al.,* 1986).

Many other implications of mysid introduction have been identified as well (Lasenby *et al.,* 1986; Nesler and Bergersen, 1991; Northcote, 1991). Mysids have been implicated in the eutrophication of lakes as their benthic feeding habits stir up sediments and stimulate the release of nutrients. Mysids also undergo diel vertical migrations from deep to near surface waters where they stimulate phytoplankton growth via their excretions. As well, mysid mandibles fractionate the phytoplankton and zooplankton they feed on releasing significant amounts of dissolved organic carbon, phosphorus and nitrogen into the upper water column. Mysids can play a major role in the bioaccumulation and transport of pollutant materials from lake sediments to lake surface. Bioaccumulation and transport of PCB's, naphthalene, lead, mercury, zinc and cadmium have all been documented (Northcote, 1991).

1.3 – The Okanagan Mysid Experience

In 1966, 240 000 *Mysis* shrimp were transported from Kootenay Lake, BC to Okanagan Lake, BC (Lasenby *et al.*, 1986). At this time, kokanee spawning estimates from Okanagan creek and shore spawning beaches were reaching all time highs of 1 million fish (Matthews and Shepherd, 1999). However, over the next decade, kokanee salmon faced a catastrophic decrease in abundance. Kokanee salmon stocks crashed to 24% of 1970 levels within a decade and were

reaching the 10% mark by 1990 (Walters, 1995). During this time, no hard data was being kept on the *Mysis relicta* population until 1989 when it is believed that the mysid population peaked (McEachern, 1999). Since then mysids have been on a downward trend (McEachern, 1999), but as of 2000 the most recent mysid estimate is still staggeringly high at 1 000 metric tons (S. Matthews, MELP, pers. comm. March 2001). Not much is known about what was happening to the rest of the lake until the 1990s as population estimates were concentrated on the lucrative kokanee salmon. What is known comes from resident fishermen and divers in Okanagan Lake as they have seen both a dramatic drop in the number of rainbow trout (*Oncorhynchus mykiss*) in Okanagan Lake and a large increase in the number of burbot (*Lota lota*) (L. Granberg, mysid boat Captain, pers. comm. September 2001). As well, it is known that *Mysis relicta* was not a successful introduction to kokanee salmon diets as very few kokanee are found to contain mysids in their guts or overlap spatially with *Mysis* for any length of time (Levy, 1991; Andrusak, 2000).

While population estimates for zooplankton in Okanagan Lake do not exist into the 1990s to my knowledge, zooplankton species counts were conducted and it is known that cladoceran species such as *Daphnia* and *Bosmina* did not completely disappear (J. Sawada, OLAP team member, pers. comm. 2000) after the introduction of *Mysis relicta* as has happened in other lakes (Byron *et al.*, 1986; Langeland *et al.*, 1991; Richards *et al.*, 1991).

While there has been no direct evidence in Okanagan Lake that mysids are involved in any form of eutrophication, levels of nitrate nitrogen have risen

slightly over the past 25 years since the mysid introduction while phosphorus and nitrogen loads to the lake have fallen dramatically (Jensen, 1999). However, there is some research to suggest that Okanagan Lake can become nitrogen-limited in the summer and is perhaps co-limited (nitrogen and phosphorus) in nutrients at this time of the year as well (Jensen, 1999; McEachern, 1999).

1.4 – Suggested Control Methods

Reiman and Falter (1981) stated that the "introduction and establishment of mysids in lakes is, in all likelihood, an irreversible action." However, since *Mysis relicta* has not always become a successful addition to fish diets, and has often had deleterious effects on zooplankton, fish and lake chemistry, there is much current research dedicated to the removal of mysids from introduced lakes.

One of the first pieces of research on methods to reduce mysid populations came from Nero (1983). Here the author describes the reduction of the mysid population in Lake 223 during a period of acidification. The pH levels for Lake 223 fell from 6.2 to 5.6 during the fall overturn of 1979. Obviously, acidification of other lakes to reduce mysid populations is not recommended due to the potential reduction of other pH sensitive species as well.

Manipulation of upwelling through the use of aeration systems has been suggested by Ken Ashley of the BC Ministry of Fisheries (Northcote, 1991) based on angler experiences with aeration systems in other lakes. Anglers tended to fish around aeration systems as lake trout seemed to congregate there, possibly to feed on macrozooplankton swept up in the upwelling current. Perhaps the

same principles could be applied to mysids. An aeration system on the bottom of a lake that delivers a plume of air bubbles 0.5 cm in diameter or greater could be capable of sweeping mysids from their daytime depths to the surface waters (Nothcote, 1991). Such mysids, stressed both thermally and by the turbulence would be easy prey for fish such as kokanee. However, the greatest issue with this suggestion is cost. In lakes over 100 m deep, the cost of pumping compressed air down to that depth become prohibitive. As well, upwelling areas would be very localized and mysids populations may evolve to avoid these areas altogether.

In small lakes, the extent, depth and sharpness of thermal stratification could be regulated by low cost circulation systems (Northcote, 1991). Perhaps this could extend the thermal refuge for zooplankters during the non-summer months. However, this method would only apply to very small lakes and none as big as Okanagan. As well, it has been noted that mysids can exceed 'thermal boundaries' as long as refuge from light is provided. Mysids in Okanagan Lake have often been reported right at the surface at night (Whall, 2000) and occasionally have been said to make the water look "as if its on fire" when a spotlight is shone on the surface (L. Granberg, mysid boat Captain, pers. comm. September 2001).

While biological control agents such as parasites or diseases have been suggested to control mysid populations, nothing has yet been found that is specific to *M. relicta* (Martinez and Bergersen, 1989). However, the introduction of a mysid predator, another exotic species introduction in order to take care of

the first one, has been more widely considered. The first candidate is the Alewife (*Alosa pseudoharengus*). Alewives are believed to be adapted to feed on vertically migrating mysids (Martinez and Bergersen, 1991; Johannson *et al.*, 1994). However, it is known that Alewives are efficient predators of more than just mysids and could cause adverse zooplankton composition shifts and eat other juvenile fish within the introduction lake (Martinez and Bergersen, 1991).

Another mysid predator candidate is the Arctic Char (*Salvelinus alpinus*). The benthic feeding, planktivorous Arctic Char are known to feed heavily on mysids, especially under winter ice conditions. They would seem a good introduction candidate except that the feeding habits of different populations of Arctic Char are known to vary widely. Some populations do not eat mysids at all (Martinez and Bergersen, 1991).

The final, and most promising candidate as a mysid predator introduction, is the Deepwater Sculpin (*Myoxcephalus thompsoni*). The Deepwater Sculpin appears to be restricted to deep cool lakes. This behaviour leads to low vagility and a decreased threat of dispersal. As well, the diet of this sculpin is known to consist almost entirely of *Mysis relicta* and therefore this fish would not effect other members of the lake community. Deepwater sculpins do have a minor diet of other benthic organism and so the threat of decreased benthic diversity is a possibility.

The control of lake trophic status is a topic of great consideration as well. In Lake Tahoe it was noticed that while the introduction effects of *Mysis relicta* in the main body of the lake were deleterious to the zooplankton community, the

more productive Emerald Bay was less affected by mysid introductions (Morgan *et al.*, 1978). Closer to Okanagan Lake, Kootenay Lake, BC has been the target of a large lake fertilization experiment which has resulted in lowered mysid abundance, higher cladoceran densities, and increased kokanee abundance (Ashley *et al.*, 1999b). However, the biggest impediments to such experiments are determining how much fertilizer should added (Northcote, 1991) and public perceptions of clean versus artificially fertilized waters (Andrusak, 2000).

1.5 – Mysid Fishery

While all the control possibilities mentioned above have been considered for Okanagan Lake, whether as serious possibilities or not, none of those methods were chosen to be implemented. Instead, it was felt that the best option available to the OLAP team, and one that the public might support, would be a selected fishery on *Mysis relicta* in order to reduce their numbers (Andrusak, 2000). A small-scale commercial fishery for mysids was attempted in the early 1990s in Pend Oreille Lake, Ohio, USA (Ashley and Shepherd, 1998). An individual who was fishing there provided the BC Ministry of Fisheries with sufficient information to begin trial fisheries here. Once a set of guidelines was established to minimize the by-catch of kokanee and other fish species, MELP decided to issue mysid fishing permits. Two permits were handed out in 1996 and by 1997 a commercial mysid fishery began on Okanagan Lake (Ashley and Shepherd, 1998). Currently two boats remain fishing on Okanagan Lake. Boat 1, Captained by Vince McGee, uses a classic beam trawl method to catch

mysids and has to haul each set onto the boat deck, sort manually, and then re-set again. As a result, only four sets can be made on an average night and catches are low (L. Granberg, mysid boat Captain, pers. comm. September 2001). Boat 2, Captained by Lee Granberg, uses a continuous fishing method that is set only once each night (there is a pump attached at the cod-end of the net which pumps the catch up to a second boat) and has the catch automatically sorted via a conveyor belt method. The catches of this boat have been much more positive, with maximum nightly catches of 910-1 364 kgs., and average nightly catches of 273-455 kgs. (personal observation). Mysids caught via this method are a prime product that is never crushed or thermally shocked and is quick frozen and sold as fish food to aquariums world-wide (L. Granberg, mysid boat Captain, pers. comm. September 2000).

1.6 – Study Objectives

1) To build an Ecopath model that reflects the status of Okanagan Lake in 1970 as accurately as possible with available data.

2) To use this base Ecopath model in Ecosim, the temporal-dynamic module of Ecopath with Ecosim (EwE) software, to portray the historical changes that have occurred in Okanagan Lake from 1970-2000 as accurately as possible. In this endeavour, both the kokanee salmon fishery (1970-1995) and the current mysid fishery (1997-2000) will be included.

3) To search for and include in the Ecosim model any relevant forcing functions that may increase the historical accuracy of this model.

4) Once an acceptable degree of historical accuracy is achieved, the Ecosim model will be extended beyond the year 2000 to try and assess the future state of Okanagan Lake and its fisheries. Particular attention will be paid to the current OLAP goal of rebuilding kokanee salmon stocks and as such a discussion regarding continued utility of the mysid fishery will be conducted.

5) Suggest and discuss alternate/concurrent possibilities that may further the OLAP goal of rebuilding kokanee salmon populations in Okanagan Lake.

Materials and Methods

2.0 – Introduction to the Ecopath Software

Ecopath is a software program that was initially created to estimate biomass and food consumption for functionally similar groups (one species or a collection of species with similar characteristics) within an aquatic ecosystem. A good overview of Ecopath and how to use it can be seen in Christensen and Pauly (1992) and Christensen *et al.* (2000). Ecopath emphasizes the analysis of trophic flows. This can be seen in Ecopath's two master equations, which describe production and consumption within a system. Ecopath Master Equation (I) is as follows (based on Edmonson and Winberg, 1971):

$$\text{Consumption} = \text{production} + \text{respiration} + \text{unassimilated food.} \qquad \ldots 1)$$

Ecopath sets a default value of 20% for unassimilated food (Winberg, 1956). However, this value is likely higher for herbivores and detritivores and can be

changed. Values for respiration are rarely entered and are usually estimated as the difference between the consumption, production and unassimilated food terms. Ecopath Master Equation (II) describes production with the system:

Production = fishery catches + predation mortality + biomass accumulation+ net migration + other mortality ...2)

Equation (2) can also be expressed as:

$$P_i = Y_i + B_i * M2_i + BA_i + E_i + P_i * (1-EE_i) \quad ...3)$$

where P_i is the total production of prey group (i), Y_i is the total fishery catch rate of (i), B_i is the biomass of group (i), $M2_i$ is the total predation rate of group (i), BA_i is the biomass accumulation rate of (i), E_i is the net migration rate (emigration – immigration) of group (i), $P_i * (1-EE_i)$ is the other mortality (unknown mortality due to disease, etc.) of group (i), and EE_i is the ecotropic efficiency of group (i) which is the fraction of group (i) that is used (consumed) within the system or taken out as fishery catch. Given that the total biomass of prey item (i) lost to predation, $B_i * M2_i$, can be re-expressed as:

$$\text{Total biomass of prey item (i) lost to predation} = \Sigma B_j * Q_j/B_j * DC_{ij} \quad ...4)$$

where Σ is the sum of all predators with item (i) in their diet, B_j is the biomass of predator group (j), Q_j/B_j is the consumption/biomass ratio of group (j), and DC_{ij} is

the fraction of prey item (i) in the average diet of predator (j). Thus equation (3) can be re-expressed as:

$$B_i * P_i/B_i * EE_i - \Sigma B_j * Q_j/B_j * DC_{ij} - Y_i - E_i - BA_i = 0. \quad \ldots 5)$$

Based on a system with *n* groups, *n* linear equations will be given and solved by the Ecopath software. Ecopath does not require a steady (static)-state model; rather biomass accumulation and emigration/immigration can all occur. On the other hand, Ecopath does assume overall ecosystem mass balance over an arbitrary period of time (usually one year). In a mass-balance equation such as equation (5), one unknown can be estimated for each group. All other information must be entered, although fishery catch (Y_i), net migration (E_i) and biomass accumulation (BA_i) terms are generally 0 for most groups. Therefore, in general, three of the remaining four parameters (plus the diet matrix) must be entered: biomass, P/B ratio, Q/B ratio and ecotrophic efficiency.

2.1 – Introduction to the Ecosim Module

Ecosim has been described in Walters *et al.* (1997). In Ecosim, the system of linear equations in (5) can be re-expressed as a system of differential equations. Under equilibrium, we have:

$$0 = B_i*(P/B_i) - F_i*B_i - M_o*B_i - \sum Q_{ij}; \quad \ldots 6)$$

where $B_i*(P/B_i)$ represents production of group (i), F_i*B_i represents fishery losses of group (i), M_o*B_i represents other mortality losses (ex. disease) of group (i) and $\sum Q_{ij}$ represents the total predation of group (i) by all predator groups (j). In order to turn equation (6) into a dynamic equation we need to replace the left side with a rate of biomass change dB_i/dt. As well, we need to provide a functional relationship for changes in primary production that takes into account competition for nutrients, light and space. Next, the static consumption estimates from equation (6) must be replaced by a functional relationship that will change with varying biomasses of predator and prey. Incorporating these changes gives us an equation of the form:

$$dB_i/dt = f(B) - M_o*B_i - F_i*B_i - \sum c_{ij}(B_i, B_j); \qquad \ldots 7)$$

where $f(B)$ is a function of B_i if (i) is a primary producer, otherwise $f(B) = g_i \sum c_{ij}(B_i, B_j)$ if (i) is a consumer, and $c_{ij}(B_i, B_j)$ is the function used to predict consumption from B_i and B_j. Given that reasonable equations for the functions above can be found, a system of dynamic equations such as equation (7) can be integrated with F_i varying in time to predict changes in group biomass. Biomass will be affected by changes in fishing and predation on any group and changes in food available to that group. Also, there will be indirect effects of fishing and predation on other groups which interact with the original group.

2.1.1 – Predicting Primary Production

The functional relationship provided for primary producers in Ecosim is a saturating production relationship of the form:

$$f(B_i) = r_i * B_i/(1+B_i * h_i); \quad \ldots 8)$$

where r_i is the maximum P/B that the primary producer can exhibit when biomass for the group is low (i.e., no limitation to production by biomass). When biomass is high, r_i/h_i is the maximum primary production rate for that group. Ecosim users must provide an estimate of the ratio between r_i and the base $(P/B)_i$ entered in Ecopath; r_i can then be computed from this ratio and h_i can be computed from Ecopath base estimates of biomass and production from the following equation:

$$h_i = [(r_i/(P/B)_i) - 1]/B_i. \quad \ldots 9)$$

The r_i to $(P/B)_i$ ratio has a default value of 2 in Ecosim.

2.1.2 – Predicting Consumption

Predation predictions are usually represented via the Lotka-Volterra assumption:

$$c_{ij}(B_i, B_j) = a_{ij} * B_i * B_j; \quad \ldots 10)$$

where a_{ij} is the instant mortality rate on (i) caused by one biomass unit of (j). a_{ij} is expressed as:

$$a_{ij} = Q_{ij}/(B_i*B_j). \quad \ldots 11)$$

This means that equation (10) does not account for processes such as predator satiation. This is usually not an issue as predators rarely reach this state in the wild. However, a more serious drawback of equation (10) is that predator-prey encounters are often connected with behavioural or physical mechanisms that limit the availability of prey to predators.

This is taken care of in Ecosim by assuming that each prey group has both an available and an unavailable component to each consumer. The available component, V_{ij}, may exchange with unavailable biomass via the equation:

$$dV_{ij}/dt = v_{ij}*(B_i - V_{ij}) - v_{ij}*V_{ij} - a_{ij}*V_{ij}*B_j. \quad \ldots 12)$$

Available biomass gains from the unavailable biomass pool at a rate v_{ij}. Biomass returns to the unavailable state at a rate $v_{ij}*V_{ij}$. Consumers may remove biomass from the available pool at a rate $a_{ij}*V_{ij}*B_j$. If we set $dV/dt = 0$, assuming equilibrium, we get:

$$V_{ij} = v_{ij}B_i/(2v_{ij}+a_{ij}*B_j). \quad \ldots 13)$$

At equilibrium, the consumption flow is predicted to vary with B_i and B_j as:

$$c_{ij}(B_i, B_j) = a_{ij}*v_{ij}*B_i*B_j/(2v_{ij}+a_{ij}*B_j). \quad ...14)$$

In Ecosim, if parameter estimates for v_{ij} and a_{ij} in equation (14) are needed, they can be obtained from the ratio of the maximum to the Ecopath base estimate of instantaneous mortality. Given this, the $ratio_{ij}$, v is then calculated from $ratio_{ij}*Q_{ij}/B_i$. Substituting this into equation (14) along with Ecopath estimates of Q_{ij}, B_i and B_j allows us to calculate a_{ij} as $2Q_{ij}*v_{ij}/(v_{ij}*B_i*B_j - Q_{ij}*B_j)$.

One should note here that equation (14) allows us to consider hypotheses of trophic structure as influenced by top-down and bottom-up control mechanisms. Setting low v_{ij} flow values corresponds to donor-controlled flow from prey to predator. High v_{ij} flow values leads to top-down control effects whereby trophic cascade effects may be seen.

2.2 – Area of Study

Okanagan Lake is a large oligotrophic lake in the Okanagan Drainage Basin located in the south-central interior of BC. It is one of four large lakes in the area that includes, from east to west, Kootenay, Arrow, Okanagan and Shuswap. All are deep lakes with a North-South axis. Okanagan Lake sits at an elevation of 345m, is 117km long, with an average width of 3.2km (Clemens *et*

al., 1939). The mean depth of the lake is 69.5m with a maximum depth of 232m (Clemens *et al.,* 1939).

2.3 – Ecopath Base Model: Okanagan Lake 1970

To begin, a small section of Thompson's (1999) thesis, which included an Ecopath model of Kootenay Lake, was used as a departure point for building this model. However, this model only had 13 groups, one of which (Bull Trout) does not exist in Okanagan Lake. As well, the Kootenay Lake model did not account for all biomass within the lake, thus violating the Ecopath assumption of mass balance. This Ecopath model of Okanagan Lake 1970 attempts to account for all biomass within the lake, includes 16 groups, and wherever possible uses independent input parameters other than ones from Thompson (1999). Details of the diets of each organism can be viewed in Appendix B.

2.3.1 – Upper Trophic Levels: Fish and *Mysis relicta*

Miscellaneous Fish (Deep Water).

This group consists of 4 species: rainbow trout, rocky mountain whitefish, eastern whitefish, fine-scaled sucker. All of these species were present during Clemens *et al.* (1939) survey and are presumed to be still present. While Rainbow trout is presumed to contribute 50% of the biomass of this group, Rocky Mountain Whitefish and Eastern Whitefish are presumed to contribute 20% of the biomass each, with the Fine-scaled Sucker making up the remaining

10%. As there are no direct biomass estimates for members of this group in Okanagan Lake, biomass was entered as 34% of the biomass of kokanee salmon. This is the approximately the same ratio of rainbow trout to kokanee as exists in Kootenay Lake (Thompson, 1999). Kokanee biomass estimates for Okanagan Lake are believed to be quite accurate.

Miscellaneous Fish (Deep Water) is split into two groups, adult and juvenile. Input parameters for the adult group are as follows:

- Biomass = 1.370 t/km^2;
- Q/B = 1.990 year^{-1} which was calculated for each species in Fishbase (2000) using an empirical regression model described in Pauly (1989). The result is a weighted average.
- P/Q = 0.182; Thompson (1999) for rainbow trout.

Input parameters for the juvenile group:

- Biomass = 0.130 t/km^2; calculated as the same ratio of adult to juveniles as Kokanee group;
- Q/B = 4.57 year^{-1};
- P/Q = 0.3; presumed similar to Johnston *et al.* (1988) for kokanee juveniles.

Kokanee Salmon (*Oncorhynchus nerka*).

Kokanee salmon were incorporated into this model as a split group, adult (age 1-3) and juveniles (age 0+). Biomass was calculated from abundance estimates obtained from Carl Walters (1995), average length at age data (Sebastian and Scholten, 1998) and length-weight relationship (Fishbase, 2000).

Adult (age 1-3) group:

- Biomass = 3.977 t/km^2;
- P/B = 0.710 year^{-1} (Sandercock, 1969);
- Q/B = 3.700 year^{-1} (Fishbase, 2000; Pauly, 1989);
- Recreational Fishery Catch (1970) = 0.090 t/km^2 (Walters, 1995).

Juvenile (age 0+) group:

- Biomass = 0.390 t/km^2;
- Q/B = 8.500 year^{-1} (Foerster, 1968);
- P/Q = 0.300 (Johnston *et al.,* 1988).

Opossum Shrimp (*Mysis relicta*).

Mysis relicta was incorporated into the model as a single-species split group. Historical biomass estimates for this group in Okanagan Lake are generally lacking. However, both the original biomass introduced to the lake (Sparrow *et al.*, 1964) and recent biomass estimates from 1989 through to the year 2000 (McEachern, 1999) are available. Therefore, linearly extrapolating from 1966 to 1989, the average biomass accumulation per year term can be

estimated. 1970 biomass, as entered into the base Ecopath model, was not taken from this linear extrapolation. Instead, the 1970 mysid biomass was estimated assuming an exponentially growing population. This was done as mysid populations have been known to take many years to become 'established' in any given lake (Sparrow *et al.*; Lasenby *et al.*, 1986). Mysids do not appear in fish stomachs or in lake sampling for years after introduction and then suddenly their populations explode within the lake. Therefore it was thought that mysid populations may grow slowly during the first few years before rapidly increasing in abundance. Input parameters for the adult mysid group include:

- Biomass = 0.240 t/km^2;
- P/B = 2.659 year^{-1} (Stockwell and Johannsson, 1997);
- Q/B = 18.250 year^{-1} (Langeland *et al.*, 1991);
- Biomass Accumulation = 0.187 t/km^2;
- Mysid Catch= 0.029 t/km^2; even though no mysid catch existed in 1970, a small number had to be entered so that the mysid fishery could later be manipulated in Ecosim.

Input parameters for the juvenile mysid group:

- Biomass = 0.053 t/km^2, i.e., 22% of adult biomass (Thompson, 1999);
- Q/B = 25.0 year^{-1}, estimated to be higher than that of adult group;
- P/Q = 0.221 (Chess and Stanford, 1999).

Miscellaneous Fish (Near Shore).

The near surface distinction for this group refers to near surface/near shore fish. This group, much like Miscellaneous Fish (Deep Water), is a multi-species split group. There are 9 species within this group: Coarse-scaled Sucker (*Catostomus macrocheilus*), Carp (*Cyprinus carpio*), Lake Shiner (*Richardsonius balteatus*), Squawfish (*Ptychocheilus oregonensis*), Chub (*Mylocheilus caurinus*), Long-nosed Dace (*Rhinichthys cataractae*), Sculpin (*Cottus asper*), burbot (*Lota lota*) and silver-grey minnow (*Apocope falcata*). Each member of this group was presumed to contribute 13% of the biomass of the group (except for long-nose dace which constituted only 5% and the silver-grey minnow which accounted for 4%). The biomass of this group, and all other groups of lower trophic level, was left to be estimated by Ecopath. All input entries for this group are the result of a weighted average of the data available for all 8 species within the group. Input parameters for adult group:

- P/B = 0.646 $year^{-1}$ (Fishbase, 2000; Pauly, 1980);
- Q/B = 3.304 $year^{-1}$ (Fishbase, 2000; Pauly, 1989);
- Ecotropic Efficiency (EE) = 0.650, set higher than that of kokanee.

Input parameters for juvenile group:

- Q/B = 7.590 $year^{-1}$, calculated to produce the same adult/juvenile Q/B ratio as that of kokanee;
- EE = 0.850, must be higher than that of adult group;
- P/Q = 0.300 (Johnston *et al.*, 1988) for kokanee 0+.

2.32 – Lower Trophic Levels: Insect Larvae, Zooplankton & Phytoplankton

Midge larvae.

Midge larvae is a multispecies group consisting of *Chironomus, Cryptochironomus, Orthocladius, Polypedilum,* and *Tanytarusus* larvae. It was included as it was recognized that these larvae were an important food item in the diet of the Miscellaneous Fish groups (Clemens *et al.,* 1939; Johnston *et al.*, 1999). The diet composition of these species was taken from descriptions of diet in Merritt and Cummins (1978), and turned into relative amounts that were averaged over the 5 species.

- Q/B = 30.0 $year^{-1}$, assumed to be at least higher than that of *Mysis relicta* juvenile group;
- EE = 0.700;
- P/Q = 0.143, similar to value for *Daphnia* group.

Aquatic Insect larvae.

Like midge larvae, this is a single group consisting of multiple species. There are three species of caddis fly, one species of dragonfly, two species of mayfly and two species of water mite (details in Appendix A). Reasons for inclusion into the model and input parameters are the same as for midge larvae. Diet composition does differ from midge larvae, but comes from the same source (Merritt and Cummins, 1978).

Copepods.

This group consists of three species: *Cyclops, Diaptomus,* and *Epischura*.

- P/B = 18.250 year^{-1} (Langeland, 1982);
- P/Q = 0.143 (Thompson, 1999);
- EE = 0.498 (Thompson, 1999).

Cladocerans.

As *Daphnia* is a separate group, the cladocerans are represented by *Bosmina* in this model.

- P/B = 47.500 year^{-1} (Langeland, 1982);
- P/Q = 0.143;
- EE = 0.757 (Thompson, 1999).

***Daphnia*.**

Daphnia was modelled as a separate group from Cladocerans as it has been shown that this zooplankter may undergo dramatic changes in lakes where *Mysis relicta* was introduced (Lasenby *et al.*, 1986; Koksvik, 1991; Langeland *et al.*, 1991; Northcote, 1991; Spencer, 1999). Therefore, as a separate group, more attention can be attributed to its dynamics in Ecosim simulations.

- P/B = 47.500 year^{-1} (Langeland, 1982);
- P/Q = 0.143;
- EE = 0.794 (Thompson, 1999).

Rotifers.

Here, the Rotifers are a single group consisting of five species, the most abundant of which is believed to be *Notholca longispina* (Clemens *et al.*, 1939).

- P/B = 50.000 year^{-1}, assumed to be higher than that of *Daphnia* group;
- P/Q = 0.099;
- EE = 0.553 (Thompson, 1999).

Phytoplankton.

Phytoplankton is the last planktonic group. As a primary producer, P/Q values are not considered.

- P/B = 150.0 year^{-1}, Thompson (1999) estimated P/B to be 113 for the 6 month summer growing period, and it was here assumed that whole year P/B would not be much higher;
- EE = 0.553 (Thompson, 1999).

Detritus.

A detritus group must be included in the model to account for all dead material within the lake. As well, it is an important food item for *Mysis relicta* (Whall, 2000) and both groups of insect larvae (Merritt and Cummins, 1978).

2.4 – Balancing the Ecopath model

Ten functional groups were originally identified to be included in the Okanagan Lake model from Thompson (1999). Groups that were added to the

original ten include: Miscellaneous Fish (deep water), Miscellaneous Fish (near shore), midge larvae, and Aquatic Insect larvae. The groups that were added later were added not only to deal with balancing the model, but to also meet the requirement that the modeller should attempt to account for all biomass within the system. Once this requirement was met, problems arose with the high mortality of *Daphnia* due to a very large kokanee biomass in 1970 and high mysid biomass later on. Splitting the zooplankton groups into near surface and deep water groups solved these problems immediately by providing a refuge for zooplankton groups. However, this solution is biologically unrealistic for Okanagan Lake as all planktonic groups intermix. As well, these spatially split groups would make the eventual exploration of nutrient addition in Ecosim difficult, as each split group consisting of the same species would react differently to nutrient addition. There is no plausible reason for them to do so in nature. Circular arguments regarding spatial hypotheses would also arise if the groups were split in the manner described above. For example, if a refuge is created where some prey items were safe from their predators, then intense fisheries and/or nutrient additions could be added to the model which would not affect those inside the refuge area or *vice versa*. Therefore, the split in the plankton groups was removed. Fortunately as more data independent from Thompson's (1999) model was added, this model began to balance itself. Here is a list of some other specific changes that were made to the original model.

Miscellaneous Fish (Deep Water).

When this group was first added, it was not split into adult and juvenile groups. When the split was added, all components of this group's diet that was near shore was transferred to the juveniles and all components considered as deep water remained in the adult diet. This is justified as juvenile species of fish tend to stay near shore where there are more hiding places and camouflage than in open water.

Kokanee (age 1-3) and (age 0+).

As kokanee biomass was high and *Mysis relicta* biomass was low in 1970, it was necessary to remove *Mysis relicta* from the diet of kokanee in this 1970 model. It is likely that kokanee were not feeding on mysids at all in 1970 as it is known that mysids often do not appear in fish stomachs until decades after introduction (Sparrow, 1964; Lasenby, 1991; Nesler and Bergersen, 1991). The lack of mysids in kokanee diet resulted in the raising of the dietary contributions of Copepods, Cladocerans and *Daphnia* to kokanee.

***Mysis relicta* (adult) and (juvenile).**

Many changes were made to this group compared to Thompson (1999). To begin, it was known that mysid biomass increased since its introduction to a year 2000 biomass of 1 000 metric tonnes. This leads to a biomass accumulation term of 0.187 $t*km^{-2}year^{-1}$. A significant change to mysid diet occurred when detritus was added as an item. According to Whall (2000), the

diet of mysid adults contain 22.5% detritus while mysid juveniles may include 35% detritus in their diet. While the 22.5% detritus diet value was used for the adult group, 25.4% detritus was entered for mysid juveniles. The lower percentage used for the juvenile group is due to the inclusion of phytoplankton into the mysid juvenile diet. Gossnickle (1982) stated that mysid juveniles depend almost entirely on phytoplankton for the first 3-4 months of their lives. Therefore a phytoplankton diet contribution of 28.6% was entered.

2.5 – Ecosim Model: Okanagan Lake 1970-2020

While the basis of how Ecosim works was presented earlier, this section will include details on the length of the model run, the linkage of juvenile and adult groups, top-down versus bottom-up flow control, the forcing function used, and which groups it was applied to.

The Ecosim model was set to run for 50 years, from 1970 through 2020, mainly because data existed for kokanee abundance and fishery catches during 1970-1995 (Walters, 1995) and for the mysid catch from 1997 to 2000 (Ashley and Smith, 1999; S. Matthews, MELP, pers. comm. March 2001).

The juvenile-adult groups linked together in Ecosim include Miscellaneous Fish (Deep Water), Kokanee (age 1-3) and (age 0+), *Mysis relicta* (adult) and (juvenile), and Miscellaneous Fish (Near Shore). All groups were assumed to mature from the juvenile group to the adult group after 1 year.

Flow control is expressed on a scale of 0 to 1, where 1 is extreme top-down control and 0 is extreme bottom-up control. In general, lower trophic levels

are more bottom-up controlled, while the highest trophic levels apply top-down pressure (McQueen *et al.*,1986). Flow control was entered for each organism as follows: Rotifers (0.10), *Daphnia* and Cladocerans (0.15), Copepods (0.20), Aquatic Insect larvae and midge larvae (0.25), Miscellaneous Fish (near shore) (0.40), Miscellaneous Fish (Deep Water) and Kokanee Salmon (0.50), *Mysis relicta* (1.00). A value for one was entered for *Mysis relicta* as it was thought that no prey items are unavailable to mysids over an entire year. As well, it is known that mysids are voracious predators that can quickly alter lake community structure (Chess and Stanford, 1999).

The only other changes made to the Group Information section from EwE default parameters included *Mysis relicta* and the fraction of 'other mortality' due to changes in feeding time as well as 'predator effect on feeding time' for the near shore Miscellaneous Fish groups (Table 1). The fraction of 'other mortality' due to changes in feeding time is the portion of unexplained natural mortality that is sensitive to changes in feeding time (default value = 1). As the density of a group increases, it generally needs to increase its feeding time in order to maintain food consumption rates. Increased feeding time can lead to a higher mortality rates due to increased exposure to predation. Setting a value of zero for this function allows 'other mortality' to remain constant even in groups that achieve high density. Predator effect on feeding time allows for a group's feeding time to be reduced by up to this factor if predators are present in large numbers (default value = 0). This allows a group to limit its exposure to predators.

Table 1. Changes from default values in Group Info section of Ecosim.

Group	Predator effect on feeding time	Fraction of other mortality	Rationale
Mysis relicta (adult)	-	0	-diel vertical migration allows avoidance of predators.
Mysis relicta (juvenile)	-	0	-juveniles are translucent and cannot be seen by predators.
Misc. Fish (near shore; adult and juvenile)	0.5	-	-when predator numbers are high, will stick close to shore.

The forcing function used can be seen in Table 2 and represents the phosphorus load to Okanagan Lake from 1970 to 1995. From 1995 to 2020 it was presumed that loading to the lake would not change dramatically. This information was obtained from Forty (1996) and Jensen (1999) and includes phosphorus loads from Forestry, Agriculture, septic tank leakage, and municipal sewage treatment plants. However, information was not provided for most groups between 1970-1980 and 1980-1990. Therefore, the forcing function was linearly extrapolated between the known points. The forcing function expresses the annual phosphorus load to the lake into values relative to the 1970 phosphorus load. While it was mentioned earlier that Okanagan Lake is probably both nitrogen and phosphorus limited, phosphorus and nitrogen loadings to the lake should have decreased at the same rate. Therefore, using phosphorus loadings as a forcing function for the lake is justifiable.

Forcing functions in Ecosim are applied to the mass action term, i.e., to a factor proportional to consumption. The above forcing function was applied to every group and its consumption of phytoplankton. This essentially results in

Table 2. Phosphorus loads to Okanagan Lake 1970-1995 and corresponding Ecosim Forcing Function.

Year	Forestry ($kg*10^3$)	Agriculture ($kg*10^3$)	Septic ($kg*10^3$)	Sewage ($kg*10^3$)	Total P ($kg*10^3$)	Forcing Function (relative values)
1970	80.0	72.0	68.0	43.2	263.2	1.000
1971						0.954
1972						0.908
1973						0.862
1974						0.816
1975						0.770
1976						0.724
1977						0.678
1978						0.632
1979						0.586
1980	52.0	42.0	33.0	14.9	141.9	0.539
1981						0.519
1982						0.499
1983						0.479
1984						0.459
1985						0.439
1986						0.419
1987						0.399
1988						0.379
1989						0.359
1990	35.0	26.0	23.0	5.0	89.0	0.338
1991	36.0	27.0	23.0	6.9	92.9	0.353
1992	37.0	28.0	24.0	7.9	96.8	0.368
1993	31.0	21.0	19.0	1.4	72.4	0.275
1994	30.0	21.0	19.0	2.6	72.6	0.276
1995	29.0	21.0	19.0	2.3	71.3	0.271

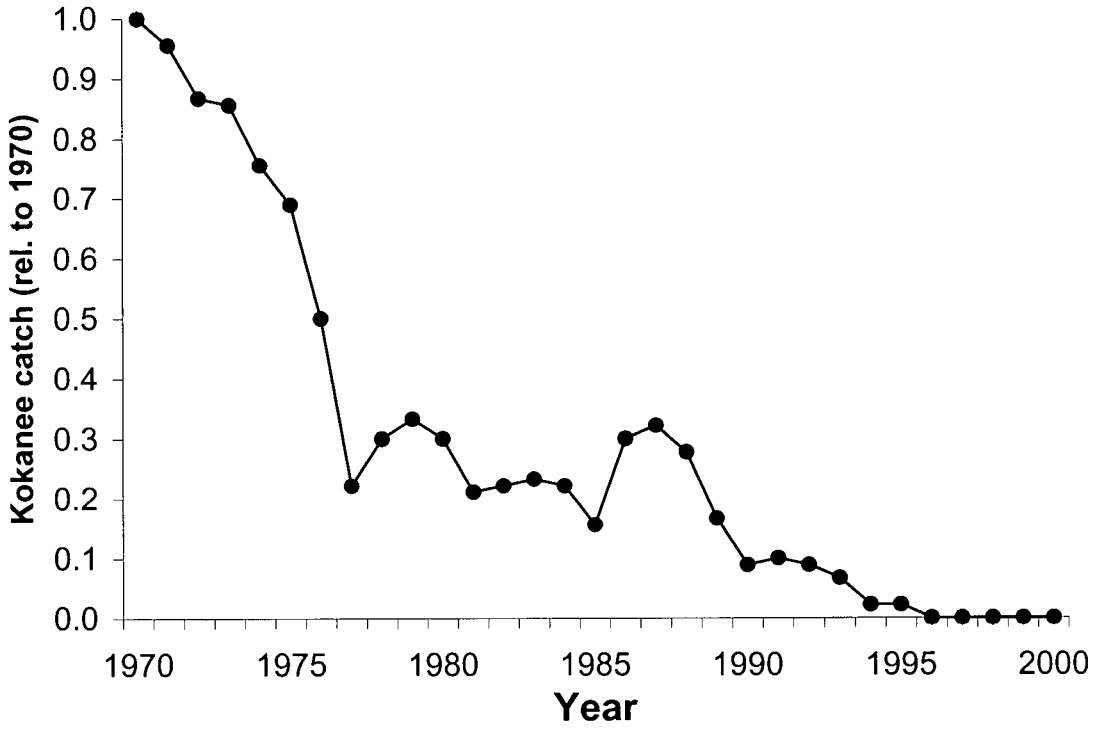

Fig. 1. Kokanee fishery data entered into ECOSIM. All values relative to 1970.

affecting the edibility of phytoplankton for each group in the model. It is known that nitrogen limitation to a lake can cause forms of inedible algae to predominate. Therefore, lowering the edibility of phytoplankton at the rate at which nutrient loads to the lake were lowered is seen as justifiable.

Two fisheries data series were entered into the model as well. One was the recreational kokanee fishery based on data from Walters (1995; fig. 1), while the other was the mysid catch based on Ashley and Smith (1999) and S. Matthews (MELP, pers. comm. March 2001). The recreational kokanee in 1970 was approximately 32 t and the fishery was closed in 1995. This Fishery was presumed to stay closed for the rest of the run of the model. The mysid fishery was not allowed to start until the experimental mysid fishery was begun by OLAP in 1997. The mysid catch was then allowed to grow to the 2000 30 t catch and was held at this level for the base runs of the Ecosim model.

2.6 – Nitrogen Ecopath Model

This model takes a closer look at nitrogen in Okanagan Lake. An Ecopath nitrogen model of Okanagan Lake will allow for the determination of whether the lake is nitrogen-limited or not. If it is, then the amount of nitrogen that is needed in order to balance the lake can be quantified. These answers are needed if there is to be any serious discussion of nutrient limitation and nutrient additions into Okanagan Lake.

The nitrogen based Ecopath model has all of the same groups as in the wet-weight Ecopath model except for two: bacteria, which were added to re-

mineralize nitrogen from the sediment and surrounding water, and Detritus (dissolved in water) which was added to create a pool of available nitrogen in the water column as opposed to Detritus (sediment). The nitrogen model is also different from the wet-weight model in that it reflects conditions in 2000, not 1970. To begin, the 1970 EwE wet-weight model was run in order to predict the biomasses of all groups in the 2000. These biomass values were used and then transferred to their respective nitrogen weights (units: mgN/m^2). This was accomplished by either transferring the groups wet-weight to dry weight, determining the group's protein weight from the dry weight and finally the nitrogen weight from the group's protein weight. However, for some groups wet-weight to protein weight conversion factors were available, allowing the dry weight conversion to be skipped (See Appendix C for details and references).

When creating the nitrogen based Ecopath model both the diet composition and P/B values were kept the same as in the 1970 wet-weight model. Each group would still be eating the same relative proportions of other groups and production relative to mass, whether of wet-weight or nitrogen, should remain the same. However, Q/B values needed to be altered. This is because each group had different wet-weight to nitrogen weight conversion factors applied to them. Therefore, each group's consumption of all other groups in its diet composition had to be transferred to consumption in nitrogen weight from consumption in wet-weight. Again, this is different for every item in a group's diet resulting in different consumption values relative to nitrogen biomass (see Appendix D for details).

The two added groups to the nitrogen model (bacteria and Detritus (water)) had no biomass values from the Ecosim model and these therefore, had to be estimated. As no groups were made to directly eat the bacteria group, Ecopath could not estimate its biomass. Instead biomass of bacteria was estimated by taking the Carbon biomass of bacteria per litre from another meso-oligotrophic lake (Lake Plusseee, Germany; Overbeck *et al.*, 1994). This was then transferred into N biomass assuming a 40C:7N weight ratio (see Appendix E for details) resulting a bacterial biomass of 36.418 mgN/m^2. Detritus (water) biomass was able to be estimated by Ecopath because phytoplankton, which became a consumer in this model, fed directly on this nitrogen source.

Next the flow of nitrogen to and from the Detritus (water) and Detritus (sediment) pools had to be determined. This was done by considering the respiration, mortality and excretions (all in units of mgN/m^2). Respiration was determined by calculating the production and consumption values for each group and subtracting one from the other. Recall equation (1) from the Ecopath section that when production and consumption are subtracted from each other, respiration and unassimilated consumption is left. However, unassimilated consumption (essentially excretion) was calculated separately from published excretion values, or experimentally determined as in the case of *Mysis relicta*. Total mortality was calculated from P/B values used in the Ecopath model. This is justified in Pauly (1980) as production should equal total mortality in any mass balance situation. Total mortality values were transferred into percent mortality values by using the formula:

$1\text{-}e^{(-z)}$, ...15)

where Z is the total mortality value and e is the basis of the natural logarithm, i.e., 2.72. This then allowed the quantification of the contribution of dead bodies (total mortality-consumption-fishery catch = dead bodies) in mgN/m^2 to the system. Once respiration, mortality and excretion were calculated for each group it was decided that respiration and 70% of excretion would flow to the Detritus (water) nitrogen pool. The remaining 30% of excretion and all of the dead bodies would flow to the Detritus (sediment) nitrogen pool. This was applied to all groups except *Mysis relicta* as summer mysid excretion experiments were to be carried out to better quantify these values.

2.6.1 – Upper Trophic Levels: Fish and *Mysis relicta*

Miscellaneous Fish (Deep Water).

This group consists of same 4 species in the same proportions as in the Ecopath wet-weight model. Miscellaneous Fish (Deep Water) is split into two groups, adult and juvenile. Input parameters for the adult group are as follows:

- Biomass = 0.265 mgN/m^2;
- Q/B = 1.458 $year^{-1}$ which was calculated for each species in Fishbase (2000) using a regression described in Pauly (1989). The result is a weighted average of Q/B values for the 4 species in this group;
- P/Q = 0.182; recalculated to keep P/B value the same as in the wet-weight model;

- Detritus fate: 0.771 (water), 0.229 (sediment).

Input parameters for the juvenile group:

- Biomass = 0.038 mgN/m^2;
- Q/B = 1.916 $year^{-1}$;
- P/Q = 0.300;
- Detritus fate: 0.764 (water), 0.236 (sediment).

Kokanee Salmon (*Oncorhynchus nerka*).

Adult (age 1-3) group:

- Biomass = 10.235 mgN/m^2;
- P/B = 0.710 $year^{-1}$ (Sandercock, 1969);
- Q/B = 1.499 $year^{-1}$;
- Detritus fate: 0.711 (water), 0.289 (sediment).

Juvenile (age 0+) group:

- Biomass = 10.235mgN/m^2;
- Q/B = 3.464 $year^{-1}$;
- P/Q = 0.300;
- Detritus fate: 0.785 (water), 0.215 (sediment).

Opossum Shrimp (*Mysis relicta*).

In the year 2000, a significant mysid fishery existed in Okanagan Lake, capturing approx. 30 t of *Mysis relicta.* This was incorporated into the model by re-expressing this wet-weight catch value as nitrogen weight. The input parameters for the adult group were:

- Biomass = 48.735 mgN/m^2;
- P/B = 2.659 $year^{-1}$ (Stockwell and Johannsson, 1997);
- Q/B = 14.855 $year^{-1}$;
- Mysid Catch = 1.471 mgN/m^2;
- Detritus fate: 0.850 (water), 0.150 (sediment).

Input parameters for the juvenile mysid group:

- Biomass = 7.542 mgN/m^2;
- Q/B = 19.867 $year^{-1}$;
- P/Q = 0.221;
- Detritus fate: 0.872 (water), 0.128 (sediment).

Miscellaneous Fish (Near Shore).

This group contains the same species in the same proportions as in the wet-weight Ecopath model. Input parameters for the adult group:

- Biomass = 13.994 mgN/m^2;
- P/B = 0.646 $year^{-1}$ (Fishbase, 2000; Pauly, 1980);

- Q/B = 1.733 $year^{-1}$;
- Detritus fate: 0.698 (water), 0.302 (sediment).

Input parameters for juvenile group:

- Biomass = 0.557 mgN/m^2;
- Q/B = 3.886 $year^{-1}$;
- P/Q = 0.300;
- Detritus fate: 0.755 (water), 0.245 (sediment).

2.62 – Lower Trophic Levels: Insect Larvae, Zooplankton and Phytoplankton

Midge larvae.

This group contains the same species in the same proportions as in the wet-weight Ecopath model. Input parameters are as follows:

- Biomass = 4.389 mgN/m^2;
- Q/B = 24.655 $year^{-1}$;
- P/Q = 0.143;
- Detritus fate: 0.784 (water), 0.216 (sediment).

Aquatic Insect larvae.

This group contains the same species in the same proportions as in the wet-weight Ecopath model. Input parameters are as follows:

- Biomass = 12.230 mgN/m^2;

- Q/B = 23.173 $year^{-1}$;
- P/Q = 0.143;
- Detritus fate: 0.778 (water), 0.222 (sediment).

Copepods.

This group contains the same species in the same proportions as in the wet-weight Ecopath model. Input parameters are as follows:

- Biomass = 14.399 mgN/m^2;
- Q/B = 18.250 $year^{-1}$;
- P/Q = 0.161;
- Detritus fate: 0.893 (water), 0.107 (sediment).

Cladocerans.

The Cladocerans are still represented by *Bosmina* only, as *Daphnia* was modelled as a separate group.

- Biomass = 3.341mgN/m^2;
- P/B = 47.500 $year^{-1}$ (Langeland, 1982);
- P/Q = 0.157;
- Detritus fate: 0.947 (water), 0.053 (sediment).

***Daphnia*.**

Input parameters are as follows:

- Biomass = 4.622 mgN/m^2;

- P/B = 47.500 $year^{-1}$ (Langeland, 1982);
- P/Q = 0.153;
- Detritus fate: 0.947 (water), 0.053 (sediment).

Rotifers.

Input parameters are as follows:

- Biomass = 7.121 mgN/m^2;
- P/B = 50.000 $year^{-1}$;
- P/Q = 0.101;
- Detritus fate: 0.965 (water), 0.035 (sediment).

Phytoplankton.

Phytoplankton is the last planktonic group. As it is no longer a primary producer, but now a consumer in the system, P/Q values needed to be entered.

- Biomass = 107.400 mgN/m^2; since phytoplankton rose by 84% during the 1970-2000 period, but the edibility of phytoplankton dropped to 27% of 1970 levels, the remaining edible phytoplankton (and nitrogen using portion) is 50% of the total phytoplankton estimated to be in Okanagan Lake (blue-green can assimilate N from the air).
- P/B = 150.000 $year^{-1}$, Thompson (1999);
- P/Q = 0.080; following pattern of lower P/Q values with falling trophic level;
- Detritus fate: 0.960 (water), 0.040 (sediment).

Bacteria.

Bacteria was added as a group that could re-mineralize nitrogen back into the system that would other wise be trapped in the Detritus (sediment).

- Biomass = 36.418 mgN/m^2; (Overbeck *et al.*, 1994) estimated by taking the Carbon biomass of bacteria per litre from the German meso-oligotrophic Lake Plusssee and assuming a 40C:7N weight ratio;
- P/B = 150.0 $year^{-1}$, Thompson (1999);
- P/Q = 0.080; following pattern of lower P/Q value with lower trophic status;
- Detritus fate: 0.330 (water), 0.670 (sediment) (Overbeck *et al.*, 1994).

Detritus (water) and (sediment).

As Detritus is a non-living group, production and consumption values were not necessary. Biomass was allowed to be estimated by Ecopath.

2.7 – Mysid Nitrogen Excretion Experiments

The purpose of this field experiment was to determine whether the net effect of *Mysis relicta*, feeding on zooplankton in near surface waters at night and then descending during the day to feed on detritus, is to remove nitrogen from near surface waters or to add nitrogen to these waters. It is known that Okanagan Lake can become nitrogen-limited during certain times of the year (July-October; Ashley *et al.* 1999) and therefore, in the wake of the government's plan to increase mysid fisheries, it would be beneficial to know

whether mysids are adding to or helping to prevent near surface nitrogen limitation.

Research was conducted during the night in the summer of 2001 aboard Boat 2 (previously mentioned in the introduction) captained by Lee Granberg on four separate dates: July 11-12, August 5-6 and 19-20, and September 23-24. As light is known to affect mysid behaviour, research was conducted on nights which had different moon phases. July 11-12 was the night before the first half moon, August 5-6 was the night after a full moon, August 19-20 was the night after the new moon, and September 23-24 was the night before the second half moon.

Materials used aboard the mysid fishing vessel included:

- 1 x 70cc Toomey syringe;
- 6 x 500ml Erynlmeyer beaker;
- 0.45 micrometer Sartorius filters;
- 6 x 500ml plastic water storage bottles;
- 3 x mercury thermometers;
- 1 x Coleman 54 quart steel cooler;
- 1 x Igloo 54 quart plastic cooler;
- 1 x Igloo 10 quart plastic cooler.

The methods used aboard Boat 2 were similar to those found in Madeira *et al.* (1982). Collection of mysids, however, differed from previous experiments. Boat 2 uses a continuous fishing method with a pump attached at the cod-end. This pumps mysids, along with the feeding depth water, up to a basin where mysids are forced into a net on a conveyor system which sorts the catch.

However, *Mysis relicta* was collected before the conveyor and in the basin of feeding depth water by submerging a small plastic cooler in the basin and allowing the mysids to flow into the cooler. Mysids were collected at the beginning, middle and end of its feeding period on each sampling night. Excretion experiments began within 30 minutes after capture. 30 mysids were picked from cooler with a 70cc Toomey Syringe and placed in 500 ml beaker which contained autoclaved water (Okanagan Lake water from the previous night) chilled to:

- feeding depth temperature for mysids caught at beginning and middle of feeding period;
- 4 degrees Celsius (lake bottom temperature) for mysids caught at end of feeding period.

Mysids were kept at feeding depth temperature by partially filling the 54 quart Igloo cooler with water from mysid feeding depth. This water placed into the cooler at least 20 min. prior to adding the containers of mysids and replaced between each trial. The Coleman steel cooler was kept at close to 4 degrees Celsius by adding two blocks of ice to the cooler by dusk on the evening experimental trials were to be conducted. This cooler was kept sealed until needed. The 500 ml beaker containing mysids was agitated to obtain a homogeneous mixture. The water without mysids was decanted off into a small water collection bottle for a control sample. The beaker with mysids contained 150 ml water and was kept for 2 hours in dark, insulated coolers (insulated at

either lake bottom temperature or feeding depth temperature depending on sample; control samples were treated identically). All experimental beakers were sealed twice over with saran wrap. For the cooler kept at feeding depth temperature, beakers containing mysids were taped to the side of the cooler and allowed to float in the feeding depth temperature water. At the end of the experimental time, a portion of the control and 150 ml of the experimental waters were filtered through 0.45 micrometer (Sartorius) filters. The filtered water was then stored at 4 degrees Celsius and was analyzed within 12 hours of collection. Collected water was analyzed for ammonia (via the phenate method described in Mackereth *et al.*, 1978) and urea (via the method described in Newell *et al.*, 1967) at the Okanagan University College (Vernon Campus) by Patricia Baird, an OUC chemistry staff member with over 25 years experience in the field. All glassware used in this experiment was washed with acid between experimental dates.

Results

3.0 – Ecosim Results: 1970-2000

From the results in Table 3, it can be seen that Ecosim was quite successful in running the Okanagan Lake system from its state in 1970 to 2000, including tracking kokanee and *Mysis relicta* quite well. Kokanee ended the run at a biomass equal to only 7% of its 1970 biomass. Kokanee salmon are known to have fallen to about 10% of 1970 levels (Walters, 1995; Ashley *et al.,* 1998). *Mysis relicta* (adult) can be seen to have reached a biomass of 2.627 t/km^2 (925

metric tonnes) which is very close to its estimated year 2000 biomass of 1 000 metric tonnes (S. Matthews, MELP, pers. comm. March 2001).

Table 3. Biomass at start and end of Okanagan Lake 1970 ECOSIM run.

Group Name	Biomass (1970) (t/km^2)	Biomass (2000) (t/km^2)	Biomass (end/start)
Adult Misc. Fish (deep water)	1.370	0.007	0.01
Juv. Misc. Fish (deep water)	0.130	0.001	0.01
Kokanee (1-3)	3.976	0.269	0.07
Kokanee (0+)	0.389	0.025	0.07
Mysis relicta (adult)	0.284	2.627	9.24
Mysis relicta (juv)	0.057	0.486	8.48
Adult Misc. Fish (near shore)	0.227	0.450	1.98
Juv. Misc. Fish (near shore)	0.010	0.018	1.80
Midge larvae	0.181	0.269	1.48
Aquatic Insect larvae	0.514	0.774	1.51
Copepods	1.468	0.908	0.62
Cladocerans	0.205	0.225	1.10
Daphnia	0.779	0.294	0.38
Rotifers	0.463	0.513	1.11
Phytoplankton	8.642	15.914	1.84
TOTAL	18.696	22.780	1.22

Figures 2 and 3 illustrate how the Ecosim program tracked the historical biomass changes in kokanee and *Mysis relicta*. The circles in Figure 2 represent a linear interpolation of mysid biomass from 1970 to 1989. The linear interpolation was added simply for reference points. As can be seen from Figure 2, mysid biomass actually grew exponentially and not linearly , as may be expected. The linear interpolation ends at 1989 as McEachern (1999) stated that

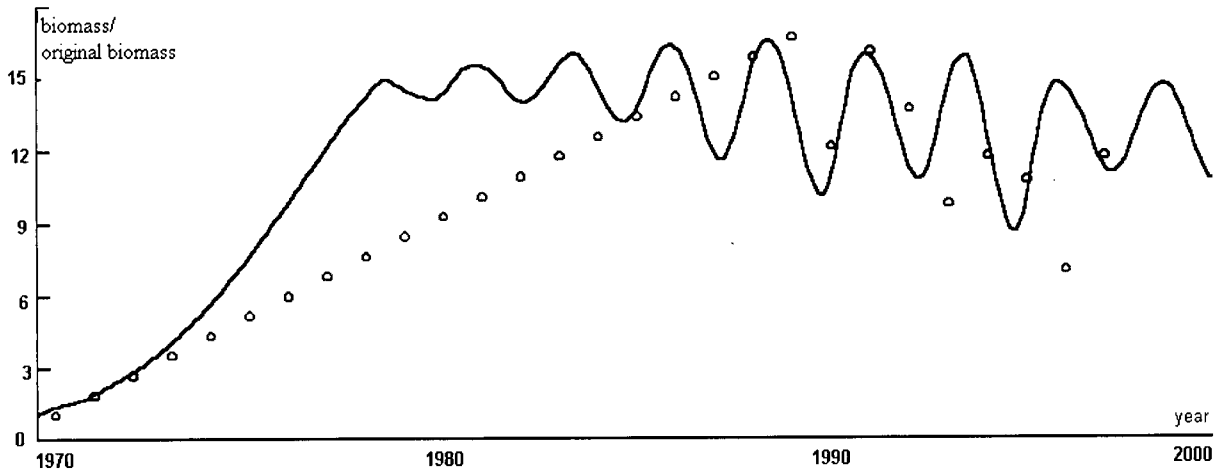

Fig. 2. Ecosim run for Okanagan Lake 1970-2000 (*Mysis relicta* (adult)). Circles represent historical biomass (linear extrapolation from 1970-1989 and historical data from 1989-2000; McEachern, 1999).

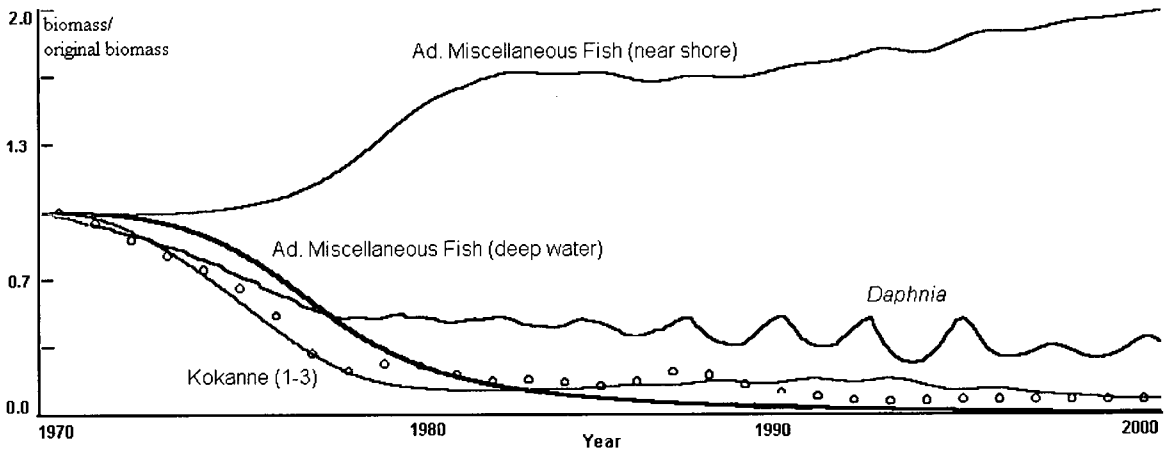

Fig. 3. Ecosim run for Okanagan Lake 1970-2000 (selected adult fish groups and *Daphnia*). Circles represent historical kokanee biomass (Walters, 1995).

mysid biomass peaked either in 1989 or sometime before. The Ecosim model shows that while mysid biomass reached high values a few years before 1989, mysid biomass did peak sometime around 1989. From 1989-1998, the data of McEachern (1999) showing that mysid biomass, while fluctuating from year to year, was on a general downward trend. The Ecosim model appears to track this quite well. However, year 2000 biomass is somewhat lower than the estimated 1 000 metric tonnes estimated for that year.

For kokanee (fig. 3), Ecosim may have tracked this group more accurately than shown if more information was available for the phosphorus forcing function between 1970-80 and 1980-90. As it is, Ecosim does lower the biomass of kokanee at the same rate as seen in the data (Walters, 1995) and shows a general slight rise and fall of kokanee biomass from 1980-2000.

Figure 3 also shows that the Adult Miscellaneous Fish (near shore) group rose from 1970-2000 while the Adult Miscellaneous Fish (deep water) group was reduced to 1% of their 1970 levels (see also Table 3). In both cases, anecdotal evidence suggests that these general trends in biomass did occur in Okanagan Lake, although the accuracy of the magnitude for change in biomass cannot be evaluated. It has been commented on by members of the OLAP team and Lee Granberg (mysid boat Captain, pers. comm. September 2001) that rainbow trout have been severely depleted in Okanagan Lake since 1970. Rainbow trout is the fish of greatest abundance in the Miscellaneous Fish (deep water) group. As for the increase in Miscellaneous Fish (near shore) group, divers in the area have seen a massive increase in the number of burbot in Okanagan Lake over the last

30 years. Burbot are one of the fish that constitute the Miscellaneous Fish (near shore) group.

The last group in Figure 3 is the *Daphnia* group. Not much is known about the abundance of *Daphnia* over the last 30 years. However, it was expected that *Daphnia* abundance would fall in the presence of increasing mysid numbers. While in some lakes mysids have completely extirpated *Daphnia* species from lakes into which they were introduced, this is not known to have occurred in Okanagan Lake.

Ecosim was best able to track historical changes in biomass when the forcing function was applied to the phytoplankton diet portion of every group. During a discussion with John Stockner (Eco-Logic Ltd., pers. comm. November 2000), regarding the nutrient imbalance (N:P ratio) taking place in Okanagan Lake, it was mentioned that this was causing inedible forms of phytoplankton to predominate. Upon learning this information, I decided that the phosphorus loading function should be added to the model. Forcing functions affect the consumption of diet items in any group. When applied to phytoplankton it essentially affects the edibility of the phytoplankton. Changing nutrient loads to Okanagan Lake may have been a cause of the nutrient imbalance and therefore the inedible forms of phytoplankton would have appeared during the same time and at the same rate as the phosphorus load decline. The phosphorus loading function was thus seen as a justifiable and necessary addition to the model. Phosphorus loads and nitrogen loads likely fell at the same rate and to the same degree of magnitude.

Another reason for including the phosphorus forcing function were the results from Ashley *et al.* (1999a) and Andrusak (2000) in which these authors speculated that the decline in kokanee abundance could be attributed to a decline in nutrients and/or competition with *Mysis relicta*. Whall (2000) also stated that simple competition over food resources between *Mysis relicta* and kokanee was unlikely to be solely responsible for the kokanee decline in Okanagan Lake. This is because nearby Kalamalka Lake supports a strong kokanee population even though mysids there remove a higher percentage of zooplankton production per day than in Okanagan Lake.

It should be noted here that Ecosim runs without the nutrient forcing function applied to the system resulted in kokanee biomass levels that did not accurately reflect the historical record (fig. 4). While kokanee abundance fell in the 1970-1980 period at the historically accurate rate, kokanee abundance rebounded to 50% of 1970 levels by 1990 and remained at that abundance level though to the year 2000.

3.1 – Ecosim Looks Ahead: 2000-2020

Once the Ecosim program was accurately calibrated, it was used in a forecasting mode. Here, Ecosim was used to predict what the Okanagan Lake ecosystem may look like over the next 20 years. This brief section looks at how the biological communities in Okanagan Lake might change if the mysid fishery remained stable at year 2000 catch levels and no alternative solution measures were applied.

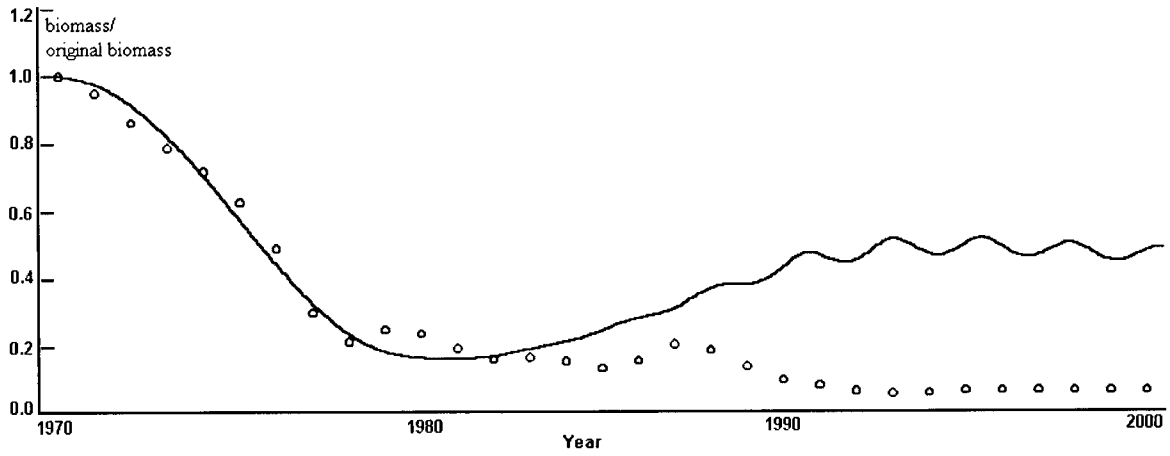

Fig. 4. Ecosim run for Okanagan Lake 1970-2000 without the nutrient forcing function applied. The Kokanee (1-3) group is shown. Circles represent historical biomass. Kokanee simulation does not follow historical biomass accurately from 1983 onwards, implying that *Mysis relicta* may be responsible for the original kokanee decline in Okanagan Lake, but is not primarily responsible for the current depressed abundance.

Figure 5 represents the Ecosim run from 1970-2020 using the stipulations stated above. As one can see, biomass levels for all groups depicted do not fluctuate greatly from year 2000 biomass levels. Kokanee remain at less than 10% 1970 levels and do not show any signs of recovery if current fishing levels are held constant. *Daphnia* remains part of the Okanagan Lake ecosystem and does not disappear. Both Miscellaneous Fish groups remain close to year 2000 biomass levels, but the Miscellaneous Fish (deep water) group is at 0.8% of 1970 levels by the year 2020.

As one might expect, mysid biomass levels do not change to any great degree if mysid catches are not increased. Mysid biomass does continue to oscillate, but only around year 2000 biomass levels of 1 000 metric tonnes. The oscillations are on the order of +/- 10% of mysid biomass.

3.2 – The Mysid Fishery

To begin, the mysid fishery was explored by changing the fishing effort values in Ecosim from the year 2002 until the year 2020. 2002 was chosen as the start year for varying the mysid fishery as catch values up to 2001 were able to be estimated (L. Granberg, mysid boat Captain, pers. comm., Sept. 2001). Fishing mortality values in Ecosim proved difficult to deal with at the beginning as changing them does not change catch values linearly. However, a fishing effort value which resulted in a year 2000 mysid catch of 30 t was found and any changes applied to future mysid fishing values were made relative to that value (see Appendix F for values used). Perhaps entering fishing

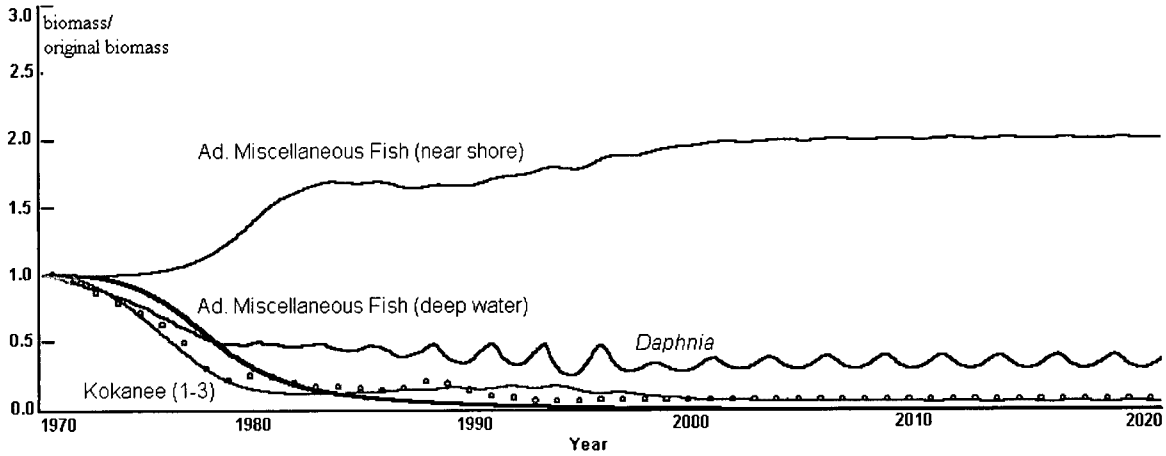

Fig. 5. Ecosim run for 1970-2020 period with no changes in mysid fishery from 2001 values and no alternative solutions applied. Circles represent historical kokanee biomass (Walters, 1995).

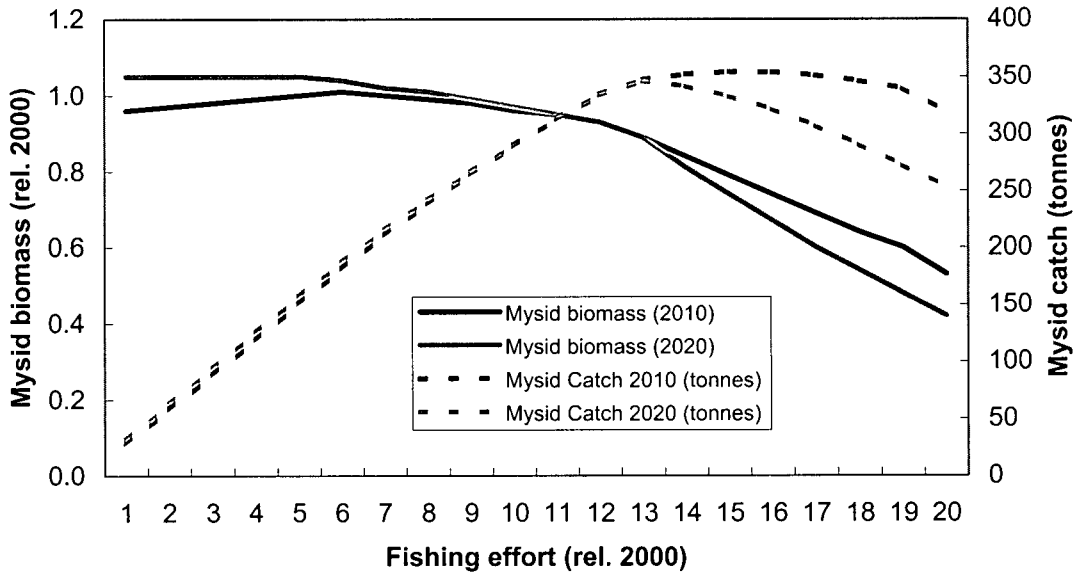

Fig. 6. Mysid biomass (relative to year 2000) and catch versus mysid fishing effort (relative to year 2000).

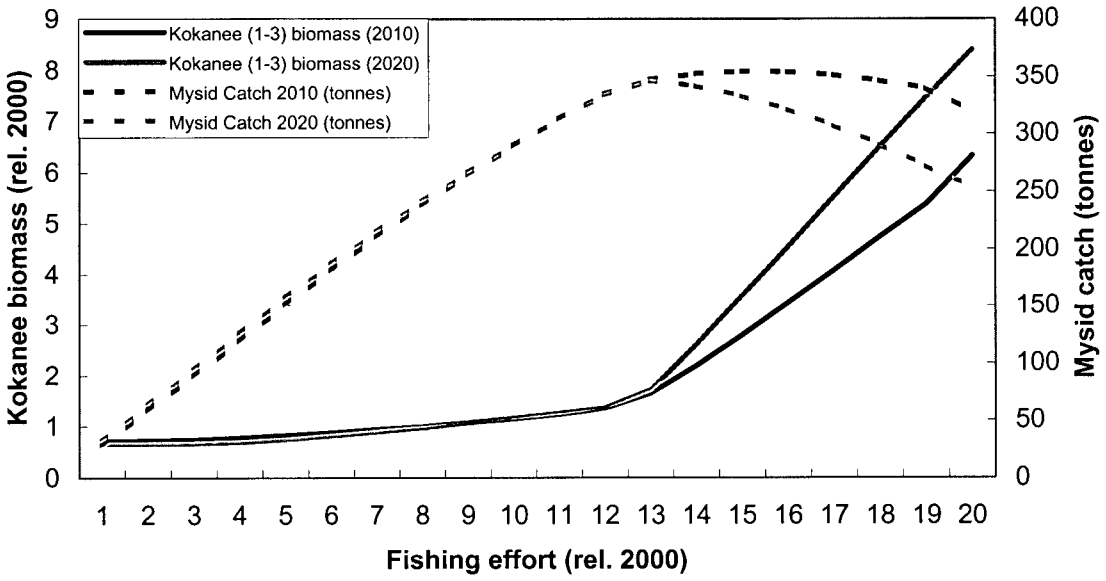

Fig. 7. Mysid catch versus fishing effort (relative to year 2000) and its effects on kokanee biomass (relative to year 2000).

effort values may prove more realistic in the end anyway. This is opposed to entering stationary catch values which could not be sustained over the long term with stationary fishing effort. As mysid biomass diminishes, catches will fall. If necessary, catch can still be quantified for any year in question.

The results of increased mysid catch on *Mysis relicta* can be seen in Figure 6. No dramatic decline in mysid biomass levels can be seen until mysid catch reaches the 350 tonne mark. This is approximately 10 times the year 2000 catch of mysids and is over 30% of the mysid population. At this catch level, the maximum sustainable yield (MSY) for mysids appears to have been passed.

Figure 7 begins to show us the effect of increased mysid catch levels on kokanee salmon. It appears that minimum catches of 250 t could have a positive effect on kokanee salmon. However, the effect is minimal as kokanee biomass appears only to have risen by 10% over year 2000 levels. As kokanee appear to be negatively affected at present mysid catch levels of 30 t, a 250 t catch would be the minimum increase necessary to produce positive results for kokanee abundance. However, Figure 7 shows that a large positive effect on kokanee biomass does not occur until mysid catch reaches the 350 t level. Once this catch level is achieved kokanee biomass increases sharply. If catches of this magnitude can be maintained for greater than 10 years, it appears that kokanee may be able to rebound to 60-80% of 1970 levels. This would be a result that all OLAP members would love to see, but in order to achieve the required mysid catch, fishing effort would need to be increased almost 20 fold.

In section 3.1 it was mentioned that maintaining the current level of mysid catch results in an oscillating mysid population around its year 2000 biomass. Mysid catch rates of less than 30% of the population appear to simply dampen these oscillations without significantly lowering the mean biomass of mysids for any given period. However, once this level has been passed, the oscillations disappear and the mysid population begins a downward trend. The reason that minimum mysid catches of 250 tonnes can have a slight positive effect on kokanee is that the peaks of the mysid biomass oscillations are lessened considerably. Without these mysid biomass peaks quickly devouring available zooplankton, the kokanee appear to be able to find more food and show positive population growth.

3.3 – Alternative Solutions: Nutrient Additions

It was mentioned earlier that increased mysid abundance was not the only reason for the kokanee population crash (Andrusak, 2000; Whall, 2000). Nutrient loading levels were believed to have changed, resulting in a nitrogen-limited or co-limited (nitrogen and phosphorus) lake that favours inedible forms of phytoplankton. Therefore, it is thought that the addition of nitrogen to the lake may allow for more edible forms of phytoplankton to return to former abundance. For all figures in this section, mysid fishery was held at year 2001 effort.

Figure 8 shows the effect of increased nutrient addition to Okanagan Lake causing the edibility of phytoplankton to increase and the

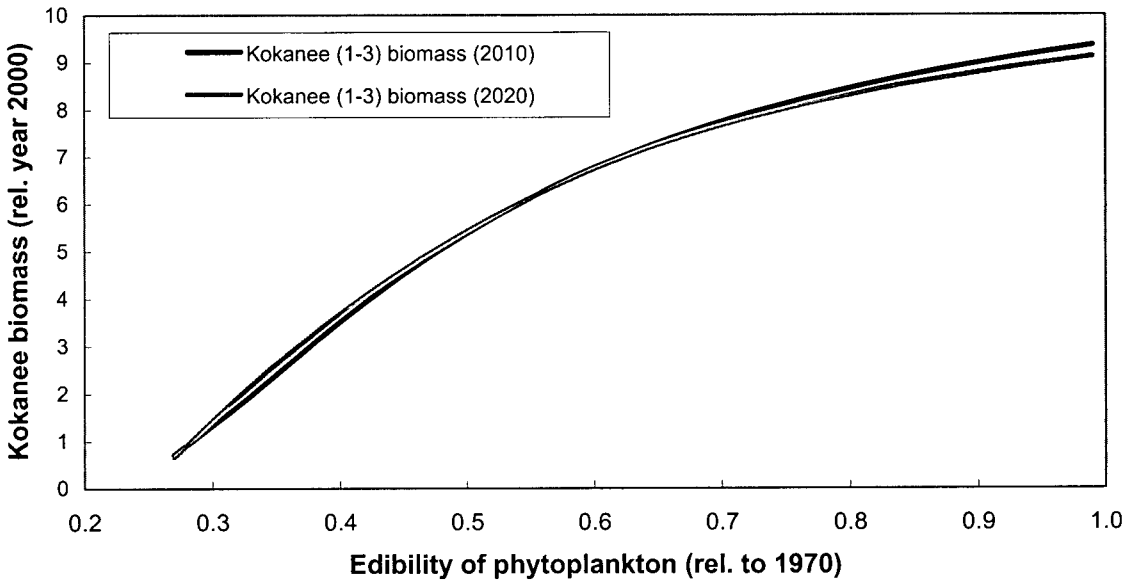

Fig. 8. Increased edibility of phytoplankton (relative to 1970) versus kokanee biomass (relative to year 2000).

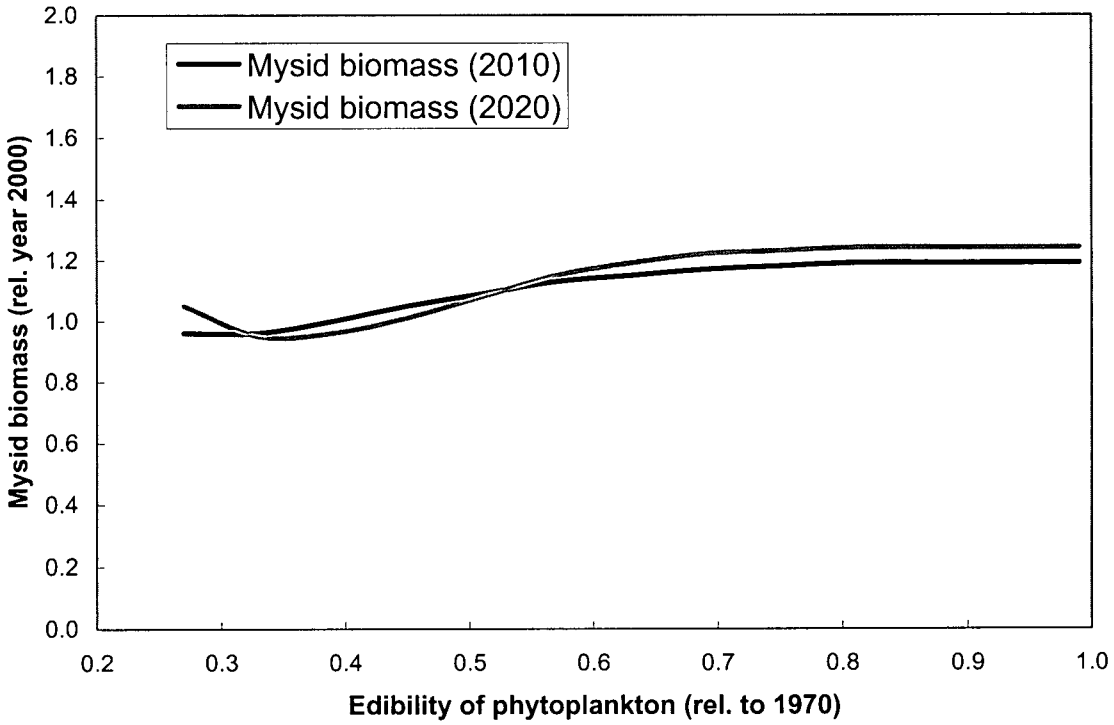

Fig. 9. Increased edibility of phytoplankton (relative to 1970) versus *Mysis relicta* biomass (relative to 2000).

response of kokanee biomass. This was achieved by increasing the forcing function controlling the edibility of phytoplankton back to 1970 levels beginning in the 2002. Edibility of phytoplankton was increased during 2002 and then held constant until 2020. This may be somewhat unrealistic as nutrient additions would likely be slowly increased rather than dramatically jacked up as in this model. As can be seen, the effect of increasing the edibility of phytoplankton on kokanee is rather quick, as the recovery of kokanee biomass by 2010 is the same as by 2020. Again, this rapid response may be somewhat quickened by the sudden jump in phytoplankton edibility applied in this model. One important point to note, however, is that even if the edibility of phytoplankton is returned to 1970 levels, kokanee biomass would only approaches 66% of its 1970 biomass.

Figure 9 shows the response of the mysid population to increased phytoplankton edibility with the rather curious result that the dramatic increases in the edibility of phytoplankton does not follow through with dramatically increased mysid biomass. A mechanism to explain this will be suggested in the Discussion section.

3.31 – Nutrient Additions and a Mysid Fishery

The next topic to explore is that of a mysid fishery in combination with nutrient additions. In this section, the mysid fishery was held at 16 (the effort at which year 2002 biomass catch was 350 000 kgs). This effort was chosen as it

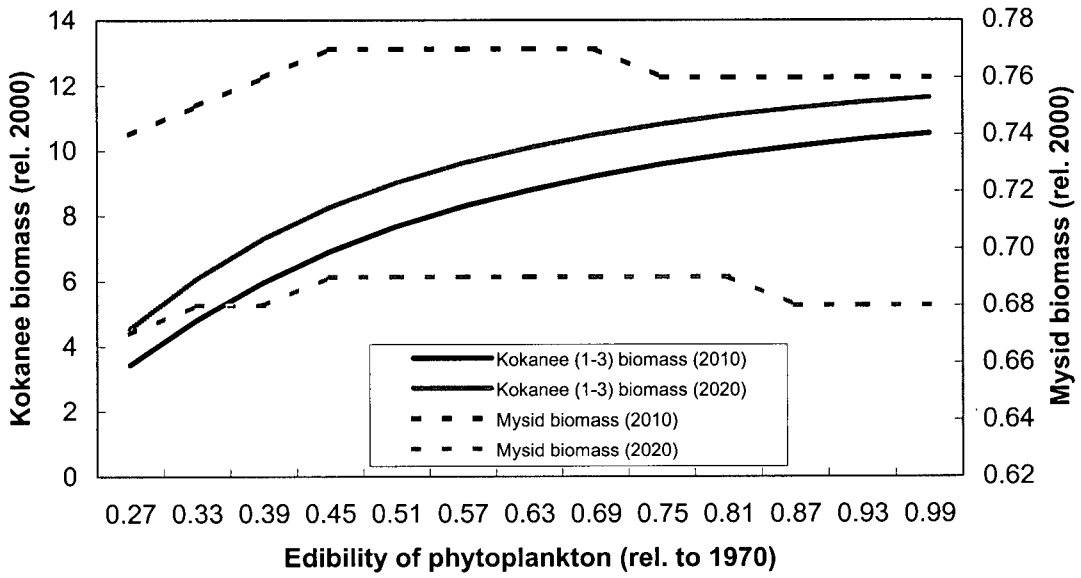

Fig. 10. Nutrient additions plus mysid fishery (at fishing effort 16) and its effect on kokanee salmon and *Mysis relicta* biomass (relative to 2000).

was the lowest level that had a large negative effect on *Mysis relicta* and a large positive effect on kokanee salmon biomass. As the edibility of phytoplankton is slowly increased by raising the forcing function applied to all Ecosim group diets, kokanee salmon can be seen to rebound strongly. It appears that kokanee could rebound to 1970 levels if the combination of strong mysid fisheries and nutrient additions were to be applied.

Nutrient additions do not seem to effect mysid biomass greatly, as a fishing effort 16 times the current 2001 mysid fishery will reduce mysid biomass to 60-70% of 2000 levels regardless of whether a nutrients are being applied or not. However, the addition of nutrients do appear to aid the kokanee population greatly. In fact, nutrient additions can achieve positive results for kokanee that are 3-4 greater than fishing alone at this effort.

3.4 – Mysid Excretion Experiments

Table 4 shows the results from summer 2001 mysid excretion experiments as carried out aboard Boat 2. The net depths used in this experiment were between 10 and 22 m (Table 4). Mysid shallow water feeding temperatures ranged from 10.3 – 12.4 °C and experimental temperatures never varied more than 2 °C from this. Mysid feeding temperatures for the bottom of Lake Okanagan were always 4 °C and experimental temperatures were within 0.4-0.9 °C of this except on the first night where the experimental temperature was 6.7 °C. In general ammonia excretion rates were higher than urea excretion rates, although not significantly (value plus standard deviation overlap) for excretion

Table 4. Mysid excretion rates of urea and ammonia at the beginning, middle and end of nightly feeding period.

Date	Time begin	Nitrogen ($\mu g\ N * mg\ wet\ weight\ mysid^{-1} * h^{-1}$) Urea	Ammonia	Total Nitrogen	Net Depth (m)	Temp. at depth (°C)	Exp. Temperature (°C)	+/- (°C)
July 11-12	22:46	0.0102	0.0252	0.0354	13.72	10.9	12.8	1.9
Sunset 21:03	2:21	0.0125	0.0297	0.0422	10.67	12.4	13.8	1.4
Sunrise 5:00	4:12	0.0249	0.0112	0.0362	10.67	4.0	6.7	2.7
August 5-6	22:32	0.0048	0.0368	0.0416	21.34	9.4	9.8	0.4
Sunset 20:33	1:43	0.0065	0.0147	0.0211	19.81	10.5	10.9	0.4
Sunrise 5:32	3:25	0.0071	0.0134	0.0205	19.81	4.0	4.4	0.4
August 19-20	21:50	0.0024	0.0119	0.0143	19.81	10.8	11.2	0.4
Sunset 20:08	1:02	0.0040	0.0262	0.0302	17.68	10.8	11.4	0.6
Sunrise 5:52	5:00	0.0030	0.0192	0.0222	20.73	4.0	5.9	1.9
Sept. 23-24	21:18	0.0112	0.0205	0.0316	16.76	10.3	11.1	0.8
Sunset 18:53	0:33	0.0092	0.0111	0.0203	16.76	10.3	10.7	0.4
Sunrise 6:44	3:40	0.0208	0.0185	0.0393	16.76	4.0	4.9	0.9

measurements at the end of mysid nightly feeding periods (see Table 5). However, this could be because the general trend of ammonia excretion rates greater than urea rates was reversed on the last night for the last trial. It should be mentioned here that mysid mortality during this trial was 6.7% whereas for the rest of the trials it was 0%.

Next, an investigation into the net effect of mysid excretions was carried out. Over a 24 hour period, mysids migrate after feeding down to the bottom of Lake Okanagan (or at least as great as 100 m; Levy, 1991), remain there during the day, and then migrate up again at dusk in order to feed again. In general, if mysid migrations were instantaneous, mysids would spend 18 hours on the

bottom of the lake and 6 hours near the surface. During this time, mysids are expected to have differential excretion rates due to stomach fullness versus

Table 5. Mean mysid excretion rates of urea and ammonia at the beginning, middle and end of nightly feeding period (n = 4 for all values).

	Nitrogen ($\mu g\ N * mg\ wet\ weight\ mysid^{-1} * h^{-1}$)		
	Ammonia start	**Ammonia middle**	**Ammonia end**
Mean	0.02359	0.02041	0.01558
Stdev	0.01039	0.00894	0.00387
	Urea start	**Urea middle**	**Urea end**
Mean	0.00714	0.00806	0.01394
Stdev	0.00421	0.00366	0.01055
	Total N start	**Total N middle**	**Total N end**
Mean	0.03073	0.02846	0.02952
Stdev	0.01170	0.01023	0.00958

emptiness and rate of metabolism at the different temperatures encountered during their migrations.

Chipps (1998) found that gut residence time (GRT) varied with temperature in the following way when fed *Diaptomus* prey:

$$GRT = 10.367 * Temp.\ (°C)^{-0.580}. \quad \ldots 16)$$

Therefore, using the average temperatures mysids encountered during this experiment at both shallow (11.3 °C) and deep depths (4 °C), gut residence time was calculated as 4.64 hours at the bottom of the lake and 2.67 hours in shallow feeding depth waters.

Mysid metabolism also changes under varying temperatures. It was found by Chess and Stanford (1999) that mysid energy conversion efficiency is much higher at cold temperatures than at warm temperatures. Energy conversion efficiency is presumed to go up as metabolism is slowed down. From this it was calculated that mysid metabolism would be 2.62 times slower at 4 °C (lake bottom temp.) than mysid metabolism at 11.3 °C (feeding depth temp.).

This information was used in compiling Table 6, which shows the total amount of nitrogen an individual is expected to excrete over a 24 hour period. When mysids descend from feeding depths to the bottom of the lake with a stomach full of zooplankton, an individual mysid can be expected to excrete nitrogen at the same rate for 4.64 hours while zooplankton remains in the stomach. This GRT can be multiplied by the total nitrogen excretion rate (ammonia excretion rate + urea excretion rate) per mg mysid to equal the total nitrogen excreted per mg mysid for that period. For the next 13.36 hours

Table 6. Excretion rates of total nitrogen per mg mysid over a 24 hour period (beginning immediately after downward migration). Deep/Deep/ Shallow/Shallow columns refer to mysid depth beginning after downward migration. Four separate time periods were identified during which mysid excretion rate differed due to temperature changes and/or GRT.

Depth level	Deep	Deep	Shallow	Shallow
Tot. N. rate used ($\mu g\ N\ mg^{-1}\ h^{-1}$)	0.02952	0.03073	0.03073	0.02846
time at level (hours)	4.64	13.36	2.67	3.33
Metabolism factor	1	2.62	1	1
Tot. N/mysid ($\mu g\ N\ mg^{-1}$)	0.1370	0.1567	0.0821	0.0948

mysids stomachs will be empty of zooplankton, but may contain detritus eaten on the bottom of the lake. Therefore, using the mysid excretion rate calculated at the beginning of each experiment (when the mysids have just come off the bottom and have not had a chance to feed on zooplankton yet) slowed by a factor of 2.62 to account for lake bottom temperatures, should allow us to calculate a reasonable estimate of the total nitrogen excreted per mg mysid for this 13.36 hour period. Once mysids have risen to begin feeding upon zooplankton, their excretion rates should remain stable until the first zooplankton they ate begins to be excreted. This should take approximately 2.67 hours at feeding depth temperatures. Therefore, using the average mysid excretion rate calculated for the beginning of the experiments multiplied by 2.67 hours gives us a good estimate of total nitrogen excreted per mg mysid for this period. Finally, mysids will remain at feeding depth for approximately another 3.33 hours before descending to the bottom of the lake. Mysid excretion rates should remain stable during this time at the average rate calculated for the middle of each experiment. Using this value multiplied by 3.33 hours should give total nitrogen excreted per mg mysid for the end of the 24 hour period.

Using the values in Table 5 for the total amount of nitrogen excreted per mg mysid upon reaching shallow and deep depths for the period of their GRT, allows us to calculate the net effect of mysids on nitrogen movements in Okanagan Lake. For 4.64 hours, mysids are excreting nitrogen that they have brought down from shallow waters into the benthos. And for 2.67 hours, mysids are excreting nitrogen into shallow waters that they have brought up from the

benthos. We know the approximate biomass of mysids to be 1 000 metric tonnes and that there are 365 days in the year. Using these values and the excretion rates calculated, we can calculate that mysids bring 30 t of total nitrogen to the shallow depths of Okanagan Lake every year via excretions. However, mysids excrete 50 t of total nitrogen that they have brought from the surface onto the bottom of every year. This leaves a net draw-down of 20 000 kgs of total nitrogen per year. Okanagan Lake contains approximately 5 240 t of total nitrogen (Jensen, 1999). Therefore, mysids remove only 0.4% year $^{-1}$ of the total nitrogen in Okanagan Lake into deep waters.

3.5 – Ecopath 2000 Nitrogen Model

The Ecopath 2000 nitrogen model was created to achieve a better understanding of the nitrogen flows in Okanagan Lake. As well, it was thought that this model could aid in determining whether the lake really is nitrogen limited. As has been mentioned, Okanagan Lake does show signs of nitrogen limitation, but there is some debate in the literature as to whether the lake is phosphorus limited, nitrogen limited or perhaps even co-limited (nitrogen and phosphorus; Jensen, 1999; McEachern, 1999). If Okanagan Lake is nitrogen limited, we would expect to see the Ecotrophic Efficiency (EE) of the Detritus (dissolved in lake) pool to have a value greater than 1.

The Ecopath 2000 nitrogen model showed that two groups had EE's greater than 1. The *Daphnia* group appeared to be overused in terms of nitrogen by a large degree, having an EE of 2.59. As well, the Detritus (dissolved in

water) group had an EE of 1.013. In order to determine how much nitrogen would be needed to balance the lake, the nitrogen import column was used to add nitrogen to the lake. Approximately 913 t of nitrogen would be needed per year to balance the model. Using a 7N:1P nitrogen to phosphorus weight ratio and using the phosphorus loading data from Table 2, 913 t nitrogen is approximately 2 times the 1995 nitrogen load to Okanagan Lake.

Discussion

4.0 – Ecosim: 1970-2000

Ecosim appeared to track the historical changes in biomass for Okanagan Lake quite well, at least for the few groups with historic data. The fact that both *Mysis relicta* and kokanee salmon appear to have been tracked closely to historical records allows for some confidence in the model. Adding to this confidence is the anecdotal evidence that rainbow trout have fallen dramatically since 1970 and burbot have increased since then as well. This model predicts the general rise and fall of the groups that include these fish. There is some concern that the dramatic increase in burbot, which are predators of young kokanee, may be partially responsible in causing kokanee to remain at its current low biomass.

However, perhaps the most interesting result for the Ecosim 1970-2000 run is not how well Ecosim tracks historical changes in biomass, but how the model responds to the application of the forcing function. Without the forcing function applied, kokanee salmon falls to the same low level and at the same rate

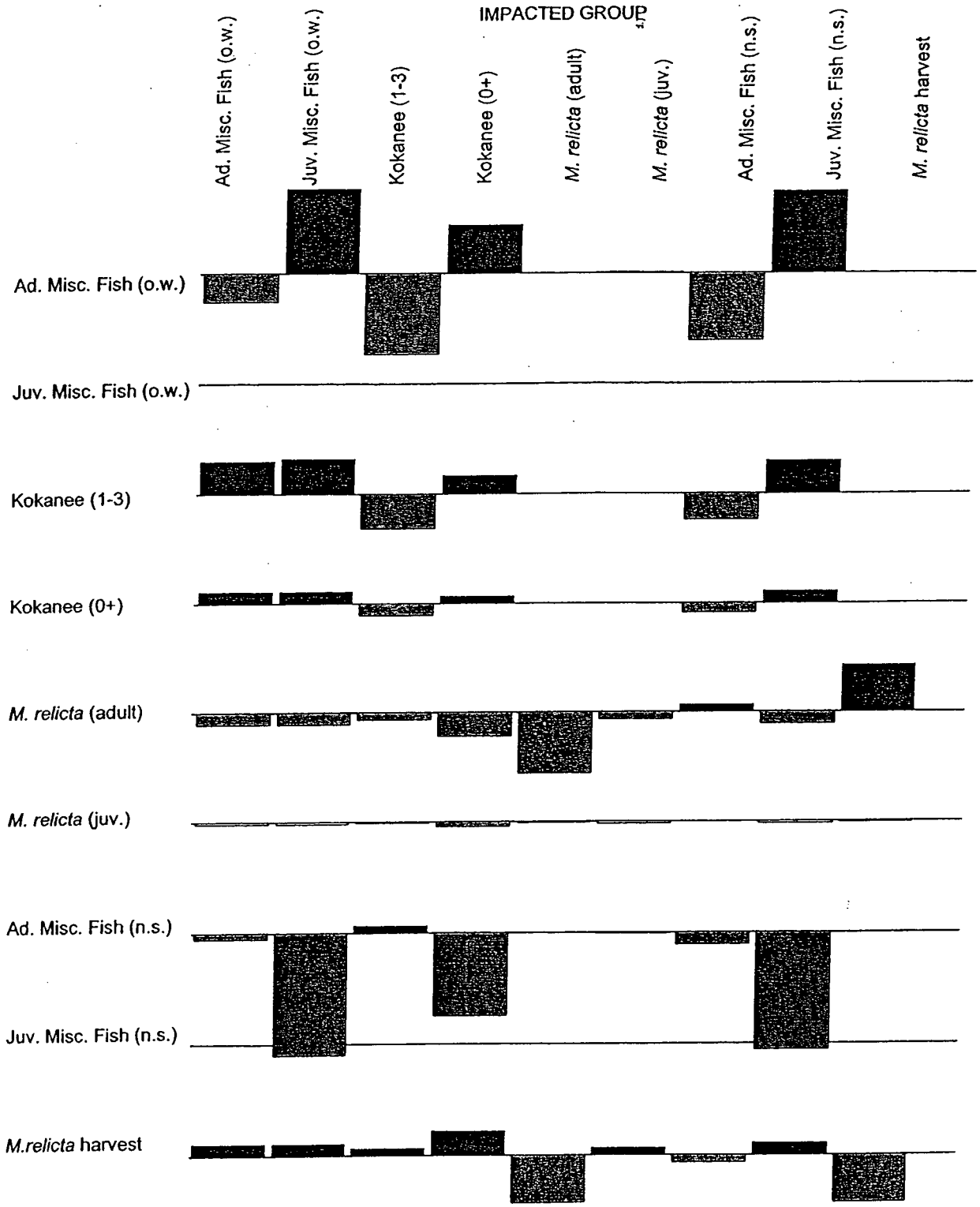

Fig. 11. ECOPATH group impact assessment for Okanagan Lake in year 2000.

as when the forcing function is not applied. However, without the forcing function kokanee salmon rebounds to 50% of 1970 levels by 1990, which we know to be historically inaccurate. Applying the forcing function to the model maintains kokanee biomass at low, historically accurate levels. This would seem to suggest that while falling nutrient loads to the lake had no effect on falling kokanee levels in the 1970s, lowered nutrient levels are at least partially responsible for keeping the kokanee biomass down at the present time. A further implication is that *Mysis relicta* is responsible for the original kokanee decline, but not for its current low levels. While *Mysis relicta* still has some negative effect on the kokanee (0+) group due to competition over zooplankton resources (see fig. 11), it is not solely responsible for the current depressed kokanee population. Figure 11 shows that the Miscellaneous Fish (near shore) group also has a negative affect on the kokanee (0+) group. However, this group was still present in the model when it was run without the forcing function. Therefore, it is not solely responsible for the depressed kokanee abundance either. Reduced nutrient input causing decreased edibility of phytoplankton appears to be the factor that is holding kokanee numbers down at less than 10% of 1970 levels. However, the increased numbers of burbot seen in Okanagan Lake is also of concern to some. Large fish have often been seen on echosounders at around 10:30 every night in late fall months that appear to be coming in from near shore areas(L. Granberg, mysid boat Captain, pers. comm. September 2001). These large fish are thought to be burbot that have come off shore to feed on juvenile kokanee salmon (L. Granberg, mysid boat Captain, pers. comm. September

2001). Members of OLAP disagree with this opinion, however, saying that the large fish seen on the echo-sounder are large kokanee.

4.1 – Ecosim: 2000-2020

It appears that if mysid catch levels are not raised well above the current 30 t catch per year, that very little will change in Okanagan Lake over the next two decades. Due to the perturbations in the past, biomass levels for all groups have adjusted and reached what appears to be some sort of equilibrium with high mysid biomass and lowered kokanee at less than 10% of 1970 levels.

The mysid biomass oscillations do appear quite large since an increase or decrease of 10% of the mysid population represents 100 tonnes of biomass. However, mysid biomass is known to fluctuate greatly in Okanagan Lake. McEachern (1999) has shown that mysid fluctuations from 1989 onwards have been greater than the 10% swings that Ecosim predicts for the future.

As was shown in McEachern (1999), mysids were on a general downward trend since 1989, but Ecosim predicts that this trend will stop and that the population will remain stable (although oscillating). Perhaps *Mysis relicta* overshot lake carrying capacity in the late 1980s and has been on a downward trend with large biomass fluctuations since.

4.2 – The Mysid Fishery

The current level of mysid fishing from Boat 2 amounts to only 0.027-0.045% (270-450 kgs.) of the current mysid biomass in Okanagan Lake each

night. Even if the fishing method and knowledge of mysid distribution were refined so that maximum nightly catch of 1 140 kgs. could be maintained, this would result in mysid catches of only 0.12% of the mysid population per night. While this is twice as high as the 0.6% of mysid population catch that the OLAP team managed during its experimental trawling program, if the calculation in Ashley and Smith (1999) is carried out, four boats such as Boat 2 trawling Okanagan Lake should be able to catch up to 0.48% of the population each night. Figure 6 shows that this would still not be enough to reduce the mysid population greatly. Not until annual catches of 350 t are reached is there any major drop in the mysid population. Any thoughts of attempting to permanently remove mysids from the lake cannot be entertained until this catch level is reached.

At a public meeting regarding the state of Okanagan Lake held in March of 2001, it was mentioned that mysid catches would hopefully reach 25% of the mysid population for the 2002 year (S. Matthews, MELP, pers. comm. March 2001). OLAP Members appear to believe that this level of mysid catch will be high enough to remove or at least severely deplete the mysid population in Okanagan Lake over the long term. Figure 6 shows that even if this 250 t mysid catch level could be reached, this may not be enough to reduce the mysid population to any great degree. As well, the major effect on kokanee salmon is not achieved until after the mysid catch reaches the 350 t mark (fig. 7). Speaking with one of the mysid catch license holders (L. Granberg, mysid boat Captain, pers. comm. September 2001), he does not feel that Okanagan Lake

will ever see a mysid catch that large, especially with only two boats fishing the lake as is the case now.

4.3 – Alternative Solutions: Nutrient Additions

As the mysid catch does not appear, at least to those involved in the actual fishery, to be able to reach the 30-35% mysid population catch level needed to have a strong positive effect on the kokanee salmon, perhaps alternative solutions should be considered. In section 4.1, it was mentioned that nutrient reductions and not *Mysis relicta* appear to be the reason for the current low levels of the kokanee population. Perhaps with the additions of nutrients, kokanee levels will respond more positively than they are to current mysid fishing efforts.

The idea of additional nutrients aiding the fish populations in mysid introduced lakes is not a new one. The most recent example is that of Kootenay Lake (Ashley *et al.*, 1999b) where both phosphorus and nitrogen were added to try to restore the declining kokanee population. The result of this experiment was increased kokanee numbers and decreased mysid abundance.

Mysis relicta introductions have proven favourable only in lakes of high productivity (Lasenby *et al.*, 1986; Northcote, 1991). Since mysids only have a limited time in which to feed (the hours between dusk and dawn), lakes that have high productivity allow for zooplankton, and cladocerans in particular, to have production rates that are high enough to offset nightly mysid predation.

Richards *et al.* (1991) give the specific example of Lake Tahoe where this appears to have occurred. Lake Tahoe used to be a lake of extremely low productivity and the introduction of *Mysis relicta* (1963-65) precipitated the virtual elimination of all cladocerans from the lake. However, from 1969 to 1979, Lake Tahoe underwent a period of cultural eutrophication. Phytoplankton production rate skyrocketed and the algal biomass doubled in 10 years. During this period the number of *Daphnia* and *Bosmina* increased dramatically. Under the increased nutrient conditions, cladocerans were able to maintain birth rates sufficient to offset mysid night-time predation. This allowed for the co-existence of mysids and cladocerans where before this was impossible.

Threlkeld (1981) who also worked on Lake Tahoe during the 1970s, showed that the return of *Bosmina* to the lake occurred immediately following a mysid crash from 380/m^2 in 1975 to 27/m^2 in 1978. Threlkeld (1981) concluded that decreased mysid predation in the later half of the 1970s could only account for <34% of the observed difference in *Bosmina* dynamics. Greater significance needed to be placed on the non-mysid mortality of zooplankton in Lake Tahoe. While it is recognized that every lake is different, this further suggests that mysid removal alone will not have the desired effects and that here too, greater significance needs to be placed on the non-mysid mortality of zooplankton.

As a final impetus to look at nutrient additions in this model, Byron *et al.* (1986) stated that "it is only with higher birth rates resulting from increased production that *Daphnia* and kokanee can co-exist with *Mysis relicta*."

Figure 8 shows the response of kokanee salmon to increased phytoplankton edibility. As one can see the response is dramatic and has the potential to be of great benefit to the kokanee salmon depending on the amount of nutrients added back into Okanagan Lake. The quick response, again, is somewhat unrealistic as phytoplankton edibility was immediately raised in 2002 and this is likely to be a more gradual process than is depicted here. However, Figure 8 is useful, as it gives one an idea of the potential for nutrient additions.

The kokanee response is mediated through a few steps in Ecosim that are useful to recognize here. First increased edibility of phytoplankton allows for *Daphnia* to increase its consumption over biomass rate without any changes in feeding time. As well, the increased phytoplankton and *Daphnia* populations in the lake allow for kokanee (1-3) and (0+) feeding times to decrease by a factor of up to 2. This decreased feeding time allows kokanee to decrease the time that it is exposed to predation. This can be seen to affect kokanee predators such as Miscellaneous Fish (near shore) which shows a slight decrease in biomass after phytoplankton edibility is increased.

Now the greatest fear of most OLAP members to nutrient additions is that this will simply lead to larger *Mysis relicta* populations in Okanagan Lake and not increased kokanee populations. However, Figure 9 suggests that this would not to be the case. Mysids appear to show a slight drop in biomass at moderate phytoplankton edibility levels. High phytoplankton edibility leads to mysids showing only a slight increase in abundance. As *Mysis relicta* has limited feeding time (the period between dusk and dawn) and that it probably is feeding at its

maximum feeding rate during this time, any addition of phytoplankton to the lake (especially in water above 90 m) would not have any effect on the mysid population. If mysids are eating for as long as they can and as fast as they can during nightly zooplankton foraging bouts, then any extra zooplankton would not benefit the mysids to any great degree. Ecosim does have restraints on feeding time so the model does have the mechanism to show this. Mysids do show an increase in feeding time to the maximum allowable (2 times the base feeding time used at the beginning of the model) and hold at this level from the 1980s onward. There is only a slight and brief drop in feeding time immediately after phytoplankton edibility is raised in 2002.

Why would mysids increase their feeding rate in the first place? As *Mysis relicta* has no major predators in Okanagan Lake (all mysid predators are visual and due to diel vertical migration behaviour, mysid predators rarely get the chance to eat *Mysis*). *Mysis relicta*'s biggest competitor is itself (see fig. 11) and as the mysid population grew, mysids had to increase their feeding time in order to maintain the same food intake for each foraging bout. However, this could only increase to a maximum as mysids return to deeper water when daylight is present.

There may be some doubt as to whether mysids could have maintained maximum feeding rates in the presence of a growing mysid population and a shrinking zooplankton prey base. However, zooplankton density is known to be patchy in any given lake and mysids appear to be adept at feeding in patches of high zooplankton density. As well, Folt *et al.* (1982) showed that the maximum

feeding rate for mysids in the field is well below that of the maximum possible feeding rate of *Mysis relicta* calculated in a laboratory setting. Maximum feeding rates in the field can be as low as ¼ the rates mysids were able to achieve in the laboratory for any given zooplankton prey (Folt *et al.*, 1982). This is likely due to mysids searching for preferred prey items in a patchy environment.

Another reason that mysids might not show an increase due to raised phytoplankton edibility is that mysids do not become more selective for any given prey item when it becomes more abundant (Bowers and Vanderploeg, 1982). Therefore, even if phytoplankton or *Daphnia* increased dramatically, mysids would not switch their diet to include more of this item in their diet.

4.3.1 – Nutrient Additions and a Mysid Fishery

Since a strong mysid fishery and increased phytoplankton edibility seem to both have positive effects on kokanee salmon biomass, perhaps a combination of both strategies would prove useful. Figure 10 shows that a combination of a strong mysid fishery (fishing effort 16 times stronger than 2000 mysid fishery) and even a moderate increase in phytoplankton edibility results in strong positive growth for the kokanee salmon population. As well, even the Miscellaneous Fish (Deep Water) group shows a positive response to the combined fishery/nutrient addition strategy, climbing from a low of 0.8% of 1970 levels in 2000 to 7% of 1970 levels by 2020.

The reason that this combined strategy appears to achieve the goals of increased kokanee biomass to a greater degree than any one strategy alone is

that *Daphnia* biomass responds to reach higher biomass levels than for any single strategy. Kokanee feeding time falls as before, but not to any noticeable greater degree than for the nutrient addition strategy.

4.4 – Mysid Excretion Experiments

The mysid excretion experiments were conducted in order to add field data to the Ecopath 2000 nitrogen model and to obtain data from Okanagan Lake that would aid in the debate of whether *Mysis relicta* is exacerbating or mediating possible nitrogen limitation in Okanagan Lake.

While it is believed that the methods used in this experiment are an improvement on previous similar experiments (Madeira *et al.*, 1982; Chipps and Bennett, 2000), confidence in the results can be taken from the fact that they are of the same order of magnitude, for both ammonia and urea, as in previous experiments. The reasons that it is felt that the methods used in this experiment were an improvement was due to the capture and handling of mysids prior to trial runs. In Madeira *et al.* (1982), vertical tows with a zooplankton net, from lake bottom to surface, were used to capture mysids. When large densities of mysids were encountered, those mysids at the bottom of the net would be crushed by the weight of the mysids on top of it when the net cleared the water surface. Perhaps, unknowingly, some damaged mysids were used in the experimental trials. Once mysids cleared the water they were then brought on deck to be sorted by hand. This could have further damaged some mysids. Madeira *et al.* (1982) also report not rinsing the net between trials to try and

avoid rinsing damaged animals into the pile of "non-damaged" mysids. However, this may only lead to having these mysids included when the next set of mysids is brought up from depths with the same net.

As was mentioned during the introduction, the boat that was used for these experiments, Boat 2, uses a continuous fishing method that allows for the net to be set only once each night. A pump at the cod-end of the net pumps the mysids, along with feeding depth water up to a basin the second boat. Mysids were taken from this basin by submerging a small plastic cooler into this water, allowing the mysids to be sucked into the cooler without ever touching them. This cooler was then transported to a low traffic working area where 30 mysids were placed via a 70 cc Toomey syringe into experimental beakers. At this point, the mysids involved in this experiment have never been touched or physically handled in any way. As well, the mysids were never thermally shocked when brought up via the pump method. Mysids were almost certainly thermally shocked and crushed under the weight of each other in the methods used by Madeira *et al.* (1982) when they were brought up from the bottom of the lake to surface and when they were brought out of the water into the warm summer air. While this could have effected the rate of mysid excretions in the Madeira experiment, these issues should not be of concern here. Mortality of mysids during the Madeira *et al.* (1982) experiment reached as high as 25% in some flasks while mysid mortality in this experiment was 0% for all beakers (except in the last trial where two mysids, or 7%, died).

Several errors in measuring mysid excretions still could have taken place in this experiment, including low nitrogen measurements due to recycling, changes in mysid excretion rates due to crowding, variability of excretion rates over time, and extra nitrogen excreted into water from introduced zooplankton. However, the short time in which the mysids were kept should limit the amount of recycling that would have taken place as well as limit the time over which excretion rates could have varied. In order to have detectable levels of nitrogen in the flasks, short experimental times and crowding of mysids were felt to be necessary. While zooplankton could have been introduced along with mysids into the experimental water, using the Toomey syringe to transfer mysids should have kept this to a minimum. As little water as possible was transferred with the mysid subjects.

Ammonia and urea were chosen as the two forms of nitrogen to be measured in this experiment for two reasons. First, total nitrogen was discussed in Madeira *et al.* (1982) as the sum of two components, ammonia and urea. Second, ammonia is said to be the primary source of nitrogen uptake for phytoplankton with urea running a close second (J. Stockner, Eco-Logic Ltd., pers. comm. May 2001). Therefore, it would be useful to know whether mysids were adding nutrients to or removing nutrients from the shallow depths of Okanagan Lake.

It was shown that mysids remove only 20 t of total nitrogen from shallow waters each year. While this is a small number, only 0.4% of the total nitrogen found in Okanagan Lake, it could still have a detrimental effect on local

zooplankton assemblages. Mysids occur at high densities at night in areas where there are high densities of zooplankton upon which mysids can feed. Therefore, in these areas where nitrogen may be a locally limiting factor on zooplankton production, having mysids remove nitrogen from these areas could be considered detrimental.

Regardless as to the amount of nitrogen that mysids are removing from the shallow depths of Okanagan Lake at night, they are not helping to alleviate the nitrogen limitation problem as was hypothesised. Therefore, the application of a mysid fishery would remain a positive measure in terms of the OLAP goal of kokanee restoration. Even though it has been mentioned that mysids are unlikely to be the sole reason for depressed kokanee numbers at present, they still compete with kokanee for zooplankton resources and are also removing nitrogen from a possibly nitrogen limited environment.

4.5 – Ecopath 2000 Nitrogen Model

Two key findings from the Ecopath nitrogen model is that Okanagan Lake does appear to be nitrogen limited and approximately 913 t of total nitrogen is needed to balance it per year. Ecopath operates on an annual basis in this model and the result of the Detritus (dissolved in lake) group having an EE greater than one shows us the there is not enough nitrogen in the lake to meet the demands of phytoplankton, at least during certain times of the year. While there may be enough nitrogen during some periods, on an annual basis there is nitrogen limitation in Okanagan Lake.

The amount of 913 t was found to be the amount of total nitrogen needed to balance the model and there are some reasons to believe that this number could be accurate. 913 t of nitrogen corresponds to 2 times the 1995 nitrogen load, or approximately 50% of the 1970 nitrogen load, to Okanagan Lake. When the forcing function in the Ecosim model, representing nitrogen limitation, was removed from the model run (i.e., no nitrogen limitation; see fig. 4) kokanee salmon returned to approximately 50% of 1970 levels. When the addition of nitrogen to Okanagan Lake was discussed (see fig. 8), and nitrogen loading (phytoplankton edibility) was returned to 50% of the 1970 nitrogen load (removing nitrogen limitation), kokanee returned to approximately 50% of 1970 levels. This shows that both the Ecopath 2000 model and the Ecosim model of Okanagan Lake agree, that nitrogen loads of 913 t or 50% of 1970 nitrogen loads, should return Okanagan Lake to a non-nitrogen limited state. While it is recognized that these two models should agree with each other (after all the Ecopath 2000 nitrogen model was adapted from wet weight biomass values in the Ecosim model) at least one can have some confidence that no errors were made in transferring the model from wet-weight biomass into nitrogen biomass.

4.6 – Conclusions

While these models of Okanagan Lake are not entirely conclusive or definitive (many groups' biomass levels are not well known for Okanagan Lake) some concepts appear to have been established. The current depressed values of kokanee salmon in Okanagan Lake are the result of more than one factor.

While *Mysis relicta* appears to be responsible for the initial kokanee salmon decline in Okanagan Lake, nutrient limitation and *Mysis relicta* appear to be responsible for the current state of kokanee salmon.

The Ecopath 2000 nitrogen model suggests that Okanagan Lake can be nitrogen limited at times, but did not solve the issue of whether Okanagan Lake is ever phosphorus limited. Once this is known, the debate of whether Okanagan Lake is perhaps co-limited may be answered.

Discussion of the mysid fishery and possible alternative measures proved to be illuminating. While mysid fisheries at their current effort in Okanagan Lake appear to be ineffective, even the OLAP projected goal of 25% mysid mortality caused by fishing appears weak in terms of kokanee response. The 30-35% mysid mortality due to fishing does not appear to be achievable unless the government is willing to support a mysid fishing fleet. Those involved in the fishery will even say that these numbers are not in the realm of possibility unless more mysid catch boats are added to the fleet. However, one has to wonder how the public might react to having 16-20 mysid catch boats running around Okanagan Lake between the hours of 6 pm and 7 am.

Due to this, nutrient additions may want to be entertained as a possible solution to the kokanee problem. It appears that kokanee would respond well to this measure and mysids would not increase greatly. Thousands of kgs of nitrogen and phosphorus were added to Kootenay Lake and perhaps not as much would be needed here (Ashley *et al.*, 1999b). However, it is recognized that there are public concerns of clean versus 'polluted' waters.

Perhaps then the best solution would be some sort of medium between these two possible solutions. A mysid fishery with nutrient additions appears to have a stronger positive kokanee response than either of the two other options alone. The public may not be as concerned with the strategy of a few extra mysid fishing boats and moderate nutrient additions. However, these things are left for the politicians to decide. Hopefully this thesis adds to the knowledge base of the issues surrounding Okanagan Lake and opens some people's eyes to possibilities that were not fully considered before.

4.7 – Future Considerations

There are some obvious gaps in the Okanagan Lake knowledge base. Another survey, beyond the 1970 benthic survey of Okanagan Lake (Saether, 1970) should be completed. People who are out on the lake every day say they have seen a major increase in the number of burbot and there is some concern as to whether these fish are preying on juvenile kokanee. This concern seems to be dismissed with no real consideration, especially since no one knows how many burbot really are in Okanagan Lake at the present moment.

While nutrient additions have been discussed here as a solution possibility, more work needs to be completed on the subject. Mysid excretions have now been quantified for the summer period in Okanagan Lake, however, there is no data for this lake, or any other lake I know of that has quantified this during other periods of the year. Mysids are known to spend more time on the bottom of the lake during winter months (Lasenby, 1991) and therefore may not

remove as much nitrogen from shallow waters as thought. As well, mysids for this nitrogen experiment were taken from the middle of the lake where mysids might not necessarily reach the sediment-water interface during their diel vertical migrations (Levy, 1991). Perhaps mysids that spend more time in contact with the sediment water interface will bring more nitrogen to the surface than previously thought. Lastly, no work was done during this project to investigate possible phosphorus limitation. This possibility should be investigated further before serious talk of nutrient additions really begins.

Where mysid fisheries are concerned, more effort needs to be applied to Okanagan Lake. It is known that the current level of mysid catch will have no tangible benefits in terms of reduced mysid biomass and increased kokanee biomass. As well, with such a small percentage of the mysid population being caught and with so little variation in this fishery, very little is known of the response of mysids to fishing mortality in Okanagan Lake. At the very least, increasing the mysid catches significantly will give us a better idea of how mysids might respond to even further increases in mysid catch levels.

4.8 – Epilogue

An update is necessary here as the mysid catch values for 2001 became available as this thesis was being completed. Mysid catch values for 2001, at 100 metric tonnes, were much higher than anticipated (K. Ashley, BC Ministry of Fisheries and OLAP member, pers. comm., January 2002).

During talks with Lee Granberg (mysid boat Captain) during the summer of 2001, it was anticipated that catches by the end of 2001 would not be greater than the 30 metric tonnes of the previous year. As this number was used as the estimated 2001 catch values for all Ecosim runs in this thesis, readers are reminded that 2000 and 2001 mysid catches were thought to be equal. In light of the high 2001 mysid catch, the suggestion during the thesis that the long-term OLAP goal of 25% mysid mortality is unrealistic may prove to be pessimistic.

OLAP goals for 2002 of 20% mysid mortality are now felt to be very achievable and the largest current impediment to reaching such a goal is that the mysid as aquarium feed world market appears to be glutted with product (K. Ashley, BC Ministry of Fisheries and OLAP member, pers. comm., January 2002). As such, the current mysid fishing groups on Okanagan Lake will not expand catches beyond 2001 levels as doing so would not be profitable. A possible solution to this issue would be a government-subsidized fishery that would create monetary incentives for higher fishery catches.

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6.0 – Appendices

Appendix A. Remarks on the Okanagan Lake 1970 Wet- weight Ecopath model.

Ad. Miscellaneous Fish (open water)
Rainbow trout, Rocky Mountain Whitefish, Eastern Whitefish, Fine-scaled sucker, Ling (Clemens et al, 1939).

Species information:
Coregonus clupeaformis. Proportion of this species: 0.2
Cotostomus catostomus. Proportion of this species: 0.1
Oncorhynchus mykiss. Proportion of this species: 0.5
Prosopium williamsoni. Proportion of this species: 0.2

Biomass : -same ratio of Kokanee to Rainbow Trout as in Thompson, 1999

Consumption/Biomass Ratio :(Fishbase, 2000).

Production/Consumption Ratio :(Thompson, 1999).

Diet Composition:

(prey on Ad. Miscellaneous fish (near shore)) :(Clemens et al, 1939).

(prey on Cladocerans) : -changed from 0.045 when juv/adult groups split (Clemens et al, 1939).

(prey on Copepods) : -changed from 0.015 when juv/adult groups split (Clemens et al, 1939).

(prey on Daphnia) : -changed from 0.19 when juv/adult groups split (Clemens et al, 1939).

(prey on Kokanee (0+)) : -Adult Rainbow trout feeds heavily on kokanee salmon

(prey on Kokanee (1-3)) : -Rainbow trout, the major fish in this group, feeds almost exclusively on kokanee salmon in Okangan Lake. (Clemens et al, 1939).

(prey on Phytoplankton) : -changed from 0.045 when juv/adult groups split (Clemens et al, 1939).

Juv. Miscellaneous Fish (open water) (Clemens et al, 1939).

Species information:
Catostomus catostomus. Proportion of this species: 0.1
Coregonus clupeaformis. Proportion of this species: 0.2
Oncorhynchus mykiss. Proportion of this species: 0.5
Prosopium williamsoni. Proportion of this species: 0.2

Biomass : -same ratio of adults to juv as kokanee

Consumption/Biomass Ratio : -Q/B is same ratio as that between Kokanee (1-3) & Kokanee (0+)

Production/Consumption Ratio : -same as kokanee (0+) group

Diet Composition:

(prey on Aquatic Insect larvae) : (Clemens et al, 1939).

(prey on Cladocerans) : (Clemens et al, 1939).

(prey on Copepods) : (Clemens et al, 1939).

(prey on Daphnia) : (Clemens et al, 1939).

(prey on midge larvae) : -juv take near shore diet from adult (Clemens et al, 1939).

(prey on Phytoplankton) : (Clemens et al, 1939).

Kokanee (1-3)

Species information:
Oncorhychus nerka. Proportion of this species: 1

Biomass : (Walters, 1995).

Production/Biomass Ratio : (Sandercock, 1969).

Consumption/Biomass Ratio : (Fishbase, 2000).

Diet Composition:

(prey on Cladocerans) : -raised from 0.025 as Mysis relicta removed from diet (Thompson, 1999).

(prey on Copepods) : -raised from 0.025 as Mysis relicta removed from diet. (Thompson, 1999).

(prey on Daphnia) : -raised from 0.675 as Mysis relicta removed from diet (Thompson, 1999).

Catches: (from Recreational Fishery) : (Walters, 1995).

Kokanee (0+)

Species information:
Oncorhynchus nerka. Proportion of this species: 1

Biomass : (Walters, 1995).

Consumption/Biomass Ratio : (Foerster, 1968).

Production/Consumption Ratio : (Johnston et al, 1988).

Diet Composition:

(prey on Cladocerans) : -raised from 0.025 as Mysis relicta juv removed from diet (Thompson, 1999).

(prey on Copepods) : -raised from 0.2 as Mysis relicta juv removed from diet (Thompson, 1999).

(prey on Daphnia) : -originally 0.725, changed due to removal of M.relicta juv from diet (Thompson, 1999).

***Mysis relicta* (adult)**

Species information:
Mysis relicta. Proportion of this species: 1

Biomass : -based on intro biomass (Lasenby,1986) and year 1989 biomass (McEachern, 1999) presuming a sigmiod population increase

Production/Biomass Ratio : -average of P/B ratios from 10 experiments (Stockwell and Johannsson, 1997).

Consumption/Biomass Ratio : (Langeland et al, 1991).

Accumulated Biomass : calculated as a linear increase from 1970 biomass to year 1989 biomass

Diet Composition:

(prey on Cladocerans) : (Thompson, 1999).

(prey on Copepods) : -lowered from 0.2 to accomodate detritus in diet (Thompson, 1999).

(prey on Daphnia) : -lowered from 0.68 to accomodate detritus in diet (Thompson, 1999).

(prey on Detritus) : (Whall, 2000; Thompson, 1999).

***Mysis relicta* (juv.)**

Species information:
Mysis relicta. Proportion of this species: 1

Biomass : -juv.. 22% biomass of adults as in Thompson, 1999

Consumption/Biomass Ratio : -juvenile Q/B higher than that of adult group

Production/Consumption Ratio : (Chess and Stanford, 1999).

Diet Composition:

(prey on Cladocerans) : -lowered from 0.025 to acommodate herbivory and detritus in diet (Thompson, 1999).

(prey on Copepods) : -lowered from 0.2 to accomodate herbivory and detriuts in diet (Thompson, 1999).

(prey on Daphnia) : lowered from 0.675 to accomodate detritus and herbivory into the diet (Thompson, 1999).

(prey on Detritus) : (Whall, 2000).

(prey on Phytoplankton) : -first four months of life, juveniles are herbivorous (Gossnickle, 1982).

(prey on Rotifers) : -lowered from 0.095 to accomodate herbivoryand detritus in diet (Thompson, 1999).

Ad. Miscellaneous fish (near shore) (Clemens et al, 1939).

Species information:
Apocope falcate. Proportion of this species: 0.04
Catostomus macrocheilus. Proportion of this species: 0.13
Cottus asper. Proportion of this species: 0.13
Cyprinus carpio. Proportion of this species: 0.13
Lota lota. Proportion of this species: 0.13
Mylocheilus caurinus. Proportion of this species: 0.13
Ptychocheilus oregonensis. Proportion of this species: 0.13
Rhinichthys cataractae. Proportion of this species: 0.05
Richardsonius balteatus. Proportion of this species: 0.13

Production/Biomass Ratio : (Fishbase, 2000).

Consumption/Biomass Ratio : (Fishbase, 2000).

Ecotrophic Efficiency : -higher then that of kokanee

Diet Composition:

(prey on Aquatic Insect larvae) : (Clemens et al, 1939).

(prey on Cladocerans) : (Clemens et al, 1939).

(prey on Copepods) : (Clemens et al, 1939).

(prey on Juv. Miscellaneous Fish (near shore)) : (Clemens et al, 1939).

(prey on Kokanee (0+)) : (Clemens et al, 1939).

(prey on midge larvae) : (Clemens et al, 1939).

(prey on Phytoplankton) : (Clemens et al, 1939).

Juv. Miscellaneous Fish (near shore) (Clemens et al, 1939).

Species information:

Apocope falcate. Proportion of this species: 0.04
Catostomus macrocheilus. Proportion of this species: 0.13
Cottus asper. Proportion of this species: 0.13
Cyprinus carpio. Proportion of this species: 0.13
Lota lota. Proportion of this species: 0.13
Mylocheilus caurinus. Proportion of this species: 0.13
Ptychocheilus oregonensis. Proportion of this species: 0.13
Rhinichthys cataractae. Proportion of this species: 0.05
Richardsonius balteatus. Proportion of this species: 0.13

Consumption/Biomass Ratio : -same adult/juvenile Q/B ratio as that of kokanee

Ecotrophic Efficiency : -juv EE always higher than that of adults

Production/Consumption Ratio : -same as kokanee (0+)

Diet Composition:

(prey on Aquatic Insect larvae) : (Clemens et al, 1939).

(prey on Cladocerans) : (Clemens et al, 1939).

(prey on Copepods) : (Clemens et al, 1939).

(prey on midge larvae) : (Clemens et al, 1939).

(prey on Phytoplankton) : (Clemens et al, 1939).

Midge larvae (Clemens et al, 1939).

Species information:
Chironomus spp.. Proportion of this species: 0.2
Cryptochironomus spp.. Proportion of this species: 0.2
Orthocladius spp.. Proportion of this species: 0.2
Polypedilum spp.. Proportion of this species: 0.2
Tanytarusus spp.. Proportion of this species: 0.2

Consumption/Biomass Ratio : -higher than M. relicta juv.

Ecotrophic Efficiency : -thought to be similar to that of zooplankton

Production/Consumption Ratio : -thought to be aproximate to that of Daphnia group

Diet Composition:

(prey on Aquatic Insect larvae) : -values approx. from text (Merritt and Cummins, 1978).

(prey on Detritus) : (Merritt and Cummins, 1978).

(prey on Phytoplankton) : (Merritt and Cummins, 1978).

Aquatic Insect larvae (Clemens et al, 1939).

Species information:
(cf) *Limnephilus spp.*. Proportion of this species: 0.125
(cf) *Polycentropus spp.*. Proportion of this species: 0.125
(cf) *Hydroptila spp.*. Proportion of this species: 0.125
(df) *Enallagama cyanthigerum*. Proportion of this species: 0.125
(mf) *Ephemera simulans*. Proportion of this species: 0.125
(mf) *Hexagenia limbata*. Proportion of this species: 0.125
(wm) *Hygorbates longipalpis*. Proportion of this species: 0.125
(wm) *Piona rotunda*. Proportion of this species: 0.125

Consumption/Biomass Ratio : -higher than M.relicta juv

Ecotrophic Efficiency : -thought to be similar to that of zooplankton

Production/Consumption Ratio : -thought to be approximate to that of Daphnia group

Diet Composition:

(prey on Copepods) : -values approximated from text readings (Merritt and Cummins, 1978).

(prey on Detritus) : (Merritt and Cummins, 1978).

(prey on Phytoplankton) : (Merritt and Cummins, 1978).

Copepods

Production/Biomass Ratio : (Langeland, 1982).

Ecotrophic Efficiency : (Thompson, 1999).

Production/Consumption Ratio : (Thompson, 1999).

Diet Composition:

(prey on Cladocerans) : (Thompson, 1999).

(prey on Copepods) : (Thompson, 1999).

(prey on Daphnia) : (Thompson, 1999).

(prey on Phytoplankton) : (Thompson, 1999).

(prey on Rotifers) : (Thompson, 1999).

Cladocerans

Production/Biomass Ratio : (Langeland, 1982).

Ecotrophic Efficiency : (Thompson, 1999).

Production/Consumption Ratio : (Thompson, 1999).

Diet Composition:

(prey on Cladocerans) : (Thompson, 1999).

(prey on Daphnia) : (Thompson, 1999).

(prey on Phytoplankton) : (Thompson, 1999).

(prey on Rotifers) : (Thompson, 1999).

Daphnia

Production/Biomass Ratio : (Langeland, 1982).

Ecotrophic Efficiency : (Thompson, 1999).

Production/Consumption Ratio : (Thompson, 1999).

Diet Composition:

(prey on Phytoplankton) : (Thompson, 1999).

Rotifers (Clemens et al, 1939).
Species information:
Collotheca mutabilis. Proportion of this species: 0.175
Conochilus unicornis. Proportion of this species: 0.175
Notholca longispina. Proportion of this species: 0.3
Ploesoma truncatum. Proportion of this species: 0.175
Synchaeta sp.. Proportion of this species: 0.175

Production/Biomass Ratio : -entered so that P/B would be higher than that of Daphnia and

Cladoceran groups

Ecotrophic Efficiency : (Thompson, 1999).

Production/Consumption Ratio : (Thompson, 1999).

Diet Composition:

(prey on Phytoplankton) :

(prey on Rotifers) : (Thompson, 1999).

Phytoplankton

Production/Biomass Ratio : (Thompson, 1999).

Ecotrophic Efficiency : (Thompson, 1999).

ECOSIM Scenario: Okanagan Lake 1970 (10)

Appendix B. Diet composition of Ecopath Okanagan Lake 1970 model.

Predator/Prey	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1 Adult Misc. Fish (deep water)														
2 Juv. Misc. Fish (deep water)														
3 Kokanee (1-3)	0.422													
4 Kokanee (0+)	0.168						0.009							
5 *M. relicta* (adult)														
6 *M. relicta* (juv)														
7 Adult Misc. Fish (near shore)	0.035													
8 Juv. Misc. Fish (near shore)							0.025							
9 Midge larvae		0.460					0.323	0.387						
10 Aquatic Insect larvae		0.357					0.290	0.357	0.200					
11 Copepods	0.020	0.005	0.125	0.211	0.100	0.071	0.108	0.075		0.050	0.050			
12 Cladocerans	0.057	0.011	0.031	0.026	0.025	0.018	0.168	0.100			0.025	0.025		
13 *Daphnia*	0.228	.0410	0.844	0.763	0.555	0.034					0.050	0.025		
14 Rotifers					0.095	0.068					0.050	0.025		0.005
15 Phytoplankton	0.070	0.126				0.286	0.077	0.081	0.500	0.150	0.825	0.925	1.000	0.995
16 Detritus					0.225	0.254			0.300	0.800				
SUM	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0

Appendix C. Conversion of Wet-weight (t/km^2) into Nitrogen weight (mgN/m^2)

Species	Year 2000 wet weight (t/km^2)	Wet weight (mg/m^2)	---->	Dry weight (mg)
Misc. Fish adult (deep water)	0.007	7000	-	-
Misc. Fish juv (deep water)	0.001	1000	-	-
Kokanee (1-3)	0.285	285000	-	-
Kokanee (0+)	0.028	28000	-	-
Mysis relicta (adult)	2.850	2850000	0.150	427500
Mysis relicta (juv)	0.440	440000	0.150	66000
Misc. Fish adult (near shore)	0.452	452000	-	-
Misc. Fish juv (near shore)	0.018	18000	-	-
Midge larvae	0.266	266000	0.150	39900
Aquatic Insect larvae	0.762	762000	0.150	114300
Copepods	0.932	932000	0.150	139800
Cladocerans	0.225	225000	0.150	33750
Daphnia	0.321	321000	0.150	48150
Rotifers	0.516	516000	0.150	77400
Phytoplankton	15.914	15914000	0.150	2387100
Detritus	13.555	13555000	0.150	2033250

Species	Dry weight	------>	Protein weight	---------->	Nitrogen weight (mg/m^2)
Misc. Fish adult (deep water)	-	(a) 0.220	1540	0.172	264.605
Misc. Fish juv (deep water)	-	0.220	220	0.172	37.801
Kokanee (1-3)	-	(a) 0.209	59565	0.172	10234.536
Kokanee (0+)	-	0.209	5852	0.172	1005.498
Mysis relicta (adult)	427500	-	-	(b) 0.114	48735.000
Mysis relicta (juv)	66000	-	-	0.114	7524.000
Misc. Fish adult (near shore)	-	(a) 0.180	81360	0.172	13993.920
Misc. Fish juv (near shore)	-	0.180	3240	0.172	557.280
Midge larvae	39900	-	-	(d) 0.110	4389.000
Aquatic Insect larvae	114300	-	-	0.107	12230.100
Copepods	139800	-	-	0.103	14399.400
Cladocerans	33750	-	-	0.099	3341.250
Daphnia	48150	-	-	0.096	4622.400
Rotifers	77400	-	-	0.092	7120.800
Phytoplankton	2387100	-	-	(c) 0.090	214839.000
Detritus	2033250	-	-	0.080	162660.000

*(a) Sidwell et al (1974)(b) Gorokhova, E. & Hansson, S. (2000) (c) Vargas, M. et al (1998)(d)linear interpolation from Mysid values to Rotifer values.

Appendix D. Conversion of Q/B for Nitrogen model (selected groups).

Kokanee (1-3)

Year 2000 wet weight (t/km^2)	Q/B	Q	N weight	N.weight eaten
0.285	**3.700**	**1.055**	**10.235**	**15.338**

	Diet composition	Amnt eaten wet weight (t/km^2)	Amnt eaten Wet weight (mg/m^2)	-------->	Dry weight	---------->	Nitrogen weight (mg/m^2)
Copepods	0.125	0.132	131.813		19.772	0.103	2.037
Cladocerans	0.031	0.033	32.690		4.903	0.099	0.485
Daphnia	0.844	0.890	889.998		133.500	0.096	12.816
							15.338

Kokanee (0+)

Year 2000 wet weight (t/km^2)	Q/B	Q	N weight	N.weight eaten
0.028	**8.500**	**0.238**	**1.005**	**3.483**

	Diet composition	Amnt eaten wet weight (t/km^2)	Amnt eaten Wet weight (mg/m^2)	-------->	Dry weight	---------->	Nitrogen weight (mg/m^2)
Copepods	0.211	0.050	50.218		7.533	0.103	0.776
Cladocerans	0.026	0.006	6.188		0.928	0.099	0.092
Daphnia	0.763	0.182	181.594		27.239	0.096	2.615
							3.483

***M. relicta* (adult)**

Year 2000 wet weight (t/km^2)	Q/B	Q	N weight	N.weight eaten
2.850	**18.250**	**52.013**	**48.735**	**723.975**

	Diet composition	Amnt eaten wet weight (t/km^2)	Amnt eaten Wet weight (mg/m^2)	------>	Dry weight	---------->	Nitrogen weight (mg/m^2)
Copepods	0.100	5.201	5201.250		780.188	0.103	80.359
Cladocerans	0.025	1.300	1300.313		195.047	0.099	19.310
Daphnia	0.555	28.867	28866.938		4330.041	0.096	415.684
Rotifers	0.095	4.941	4941.188		741.178	0.092	68.188
Detritus	0.225	11.703	11702.813		1755.422	0.080	140.434
							723.975

***M. relicta* (juv)**

Year 2000 wet weight (t/km^2)	Q/B	Q	N weight	N.weight eaten
0.440	**25.000**	**11.000**	**7.524**	**149.482**

	Diet composition	Amnt eaten wet weight (t/km^2)	Amnt eaten Wet weight (mg/m^2)	-------->	Dry weight	---------->	Nitrogen weight (mg/m^2)
Copepods	0.071	0.781	781.000		117.150	0.103	12.066
Cladocerans	0.018	0.198	198.000		29.700	0.099	2.940
Daphnia	0.304	3.344	3344.000		501.600	0.096	48.154
Rotifers	0.068	0.748	748.000		112.200	0.092	10.322
Phytoplankton	0.286	3.146	3146.000		471.900	0.090	42.471
Detritus	0.254	2.794	2794.000		419.100	0.080	33.528
							149.482

*Wet weight to dry weight conversion factor chosen to be 0.15. For most groups, dry weight was converted directly into nitrogen weight. However, other groups required the extra conversion of dry weight into protein weight.

Appendix E. Calculation of Bacterial Nitrogen Biomass.

2.62E+11 L	Volume of Okanagan Lake	(Clemens *et al*, 1939)
*278ug C/L=	7.2836E+13μg C bacteria	(Overbeck *et al*, 1994)
/ 1000 ug/mg=	72836000000mg C bacteria	
*.175=	12746300000mg N bacteria	-assuming 40C:7N by weight
/350000 m^2=	36418mg N bacteria/m^2	

Appendix F. Data used to produce Figures 6-10.

Data used for figures 6 and 7	**2010**	**2010**	**2010**	**2020**	**2020**	**2020**
Fishing effort (relative to year 2000 effort)	Kokanee (1-3) biomass (2010)	Mysid biomass (2010)	Mysid catch 2010 (tonnes)	Kokanee (1-3) biomass (2020)	Mysid biomass (2020)	Mysid catch 2020 (tonnes)
1	0.71	0.96	28.70	0.66	1.05	31.50
2	0.72	0.97	58.45	0.66	1.05	63.00
3	0.74	0.98	88.55	0.67	1.05	94.15
4	0.78	0.99	119.00	0.70	1.05	125.65
5	0.83	1.00	150.85	0.75	1.05	157.15
6	0.88	1.01	181.30	0.82	1.04	186.90
7	0.94	1.00	210.70	0.90	1.02	214.90
8	0.99	0.99	238.35	0.98	1.01	241.50
9	1.07	0.98	264.60	1.07	0.99	266.35
10	1.15	0.96	289.45	1.16	0.97	289.80
11	1.24	0.95	312.55	1.26	0.95	312.20
12	1.36	0.93	334.25	1.36	0.93	333.20
13	1.65	0.89	347.20	1.71	0.89	346.15
14	2.19	0.84	352.10	2.61	0.81	341.25
15	2.79	0.79	354.20	3.57	0.74	332.50
16	3.43	0.74	353.85	4.54	0.67	320.95
17	4.08	0.69	351.05	5.53	0.60	306.60
18	4.74	0.64	346.15	6.50	0.54	290.15
19	5.38	0.60	339.50	7.47	0.48	271.95
20	6.32	0.53	318.85	8.40	0.42	253.05

Data used for figures 8 and 9

Nutrient Level (rel. 1970)	% Nutrient increase	Kokanee (1-3) biomass (2010)	Mysid biomass (2010)	Kokanee (1-3) biomass (2020)	Mysid biomass (2020)
0.27	0	0.71	0.96	0.66	1.05
0.33	22	1.96	0.96	2.18	0.95
0.39	44	3.30	1.00	3.48	0.96
0.45	67	4.51	1.05	4.61	1.01
0.51	89	5.54	1.09	5.58	1.08
0.57	111	6.40	1.13	6.39	1.15
0.63	133	7.09	1.15	7.06	1.19
0.69	156	7.66	1.17	7.59	1.22
0.75	178	8.13	1.18	8.02	1.23
0.81	200	8.52	1.19	8.37	1.24
0.87	222	8.85	1.19	8.66	1.24
0.93	244	9.12	1.19	8.91	1.24
0.99	267	9.36	1.19	9.12	1.24

Data used for figure 10

Nutrient Level (rel. 1970)	% Nutrient increase	Kokanee (1-3) biomass (2010)	Mysid biomass (2010)	Kokanee (1-3) biomass (2020)	Mysid biomass (2020)
0.27	0	3.43	0.74	4.54	0.67
0.33	22	4.81	0.75	6.08	0.68
0.39	44	5.96	0.76	7.30	0.68
0.45	67	6.91	0.77	8.26	0.69
0.51	89	7.67	0.77	9.01	0.69
0.57	111	8.28	0.77	9.61	0.69
0.63	133	8.78	0.77	10.09	0.69
0.69	156	9.21	0.77	10.49	0.69
0.75	178	9.58	0.76	10.81	0.69
0.81	200	9.88	0.76	11.08	0.69
0.87	222	10.13	0.76	11.30	0.68
0.93	244	10.35	0.76	11.48	0.68
0.99	267	10.53	0.76	11.63	0.68

Appendix G. Urea and Ammonia standards. Concentration of Ammonia = 0.0012 * absorbance; concentration of Urea = 0.0004 * absorbance.

Ammonia standards

Trial	Volume (ml)	Absorbance @ 636 nm	Conc. NH_4-N (g/L)
A	0.175	0.12308	0.00014
B	0.250	0.32547	0.0002
C	0.500	0.57407	0.0004
D	1.000	0.96840	0.0008
E	2.000	1.68800	0.0016
F	3.000	2.06410	0.0024
G	4.000	2.30090	0.0032

Urea standards

Trial	Volume (ml)	Absorbance @ 520 nm	Conc. urea (g/L)
A	0.500	0.25887	0.0001532
B	1.000	1.05050	0.0003065
C	1.500	1.46380	0.0004597
D	2.000	1.70700	0.0006130
E	2.500	2.00350	0.0007662
F	3.000	2.16420	0.0009195

Appendix H. Calculations of urea and ammonia excretions (Trial #1 only) for *Mysis relicta.*

Ammonia trial #1

Trial	Absorb @ 636 nm	Conc. NH_4-N (mg/L)	Conc. NH_4-N (mg)	Exp-Control	mg/hr	g/(mg mysid*hr) $*10^8$ 42.33mg/mysid	microg/(mg mysid*hr)
1	0.218	0.262	0.0393	-	-	-	-
2	0.573	0.688	0.1032	0.0639	0.0319	2.52	0.0252
3	0.192	0.231	0.0347	-	-	-	-
4	0.611	0.734	0.1101	0.0754	0.0377	2.97	0.0297
5	0.156	0.188	0.0282	-	-	-	-
6	0.315	0.378	0.0567	0.0285	0.0143	1.12	0.0112

Urea trial #1

Trial	Absorb @ 520 nm	Conc. urea (mg/L)	Conc. urea (mg)	Exp-Control	mg/hr	g/(mg mysid*hr) $*10^8$	microg/(mg mysid*hr)
1	2.02	0.808	0.121	-	-	-	-
2	2.45	0.980	0.147	0.0259	0.0129	1.02	0.0102
3	2.11	0.846	0.126	-	-	-	-
4	2.64	1.054	0.158	0.0319	0.0159	1.25	0.0125
5	1.23	0.493	0.074	-	-	-	-
6	2.29	0.914	0.137	0.0633	0.0317	2.49	0.0249