THE DECLINE OF AMERICAN EEL (*Anguilla rostrata)* IN THE LAKE ONTARIO/ST. LAWRENCE RIVER ECOSYSTEM: A MODELING APPROACH TO IDENTIFICATION OF DATA GAPS AND RESEARCH PRIORITIES

Prepared for:

Lake Ontario Committee
Great Lakes Fishery Commission
2100 Commonwealth Blvd., Suite 209
Ann Arbor, Michigan
48105-1563

Prepared by:

BEAK INTERNATIONAL INCORPORATED
14 Abacus Road
Brampton, Ontario
L6T 5B7

March 2001
BEAK Ref: 21852.1

ABSTRACT

Hypotheses concerning the observed decline in recruitment and abundance of American eels, *Anguilla americana*, in Lake Ontario and the upper St. Lawrence River are summarized. These hypotheses were presented in a questionnaire to managers and biologists with knowledge of eels for scoring with regard to their importance in determining eel population dynamics. As well, the hypotheses were used to construct a life history model based on disaggregated Beverton-Holt recruitment dynamics. The population is modelled as six sub-stocks with panmictic reproduction and unique parameter sets and recruitment dynamics within each sub-stock.

Eleven responses were received to the questionnaire. Habitat reduction ranked as most important influence on recruitment and abundance, followed by mortality associated with downstream passage at dams and overfishing on resident eels. The impacts of microcontaminants and impacts in the oceanic environment ranked lower and mortality associated with infestations of swimbladder nematode was ranked very low. None of those polled offered an opinion on the importance of harvest of sargassum weed in the Sargasso Sea as an influence on recruitment and abundance.

Data from which to estimate parameters are sparse, and in some cases nonexistent. The modeling approach was limited to assessing the influence on model outcomes of varying the parameters within plausible ranges based on literature reports, consultation with experts and life history theory. The impact of varying individual parameters was examined in two ways: by comparing single trials of the model with one parameter varied from a base case, and comparing outcomes; and by Monte Carlo simulations which compared the influence of individual parameters by computing rank correlations of random values of the parameters with outcomes over a thousand trials of the model. Total eel population capacity was allowed to vary in some runs, and the age structure of the Lake Ontario – upper St. Lawrence sub-stock was run with assumed residence of 12 or 17 years before onset of maturity.

Based on sensitivity analyses the top five plausible impacts on the entire population in terms of model sensitivity, from greatest to least influential, are oceanic effects on early life stages, cumulative effects of fishing (and other anthropogenic mortality) on resident (juvenile) eels, dam passage effects, habitat impacts throughout the entire range, habitat impacts in the Lake Ontario/upper St. Lawrence sub-stock. The five most plausible impacts on the Lake

Ontario/upper St. Lawrence River contribution to total reproduction, from greatest to least influential, in terms of model sensitivity are cumulative effects of fishing (and other anthropogenic mortality) on resident eels, oceanic effects, dam passage effects, habitat impacts in the Lake Ontario/upper St. Lawrence sub-stock and habitat impacts throughout the entire range.

We conclude that reduction of fishing pressure on resident eels and mitigation of upstream and downstream passage impacts from dams would likely have a positive effect on the Lake Ontario/upper St. Lawrence sub-stock.

We identify areas for further research that would significantly decrease the uncertainty attached to models characterizing American eel population dynamics.

ACKNOWLEDGEMENTS

This research was sponsored by the Lake Ontario Committee of the GLFC. Drafts were reviewed by Alastair Mathers and Tom Stewart of MNR, and Steve LaPan of NYSDEC. The paper benefited greatly from these reviews. James McKenna, Jr. of the U.S. Geological Survey also provided a useful review, as did W. Dieter-Bush of the Atlantic States Marine Fisheries Commission. Brian Jessop (DFO) provided valuable insight with respect to plausible ranges for glass eel and elver mortality rates. Ann Barse (Salisbury State University, Salisbury, MD) provided the interesting and useful information on the exotic swim bladder nematode.

TABLE OF CONTENTS

		Page
ABSTRACT		i
ACKNOWLEDGEMENTS		iii
1.0	INTRODUCTION AND OBJECTIVES	1.1
2.0	BACKGROUND	2.1
	2.1 Life History of American Eel	2.1
	2.1.1 General Life History	2.1
	2.1.2 Oceanic Life Stages	2.1
	2.1.2.1 Silver-phase Eels	2.2
	2.1.2.2 Eggs and Leptocephalus (Larval) Stages	2.3
	2.1.2.3 Glass Eels/Elvers	2.3
	2.1.3 Estuarine and Freshwater Life Stages	2.4
	2.1.3.1 Glass Eels/Elvers	2.4
	2.1.3.2 Juveniles (Yellow-phase Eels)	2.4
	2.1.3.3 Maturing Silver-phase Eels	2.6
	2.2 Potential Causes of the Decline in Recruitment to the Lake Ontario-Upper St. Lawrence River Ecosystem	2.6
3.0	EVALUATING EFFECTS ON THE LAKE ONTARIO/UPPER ST. LAWRENCE RIVER EEL SUB-STOCK	3.1
	3.1 Questionnaire	3.1
	3.2 Development of a Life History-based model	3.1
4.0	RESULTS	4.1
	4.1 Questionnaire	4.1
	4.2 Model Implementation and Sensitivity Analyses	4.1
5.0	DISCUSSION	5.1
6.0	REFERENCES	6.1

APPENDIX A: Graphical Model Output

APPENDIX B: Sensitivity Results: Frequency Distributions and Descriptive Statistics

1.0 INTRODUCTION AND OBJECTIVES

Numerous scientific reports (e.g., Castonguay *et al.*, 1994a,b; Marcogliese *et al.*, 1997; Casselman *et al.*, 1997a,b) and resource agencies (e.g., ASMFC, 2000), suggest that the American eel, *Anguilla rostrata*, is experiencing a rapid decline in abundance in the Lake Ontario/St. Lawrence River (LO-SLR) ecosystem. Haro *et al.* (2000) present evidence for a decline in the population of the American eel from several widely distributed regions of North America from 1984 to 1995. Reductions in the number of juvenile (yellow-phase) eels ascending the eel ladder at the R.H. Saunders dam on the St. Lawrence River (Casselman *et al.*, 1997a) was the earliest indicator of a possible precipitous decline in eel abundance. Between 1982 and 1995, the number of juveniles passed at the ladder during the peak migration period dropped from over 25,000 per day to less than 1,000 per day. Marcogliese *et al.* (1997) provided evidence that the substantial declines in recruitment to the Lake Ontario/upper St. Lawrence River system since 1982 have been reflected in the catch per unit effort (CUE) in the commercial juvenile eel fishery in the Ontario waters of Lake Ontario. In the Quebec silver eel fishery, catches steadily declined through the 1990s despite a substantial increase in the price offered to eel fishers (Casselman, 1997; Caron and Verreault, 1997). A significant decline in abundance is also evident in the silver-phase eel commercial weir fishery dataset for the St. Lawrence River estuary (Haro, 2000). A similar decline in catch, in spite of a five-fold increase in price, also occurred in the Atlantic States in the mid-1990s (Jessop, 1997; Richkus and Whalen, 1999).

A number of factors have been suggested as the cause, or causes, of this decline in recruitment to, and the abundance of, the Lake Ontario-upper St. Lawrence River sub-stock, e.g.:

- habitat loss/fragmentation due to blockage and/or impedance of upstream passage;
- turbine mortality on silver eels during downstream passage;
- overexploitation of multiple life stages, e.g., glass eels/elvers, yellow-phase eels, silver-phase eels;
- microcontaminants and their effects on survival and reproduction;
- oceanic environmental change;
- pre-spawning mortality associated with swim bladder worm infections; and
- the unregulated commercial harvest of Sargassum (*Sargassum* spp.) in the spawning zone.

One of the key issues involved in determining the effects of these factors is the high degree of uncertainty (due to a lack of information associated with the unique and complex life history of *A. rostrata*) with respect to age structure, growth, life stage-specific mortality, fecundity, density-dependence and other important data needed to draw scientifically-defensible conclusions (ASMFC, 2000). This large uncertainty is also problematic in any attempt to quantify, or estimate the relative effectiveness of potential mitigative measures that might help stimulate a recovery of recruitment to the Lake Ontario-upper St. Lawrence River (LO-SLR) ecosystem. At present, we are not aware of any attempt to determine the relative population-level and sub-stock-level effects associated with each of these potential causes of eel decline in the LO-SLR system.

The Lake Ontario Committee (LOC) of the Great Lakes Fishery Commission (GLFC) has become concerned with the current status of American eel in Lake Ontario and the upper St. Lawrence River. This concern has lead the LOC/GLFC to assign the task of development of an adaptive modeling approach to address the possible reasons for the observed decline in this part of the range of *A. rostrata*. The initial objective of this effort is the development of a model that employs established ecological theory to describe the life history and population/sub-stock dynamics of *A. rostrata*, with explicit representation of the Lake Ontario-upper St. Lawrence River sub-stock. Other objectives are:

- to conduct Monte Carlo simulations to analyze model sensitivity;
- to use the results of these sensitivity analyses to identify critical data gaps and research priorities; and
- attempt to rank the potential causes of the decline, and potential mitigative measures.

This discussion paper includes background information describing the life history of American eel and detailing the suspected causes of the decline in the LO-SLR sub-stock. It also includes the development and implementation of a life-history-based population dynamics model for American eel, and the use of sensitivity analyses to examine data gaps and rank the sensitivity of various model configurations to factors which may be affecting the population and the LO-SLR sub-stock. These rankings are interpreted and used to identify data gaps and research priorities for management.

2.0 BACKGROUND

2.1 Life History of American Eel

The panmictic nature of American eel life history implies that factors affecting any life stage, in any of the geographic areas of the range, have the potential to affect the abundance of other life stages throughout the range of the population. Depending on the nature of the factors, the effect(s) may be very different in various portions of the range. Some knowledge of American eel life history is required to develop a life history-based model of the population; therefore, the following sections consist of a brief review of the life history of *A. rostrata* with an emphasis on the Lake Ontario/St. Lawrence River (LO-SLR) component of the population.

2.1.1 General Life History

The life history of *A. rostrata* encompasses freshwater, estuarine and oceanic environments. The species is catadromous, i.e., spawning in the marine environment and migrating into freshwater habitats to feed and mature, before migrating back to sea as mature adults to spawn. American eels spawn in the vicinity of the Sargasso Sea, with transport and distribution of early life stages to coastal waters from northern South America to Greenland. Juveniles tend to migrate considerable distances up rivers to become long-term residents of lacustrine and riverine habitats. As juveniles become mature, they begin to metamorphose into adult eels which move downstream to the sea as they migrate to the spawning habitat in the Sargasso sea.

The fisheries literature related to *A. rostrata* employs a classification of life stages that is only loosely related to ontogeny. The stages identified by fishers and fisheries workers do have the virtue of generally corresponding to changes in habitat use and migratory behaviour. We have therefore employed the common usage in naming stages.

2.1.2 Oceanic Life Stages

Life stages which occur in the oceanic environment include silver-phase migrants, spawners, eggs, leptocephalus larvae and glass eels.

2.1.2.1 Silver-phase (= Bronze-phase) Eels

Maturing silver-phase *A. rostrata* enter the Atlantic Ocean after completing downstream migrations from freshwater lakes and rivers, and through estuaries. Metamorphosis from the yellow-phase begins in freshwater and results in rapid morphological and physiological changes which are widely thought to better adapt silver-phase eels to swimming and survival during the oceanic, adult phase of the life cycle (Kleckner, 1980; Pankhurst, 1982). The changes include:

- colour change to a metallic silver or bronze sheen dorso-laterally and white or cream ventrally (Parkhurst and Lythgoe, 1982);
- accumulation of body fat content (Sorensen and Pankhurst, 1988);
- thickening of the integument (Sorensen and Pankhurst, 1988);
- enlargement of eyes and changes in visual pigments in the retina (Pankhurst, 1982);
- enlargement of swim bladder rete (Kleckner and Krueger, 1981);
- degeneration of the digestive tract (Parkhurst and Sorensen, 1984); and
- beginning of gamete maturation (Krueger and Oliveira, 1997).

The oceanic portion of adult migration is poorly understood. Only a few specimens have been collected in offshore waters, e.g., Wenner (1973).

Tesch (1977, 1991) synthesized available data from a variety of sources to contend that the spawning zone is located in the Sargasso Sea south of Bermuda and north of the Bahamas (Facey *et al.*, 1987). Distance traveled to reach the spawning zone varies substantially over the range of *A. rostrata*. Silver eels from the western end of Lake Ontario must migrate well over 6000 km to reach the spawning zone whereas eels outmigrating from rivers in Georgia are required to migrate only about 1300 km. Spawning is thought to occur between February and April in the upper 300 m of the spawning zone (Kleckner *et al.*, 1983; McCleave and Kleckner, 1985). It is very probable that the timing of the onset of the migration varies with distance from the spawning zone so that eels from Lake Ontario or Lake Champlain begin to outmigrate in June and the silver eel outmigration in the Delaware River begins in late August or September. This timing is thought to synchronize the arrival of all components of the spawning population at the spawning zone (Helfman *et al.*, 1987).

The fecundity of *A. rostrata* varies with body size (e.g., Wenner and Musick, 1974), and female body size varies such that the largest (and oldest) silver-phase females are found in the St. Lawrence River estuary and smaller (younger) silver-phase females are found in Georgia (Helfman *et al.*, 1987). Krueger and Oliveira (1997) suggest that this size trend is related to the minimum size required to complete the seaward migration to the Sargasso. Fecundity per female is thought to range from 0.4 to 8.5 million eggs (Facey *et al.*, 1987), although Krueger and Oliveira (1999) report fecundity as high as almost 20 million eggs. *A. rostrata* is assumed to be semelparous, and eels from throughout the range are assumed to mix randomly during spawning (Avise *et al.*, 1986, 1990).

2.1.2.2 Eggs and Leptocephalus (Larval) Stages

Eggs are small, about 1.1 mm (Tesch, 1991) and probably hatch within a week of deposition. McCleave *et al.* (1987) suggest that hatching peaks in February and may continue into April. The larval stage is termed the leptocephalus and is transported by a variety of oceanic currents to the coastal waters of the range of *A. rostrata* (see Kleckner and McCleave, 1982; Power and McCleave, 1983). The duration of this stage is thought to be up to one year (Facey *et al.*, 1987) but may last longer (Fahay, 1978). Drifting in the Gulf Stream is probably the means by which larvae reach Canadian coastal waters and the Gulf of St. Lawrence and metamorphose to the glass eel and elver stages. This metamorphosis essentially transforms the eel from a pelagic animal to a benthic animal. This process is thought to occur as the animals enter coastal waters at 8 to 12+ months after spawning.

Mortality rates for the larval stage are unknown; however, evidence from other ocean spawning species with long-term pelagic larvae suggests that mortality through this stage is very high (Bond, 1979). No commercial or recreational fishery exists for the leptocephalus stage; however, the potential effect of commercial harvesting of Sargasso weed in the Sargasso Sea is presently unknown.

2.1.2.3 Glass Eels/Elvers

The commonly used terminology of eel life history differentiates juvenile stages based on superficial appearance for which there is no real biological basis. Glass eels are unpigmented animals which have metamorphosed into the general morphology of juvenile eels, but without the dark pigmentation of elvers or yellow-phase juveniles. The glass eel is a short transitional phase during which active inshore and upstream migration begins. As a result, glass eels occur in both coastal and estuarine habitats.

Most glass eels and elvers reach estuarine waters of New England in the late winter/spring approximately one year after spawning (Facey *et al.*, 1987). Historically, this timing was probably similar for most glass eels and elvers entering the estuaries of the northern parts of the range, i.e., Nova Scotia, the Gulf of St. Lawrence, Newfoundland, Labrador, Greenland. Glass eels, partially pigmented elvers, and fully pigmented elvers begin to actively move upstream as they become highly rheotactic.

2.1.3 Estuarine and Freshwater Life Stages

These life stages of *A. rostrata* include glass eels/elvers, a transitional phase between the oceanic and freshwater/estuarine environments, yellow-phase or juvenile eels, and maturing, i.e., silver-phase, eels but only during the freshwater/estuarine portion of the downstream, seaward migration.

2.1.3.1 Glass Eels/Elvers

The glass eel/elver stages are of short but variable duration, likely about three to twelve months, much of which is spent migrating upstream through the marine and freshwater tidal zone of estuaries (e.g., Haro and Krueger, 1991; Jessop, 1998). Glass eels/elvers may migrate upstream using flood tides to travel considerable distances into freshwater environments. Elvers entering the Gulf of St. Lawrence probably use a variety of mechanisms to move upstream.

2.1.3.2 Juveniles (Yellow-phase Eels)

There does not appear to be a clear distinction between the late elver stage and early juvenile (yellow-phase) stage. Eels larger than about 150 mm are considered to be juvenile or yellow-phase eels. These juveniles may continue to actively migrate upstream for many years, or may establish home territories in estuaries and brackish tidal zones of rivers. Active upstream migrants may move considerable distances over very long periods. A juvenile eel ladder was installed in an ice sluice at the Moses-Saunders dam near Cornwall, Ontario, and began operation in 1974 (Liew, 1982). Juveniles passing the eel ladder are considered to be 3- to 8-years-old (J. Casselman, Glenora Fisheries Research Station, Picton, ON, pers. comm.).

The standardized peak juvenile migration period at the Moses-Saunders juvenile eel ladder is 31 days in duration and generally occurs in July/August. The number of eels passing the ladder during this peak period was demonstrated to be an index of recruitment of eels to the

Lake Ontario yellow eel fishery (Marcogliese *et al.*, 1997). Juveniles commonly move even further upstream, to the waters of western Lake Ontario and lower Niagara River. Historically, the other large tributary rivers of Lake Ontario, e.g., the Oswego, Genessee and Black Rivers and the tributaries of the upper St. Lawrence River., e.g., the Ottawa and Richelieu Rivers are thought to have harboured a very large proportion of the juvenile eel population in the LO-SLR ecosystem, e.g., Lary and Busch (1997). Dams on many of these rivers have essentially excluded juveniles from vast areas of habitat upstream of these migration barriers. A similar situation exists in many parts of the range of *A. rostrata* (ASMFC, 2000).

Helfman *et al.* (1987) show that juvenile females are distributed throughout the range of *A. rostrata*, but that males are generally restricted to estuarine habitats and are proportionally more abundant in the southeastern U.S. The LO-SLR portion of the stock is exclusively females (Facey *et al.*, 1987). The duration of the juvenile stage varies considerably over the range of *A. rostrata*. Females mature at greater size than do males and females from geographical extremes of the range, e.g., LO-SLR, mature later and at greater sizes than females from more southern waters (Helfman *et al.*, 1987).

Juvenile mortality rates have not been determined for *A. rostrata*. DeLeo and Gatto (1995) report that the natural mortality rate for juvenile *A. anguilla* was 65 percent. Fisheries exist for juvenile *A. rostrata* in many jurisdictions (ASMFC, 1997). Richkus and Whalen (1999) observe that all fishing mortality in *A. rostrata* is pre-spawning mortality; therefore, long-lived juveniles are potentially subjected to high cumulative fishing mortality during their residence in rivers and estuaries. The commercial juvenile eel fishery in the LO-SLR system is presently limited to Canadian waters. Juvenile eel fisheries, using a variety of gears, occur in the Bay of Quinte, the eastern outlet basin of Lake Ontario, parts of the upper SLR-Thousand Islands area, Lake St. Francis and Lake St. Pierre. No data are available on fishing mortality rates for juvenile *A. rostrata*. Juvenile fishing mortality rates can be expected to vary widely depending on the habitat (lake, river, estuary) jurisdiction, gear restrictions, seasons, etc. Marcogliese *et al.* (1997) showed that the relative abundance of juvenile eels caught in a Lake Ontario yellow eel fishery was closely related to the numbers of juveniles passing the eel ladder at the Moses-Saunders Dam, with lags of five to eight years for different fishing techniques.

2.1.3.3 Maturing Silver-phase Eels

In LO-upper SLR sub-stock, metamorphosis from the juvenile to the adult stage begins in freshwater. Except for a series of artificial maturation experiments on *A. anguilla*, (e.g. Pankhurst and Sorensen (1984), Pankhurst (1982), Pankhurst (1984), and Sorensen and Pankhurst (1988)), the process is poorly understood. During the downstream migration, maturing eels may move at considerable rates if conditions are suitable. Downstream movement rates can exceed 30 km per day (Stasko and Rommel, 1997; K. McGrath, New York Power Authority, 123 Main St., White Plains, NY, 10601, pers. comm.). During the downstream migration, silver-phase eels are subjected to several potential sources of natural mortality, turbine-induced mortality and fishing mortality. Dutil *et al.* (1987) observed an apparently higher than expected number of natural mortalities in the St. Lawrence estuary, which was thought to be associated with osmotic stress during the transition from freshwater to marine conditions. Some level of silver eel mortality is attributable to the passage of downstream migrants through turbines at hydroelectric generating stations and has been estimated as 25 to 40% by some authors (Castonguay *et al.*, 1994a; Hadderingh, 1994). Long-standing tidal weir fisheries occur on many of the larger rivers and estuaries in the range of *A. rostrata*, e.g., the St. Lawrence estuary and the Richelieu (Eales, 1968) and Delaware Rivers. Fishing mortality rates have been investigated only in the St. Lawrence River estuary where mark-recapture experiments have indicated an annual exploitation rate of about 23 percent (Caron and Verreault, 1997).

2.2 Potential Causes of the Decline in Recruitment to the Lake Ontario-Upper St. Lawrence River Ecosystem

Although the decline of recruitment and abundance in the LO-SLR sub-stock are well-documented, there are at least seven generally known, or suspected, causes of the decline, i.e.:

- habitat loss/fragmentation due to blockage and/or impedance of upstream passage;
- turbine mortality on silver eels during downstream passage;
- overexploitation of multiple life stages, e.g., glass eels/elvers, yellow-phase eels, silver-phase eels;
- microcontaminants and their effects on survival and reproduction;
- oceanic environmental change; and

- pre-spawning mortality associated with swim bladder worm infections, and
- the unregulated commercial harvest of Sargasso weed (*Sargassum* spp.) in the spawning zone.

These suspected "causes of decline" in recruitment to the LO-SLR ecosystem are not exhaustive, but this list is thought to include most of the major factors that could be functioning to limit eel abundance in the system. Although recruitment to the LO-SLR, at least recruitment to those portions of the sub-stock upstream of the Moses-Saunders generating station, is in dramatic decline, and there is some evidence of a continent wide decline (Richkus and Whalen, 1999), some eel researchers suggest that comparable elver recruitment declines have not occurred in other areas in the range of *A. rostrata,* (e.g. New Brunswick and New England.

Castonguay *et al.* (1994a,b), Casselman *et al.* (1997), Marcogliese *et al.* (1997), and Richkus and Whalen (1999) analyzed five of the above causes:

- dam-induced fragmentation of upstream passage habitat preventing and/or delaying juvenile migration into rearing habitats, e.g., Lary and Busch (1997);
- mortality of silver-phase eels passing through hydroelectric turbines during downstream migration (e.g., Hadderingh, 1990);
- cumulative fishing mortality of multiple life-stages (Richkus and Whalen, 1999);
- microcontaminants affecting reproductive success, e.g., Giesy *et al.* (1986), Hodson *et al.* (1992); and
- oceanic environmental change (e.g., Greatbatch *et al.*, 1991) affecting transport (McCleave, 1987) and/or survival of early life stages.

These competent reviews consistently conclude that insufficient information is available to definitively determine that the decline is attributable to one or more of these causes. Therefore, the literature on the five potential causes listed above will not be extensively reviewed here. Two additional potential causes of the decline, which were not included in previous reviews, i.e., the potential effects of the exotic swim-bladder nematode, *Anguillicola crassus,* on the American eel population and respective sub-stocks, and the potential effects of the unregulated commercial harvesting of Sargassum (*Sargassum* spp.) in the spawning zone and nursery habitat of the American eel, deserve additional attention and are addressed below.

Anguillicola crassus

The swimbladder nematode, *A. crassus*, parasitizes three anguillid species of eels: the Japanese eel, *A. japonica*, the European eel, *A. anguilla*, and the American eel, *A. rostrata* (Barse and Secor, 1999). The life cycle, known only from studies on European eels, includes a required crustacean intermediate host, which is usually a copepod, and an optional paratenic host (i.e., transport hosts), which could be one of many species of finfish, as well as various species of insect larvae, snails, and amphibian larvae (Moravec and Konecny, 1994; Moravec and Skoríková, 1998). Thus far, no work has been done to identify species of intermediate or paratenic hosts in North American systems.

An important gap in our knowledge of eel biology is the contribution of *A. crassus* infections to the natural mortality, growth, and fecundity of American eels. This nematode parasite has been shown to cause mass mortalities of eels in Europe (*A. anguilla*) at least in Lake Balaton in Hungary. It has also been implicated as a source of mortality in various aquaculture ponds. And there is much literature on sublethal (pre-lethal?) effects of this parasite on the health of the eel (Würtz and Taraschewski, 2000).

Infections cause thickened swimbladder walls, inflammation, and dilation of blood vessels; but the effects of these pathological changes on the ability of the swimbladder to function as a hydrostatic organ are not known. Kirk *et al.*(2000) reported on such pathological changes, as have been observed in many previous studies. They proposed that because migrating silver eels undergo vertical migrations to the surface at night, and swim at 700 m depth by day, that the swimbladder pathologies caused by infections with *A. crassus* may impair the ability of eels to migrate to the Sargasso Sea for spawning.

Eggs and leptocephali most likely cannot become infected because this parasite is infective for only eight days in full strength seawater, and no intermediate hosts (crustaceans, usually copepods) that live in marine systems have been identified (Kirk *et al.*, 2000). All other life stages of eels can become infected, from glass eels to the silver eel stage (De Charleroy *et al.*, 1990; Thomas and Ollevier, 1992).

Kirk *et al.* (2000) showed that, under laboratory conditions, most *A. crassus* can survive in eels maintained in 50% and 100% seawater for up to six months, and therefore, an infected silver eel could carry the physiological burden of this infection to its spawning grounds. Only about 10% of the worms in these 50% and 100% seawater-maintained eels were “damaged”. Furthermore, these authors demonstrated that a dominant calanoid copepod of estuaries of

the northern hemisphere *Eurytemora affinis*, can serve as an intermediate host, so that transmission in coastal brackish water is probable. In the Baltic Sea, field studies have shown that two marine species of fish can serve as paratenic host: the black goby (*Gobius niger*), and the deep-snouted pipefish (*Syngnathus typhle*) (Höglund and Thomas, 1992; Reimer e*t al*., 1994).

Kirk *et al.* (2000) observed from infection experiments that the ability of juvenile stage *A. crassus* to infect intermediate and paratenic hosts was greatest in fresh water, and declined with increases in salinity. However, larvae were infective to intermediate and paratenic hosts for 21 days in 50% seawater. Thus, transmission in brackish water is probable. Transmission is possible in fresh and brackish water systems, therefore it is unlikely that salinity will have a limiting effect on the spread of *A. crassus* in any of the sub-stocks of American eel.

A. crassus has successfully colonized much of the east coast of North America from Florida to New York, yet it has not been found in the St. Lawrence River or in Nova Scotia (based on publications and personal communications with various scientists in the U.S. and Canada). This finding supports the prediction of Knopf *et al*. (1998) that *A. crassus* will not invade eel populations in the St. Lawrence River or northward due to the cold winter temperatures which predominate there. They base this prediction on their experimental data showing significant reductions in *A. crassus* larval development rates below 10°C. At 4°C, juveniles are unable to invade the swimbladder wall. However, in eels maintained for 115 days at 4°C and then for 115 days at 19°C, the nematodes resumed normal development. Thus, wherever *A. rostrata* are subjected to extended temperatures of 4-9°C or less, there may be little or no transmission, or otherwise deleterious effects of this parasite. Where summer temperatures are above 9°C, the parasite could be transmitted during those warmer months. Survey data are needed to test these predictions.

Commercial Harvesting of Sargassum (*Sargassum* spp.)

The unregulated commercial harvest of Sargassum has been implicated as a potential factor in the decline of *A. rostrata* (ASMFC, 2000). Sargassum is a combination of several species of large-bodied pelagic macroalgae which arise in the Sargasso Sea and drift into other potions of the Atlantic. Floating masses of sargassum are known to provide critical habitat for a wide variety of sea life including dolphin fish (*Coryphaena hippurus*) (also called mahi mahi), juvenile sea turtles, and seabirds and may represent the single most important fish habitat in the blue waters off the Atlantic Coast. It is possibly one of the few sources of energy in an otherwise nutrient-poor and energy-poor part of the ocean. Despite its importance, this plant is not protected by any treaty, and it is routinely harvested for use in such products as plant fertilizers and hog feed supplements. The South Atlantic Marine Fisheries Council has voted to phase out the harvest of pelagic Sargassum seaweed in U.S. waters. Any possible role of sargassum in the spawning and/or early life history of *A. rostrata* is undetermined.

3.0 EVALUATING EFFECTS ON THE LAKE ONTARIO/ UPPER ST. LAWRENCE RIVER EEL SUB-STOCK

3.1 Questionnaire

Regulators and biologists involved in the management of eels in Canada and the United States were polled regarding their opinions concerning the relative importance of factors contributing to the state of the Lake Ontario/upper St. Lawrence sub-stock. They were asked to indicate the importance of seven factors:

- habitat destruction and fragmentation, especially with reference to the impedance by dams of upstream passage into suitable habitat;
- mortality of silver eels caused by downstream passage of hydroelectric facilities;
- over-exploitation related to the harvest of eels over several life stages;
- the effects of microcontaminants, especially on reproductive success;
- oceanic environmental change;
- mortality associated with swimbladder infections by nematode worms; and
- harvesting of Sargassum.

Respondents were asked to rank the importance of each factor from 0 to 10, with 0 representing no importance at all, and 10 representing the greatest possible importance.

3.2 Development of a Life History-based Model

The role of uncertainty in living natural resource management, and methods for dealing with it, have received increasing attention in recent years (Hilborn and Walters, 1992). In particular, the problem of modeling populations for which population estimates and life history parameters are poorly known has prompted development of new approaches based on alternatives to the widely employed statistical hypothesis testing techniques (often referred to as frequentist statistics) in which the likelihood of detecting trends in the data decreases with increasing uncertainty (Taylor, 1993; Taylor and Gerodette, 1993; Taylor *et al.*, 2000; Wade, 2000).

Among the features common to many such efforts has been the use of simple, theoretically based population dynamical models for which uncertainty may be modelled explicitly. The methods of Bayesian statistics have informed much of the discussion, with the use of assumed

prior distributions gaining wider acceptance as a point of departure for modeling exercises (Wade, 2000).

A full statistical treatment of the hypotheses competing as explanations for trends in American eel population data is beyond the scope of this report. It is possible, however, to structure discussion around a plausible population dynamical model as a first step toward such an approach. Such a model can also be analyzed regarding its sensitivity to variation in model parameters, permitting structured discussion of the plausibility of competing hypotheses under a range of assumptions.

The Beverton-Holt model of stock recruitment (Beverton and Holt, 1957) has been widely used as a management tool by fisheries managers throughout the world. It is generally used to model the density-dependent contribution of a spawning stock to a subsequent generation's recruitment to a year class, life stage, or fishery.

As demonstrated by Mousalli and Hilborn (1986), it (and any other stock recruitment model) can be employed in disaggregated form to model a sequence of steps in a stock's life history. Put another way, transition to any life history stage from the previous stage can be modelled as a stock-recruitment relationship.

The Beverton-Holt stock-recruitment function is employed for all life-history transitions in this model. The form:

(1) $$N_{stage} = p_{stage} N_{stage-1} / (1 + N_{stage-1} p_{stage} / c_{stage})$$

where: N_{stage} = stage abundance
p_{stage} = a stage production parameter, and
c_{stage} = a stage capacity parameter

permits the explicit inclusion of effects on recruitment at each stage through the introduction of variables or functions that moderate production and capacity. The production parameter is related to survivorship in all cases but egg production. Egg production is a function of fecundity. The effect of fishing mortality on stage production can be introduced by expanding equation (1) to:

(2) $N_{stage} = p_{stage} F_{stage-1} N_{stage-1} / (1 + F_{stage-1} N_{stage-1} p_{stage} / c_{stage})$

where: F_{stage} = stage fishing mortality

Other sources of mortality could be modelled in the same way. Similarly, the effects of habitat availability or suitability can be modelled through effects on capacity, which is analogous to the carrying capacity parameter in the familiar logistic growth function on which much ecological theory is based.

The model can further be structured around sub-stocks in which growth and life-history schedules, as well as anthropogenic influences, will differ. American eel life history involves a series of life stages in different environments and migrations between and transitions to the various habitats. It is therefore generally suited to the modeling approach of Mousalli and Hilborn (1986).

In its initial implementation, we employed five sub-stocks: Lake Ontario- upper St. Lawrence River (LO-SLR), i.e., upstream of the Beauharnois dam; lower St. Lawrence River (SLR); Newfoundland and northern (NO); Nova Scotia - New York (NY); and southern (S). These sub-stocks were based on our reading of reports which indicate geographic trends in many aspects of the life history, e.g., Helfman *et al.* (1987), Facey *et al.* (1987), but on discussions with several eel researchers we added an additional stock on the US mid-Atlantic coast. It extends from the Hudson River to North Carolina and is designated as the Chesapeake sub-stock. Migrant juveniles are assumed to arrive in each sub-stock at different ages; the three most southern sub-stocks in their first year, Lake Ontario in its third year, and the others in their second year. Egg production is the sum of contributions from all sub-stocks and the recruitment of eels to sub-stocks is modelled as a proportion of total recruitment to the glass eel stage. Ranges for the proportions recruiting to each sub-stock employed in the model are presented in Table 3.2. This process could be modelled as a function of factors such as Gulf Stream strength to investigate hypotheses related to the influence of the oceanic environment on sub-stock and overall population dynamics in future implementations.

Both egg production and leptocephalus recruitment are modelled as density dependent processes with high values for c. In the case of egg production, it is calculated as the summed production of females from each sub-stock, described by the equation:

(3) $N_{egg} = p_{egg} (1-F_{silver}) S_{mig} N_{silver} / (1+ (1-F_{silver}) S_{mig} N_{silver} p_{egg} / c_{egg})$

where:
- N_{egg} = number of eggs produced per year
- p_{egg} = egg production parameter
- F_{silver} = fishing mortality on silver eels
- S_{mig} = natural survivorship of migrating silver eels
- N_{silver} = number of silver eels
- c_{egg} = habitat capacity for eel eggs

Recruitment to the leptocephalus stage follows the form:

(4) $N_{lepto} = p_{lepto} S_{egg} N_{egg} / (1+ p_{lepto} S_{egg} N_{egg} / c_{lepto})$

where:
- N_{lepto} = number of leptocephalus recruited
- p_{lepto} = leptocephalus production parameter
- S_{egg} = natural survivorship of eggs to hatching
- c_{lepto} = habitat capacity for leptocephalus eels

Recruitment to the glass eel stage is modelled as occurring prior to distribution to each sub-stock.

(5) $N_{glass} = p_{glass} N_{lepto} / (1+ p_{glass} N_{lepto} / c_{glass})$

where:
- N_{glass} = number of glass eels recruited
- p_{glass} = glass eel production parameter
- c_{glass} = habitat capacity for glass eels

Recruitment to each sub-stock is defined at the first elver stage as:

(6) $N_{elver(1)} = p_{elver(1)}(1-F_{glass}) ppn_{glass} N_{glass}/(1+ p_{elver(1)}(1-F_{glass}) ppn_{elver} N_{glass}/c_{elver(1)})$

where:
- $N_{elver(1)}$ = number of glass eels recruited
- $p_{elver(1)}$ = elver(1) production parameter
- F_{glass} = fishing mortality on glass eels

ppn_{elver} = the proportion of total glass eel production entering a sub-stock as elvers

$c_{elver(1)}$ = habitat capacity for elvers in age class elver(1)

For sub-stocks in which multi-year juvenile migration is assumed (e.g. Lake Ontario-upper St. Lawrence River), recruitment to additional stages is described by:

(7) $$N_{elver(k)} = p_{elver(k)} N_{elver(k-1)} / (1 + p_{elver(k)} N_{elver(k-1)} / c_{elver(k)})$$

where:

$N_{elver(k)}$ = number of glass eels recruited to age class elver(k)

$p_{elver(k)}$ = elver(k) production parameter

$c_{elver(k)}$ = habitat capacity for elvers in age class elver(k)

Recruitment to resident age classes is defined by the equation:

(8) $$N_{yellow(1)} = p_{yellow(1)}(1-F_{elver}) N_{elver} / (1 + p_{yellow(1)}(1-F_{elver}) N_{elver} / h\, c_{yellow})$$

where:

$N_{yellow(1)}$ = number of glass eels recruited

N_{elver} = number of elvers in the last elver age class

$p_{yellow(1)}$ = age class yellow(1) production parameter

F_{elver} = fishing mortality on elvers

c_{yellow} = habitat capacity for eels in age class yellow(1)

h = proportion of original habitat currently available to resident eels.

Recruitment to subsequent resident fully juvenile age classes (i.e. none metamorphose to silver eels) is defined by:

(9) $$N_{yellow(i)} = p_{yellow(i)}(1-F_{yellow(i-I)}) N_{yellow(i-I)} / (1 + p_{yellow(i)}(1-F_{yellow(i-I)}) \; ?^{m-1}_{i-1} N_{yellow(j)} / h\, c_{yellow})$$

where:

$N_{yellow(i)}$ = number of eels in age class yellow(i)

m = yellow age class in which metamorphosis to silver stage is assumed to begin

$p_{yellow(i)}$ = age class yellow(i) production parameter

$F_{yellow(i)}$ = fishing mortality on age class yellow (i)

c_{yellow} = habitat capacity for eels in age class yellow(1)

h = proportion of original habitat currently available to resident eels.

Abundance of immature eels old enough to become sexually mature is calculated as

(10) $N_{yellow(m+,t)} = (p_{yellow(m)}((1-F_{yellow(m)}) (N_{yellow(m+,t-1)}-N_{\boldsymbol{silver(t)}}) + (1-F_{yellow(m-1)}) (N_{yellow(m+,t-1)}) /(1+ (p_{yellow(m)}((1-F_{yellow(m)}) (N_{yellow(m+,t-1)}-N_{\boldsymbol{silver(t)}}) + (1-F_{yellow(m-1)})(N_{yellow(m+,t-1)}) / h\, c_{yellow})$

where: $N_{yellow(m+,t)}$ = number of eels in age classes yellow(m) and older in year *t*

$N_{\boldsymbol{silver(t)}}$ = number of silver eels produced in year *t*

Silver eel recruitment is assumed to be density independent and is modelled as:

(11) $N_{\boldsymbol{silver}} = p_{\boldsymbol{silver}} (1-F_{yellow(m+)}) (N_{yellow(m+)})$.

This form does not look like equation (1) but is the same relationship with an assumed infinite capacity. This was concluded to be a reasonable assumption given the onset of outmigration as the metamorphosis from yellow to silver is completed, and the cessation of feeding associated with that process. There did not seem to be any hypothesized mechanism through which density dependence could be mediated.

A complete list and description of model parameters is shown on Table 3.1. Data with which the model might be fitted are sparse for all populations of American eel. There are some data regarding the age structure and fecundity of sub-stocks, e.g., Dutil *et al.* (1987), Facey *et al.* (1987), Krueger and Oliveira (1997). There remains considerable room for interpretation and disagreement, however, and mortality rates, age of maturity, and mean fecundities for eels from different parts of their range are known only imprecisely.

There are some data for gross fishing mortality (Caron and Verreault, 1997), but they are generally restricted to harvest data, with limited information on effort that would permit estimation of abundance indices (Richkus and Whalen, 1999). Ranges for fishing mortality estimates were assigned on the basis of previous analyses (e.g., Caron and Verreault, 1997; ICES, 2000). Virtually all other elements of the model can only be approximated.

Some effort has been made to quantify habitat loss over much of the range (Lary and Busch, 1997). These data form the basis for estimates of habitat loss in the model. However,

Table 3.1 Model parameter designations

c(yellow)	= combined capacity (parameter c) for all substocks
dams	= mean number of passable hydroelectric dams per unit capacity
F(elver)	= annual fishing mortality on the last elver stage
F(glass)	= annual fishing mortality on the glass eel stage
F(silver)	= annual fishing mortality on the silver stage
F(yellow)	= annual fishing mortality on the yellow stage
h(yellow)	= proportion remaining capacity after habitat exclusion and destruction
p(egg)	= production parameter for the egg stage
p(elver)	= production parameter for the elver stage (substocks with one elver stage)
p(elver1)	= production parameter for elver stage 1 (substocks with multiple elver stages)
p(elver2)	= production parameter for elver stage 2 (substocks with multiple elver stages)
p(elver3)	= production parameter for elver stage 3 (substocks with three elver stages)
p(glass)	= production parameter for the glass eel stage
p(lepto)	= production parameter for the leptocephalus stage
p(silver)	= production parameter for the silver eel stage
p(yellow1)	= production parameter for yellow stage 1
p(yellow2)	= production parameter for yellow stage 2
p(yellow3)	= production parameter for yellow stage 3
p(yellow4)	= production parameter for yellow stage 4
p(yellow5)	= production parameter for yellow stage 5
ppn(elver)	= proportion of all elver production entering a given substock
ppn(yellow)	= proportion of total yellow eel capacity (parameter c) in a given substock
S(dspassage)	= mean survivorship of downstream passage of hydroelectric dams
S(silver)	= silver eel natural survivorship on migration

Stock designation Postscripts

C	= Chesapeake – Hudson River to North Carolina
NO	= Newfoundland and northern
NY	= Nova Scotia to New York (Hudson River)
O	= Lake Ontario and upper St. Lawrence River
S	= southern – south of North Carolina
SL	= lower St. Lawrence River and Gulf of St. Lawrence

estimates of carrying capacity for the population or sub-stocks are lacking. We employ a range of possible carrying capacities for the entire population and vary the relative proportions of that total in each sub-stock. The model was also run with total yellow eel capacity fixed at 50,000,000 to examine the sensitivities of other parameters in the absence of variation in capacity.

Possible changes in the relative contribution to total reproduction from each sub-stock forms the basis of some hypotheses regarding observed changes in migrant juvenile numbers arriving at eel ladders, especially for the LO-SLR and SLR sub-stocks (Castonguay *et al.*, 1994). Therefore, proportions contributed to each sub-stock were permitted to vary among trials. The proportion of reproduction recruiting to the Lake Ontario population was calculated as the proportion remaining after all other sub-stocks recruited.

Oceanic effects are arguably the least tractable to management. Model runs were therefore implemented in which production parameters of leptocephaplus larvae and glass eels were held constant (0.95 and 0.01, respectively). All other aspects of these runs were identical to the fixed yellow eel capacity implementations with unequal sub-stock capacities.

It was our original intention to use actual statistical distributions for at least some parameters, but the uncertainty regarding the extent to which published estimates were representative of the sub-stocks from which they were drawn led us to employ uniform distributions for all parameter ranges, as would be the assumed prior distribution in a Bayesian analysis (Wade, 2000). Such a distribution significantly increases the influence of parameter values at the extremes of the range and will undoubtedly have played a role in the ranking of influences. There did not seem to be any way to legitimately employ normal, lognormal, gamma or other commonly used statistical distributions and the risk averse approach seemed to be one which encompassed the uncertainty of the data.

Plausible ranges for parameters (Table 3.2) were estimated from available literature and discussions with eel researchers. The metapopulation software which we had hoped to be able to use for this work could not handle the panmictic nature of American eels sub-stocks. Rather than implement the model in a programming language such as Fortran or C++, we decided to use off-the-shelf software available to all fisheries managers. The model was implemented as a set of Excel spread sheets. The Crystal Ball risk assessment package (Wainwright, 1998) was used to conduct sensitivity analyses.

Silver eel and egg production for LO-SLR and all sub-stocks combined were calculated over 1,000 trials. Proportion of total silver eel numbers and egg production were also calculated for the LO-SLR sub-stock. Sensitivity of these outcomes to all parameters was output as rank correlations.

TABLE 3.2: PARAMETER VALUES EMPLOYED FOR SENSITIVITY ANALYSIS

Parameter	Stage	All	L. Ontario (LO-SLR)	St. Lawrence (SLR)	North (NO)	NS-NY (NY)	Ches. (C)	South (S)
	egg		3.5-8 x 10^6	2.5-6 x 10^6	2.5- 6 x 10^6	2.5-6 x 10^6	2-5 x 10^6	0.8-2 x 10^6
	lepto	0.7-0.99						
	glass	0.001-0.05						
	elver 1	0.15-0.25						
	elver 2		0.2-0.3	0.2-0.3	0.2-0.3			
	elver 3	0.25-0.35						
p	yellow 1	0.34-0.44						
	yellow 2	0.4-0.5						
	yellow 3	0.55-0.69						
	yellow 4	0.74-0.89						
	yellow 5+	0.75-0.9						
	silver		0.1-0.3	0.2-0.4	0.1-0.4	0.2-0.4	0.3-0.5	0.4-0.6
	egg	1 x 10^{18}						
	lepto	1 x 10^{18}						
c	glass	1 x 10^{18}						
	elver	1 x 10^{18}						
	yellow	10-100 x 10^6						
	elver			0.1-0.3	0.05-0.15	0.05-0.15	0.05-0.15	0.05-0.15
ppn	yellow			0.2-0.3	0.05-0.15	0.15-0.25	0.05-0.15	0.05-0.1
	F (glass)					0-0.01	0-0.01	0-0.1
F	F (elver)	0-0.05						
	F (yellow)	0-0.18						
	F (silver)	0-0.2						
h	yellow	0.5-1						
dams	silver	0-2						
S(ds)	silver	0.5-0.85						
S(mig)	silver	0.5-0.9						

Individual deterministic outcomes were also calculated for intermediate and high values of key parameters, in isolation from other effects. Model output without variability under various assumed effects for individual parameters, intermediate and high combined effects is presented in Section 4.0. Base case runs are premised on no habitat reduction, fishing effects or perturbation from original conditions. Parameter values for base case runs were therefore either 0 (e.g., fishing mortality parameters, number of dams) or 1 (e.g., habitat reduction parameter), depending on their form. Parameter values used in other runs were selected to provide some indication of the relative effect on the model of varying factors acting in isolation, and should not be read as predictive results for each case. Parameters other than those under comparison were equal in all runs, and from within the range employed in the sensitivity analyses (see Table 3.2), but were arbitrarily assigned. Outcomes with total carrying capacity equally divided among sub-stocks and apportioned unequally are presented. Total resident capacity is fixed at 50 million yellow eels for deterministic runs.

4.0 RESULTS

4.1 Questionnaire

We received eleven responses to the questionnaire. Respondents included representatives of the Ontario Ministry of Natural Resources, New York Department of Environment and Conservation, Department of Fisheries and Oceans, United States Geological Survey, National Marine Fisheries Service, the St. Regis Mohawk and the New York Power Authority, Ontario Power Generation (formerly Ontario Hydro). The mean values and standard deviation of responses to the questionnaire are summarized in Table 4.1.

Table 4.1: Questionnaire Results. Respondents were asked to rank the importance, from 0 to 10 of the following factors to American eel population dynamics with reference to contemporary management issues. A rating of 0 mean no importance and 10 would be the utmost importance.

Issue	**Mean**	**SD**
Habitat loss/upstream passage	8.0	2.6
Downstream passage	7.3	2.3
Overexploitation of all life stages	6.5	2.5
Contaminant effects on reproduction	4.8	2.8
Ocean environment	4.2	2.0
Swimbladder mortality	3.3	3.0
Sargassum harvest	-	-

4.2 Model Implementation and Sensitivity Analyses

Runs with Fixed Values

Model implementation with combined effects at the high end of assumed ranges led to an order of magnitude drop in total egg production (Tables 4.2 and 4.3) and, in the case with late onset of maturation in the Lake Ontario sub-stock, a reduction by approximately half in the proportion of production originating in the Lake Ontario sub-stock (Table 4.2).

Reduction of the available habitat in Lake Ontario (L_{ONT}) to very low levels had a limited effect on total production (Tables 4.2 and 4.3). Fishing yellow and silver eels at an annual exploitation rate of 9% had the greatest effect, followed by an average of 2 dams per unit of available habitat with 75% passage survivorship at each dam, and loss of 33% of total habitat (all stocks). An elver fishery at 5% annual exploitation rate has a negligible effect on production (Tables 4.2 and 4.3).

Sensitivity to Parameters

Sensitivity analyses involved calculating the rank correlation of parameter values with results, and were carried out on six model configurations:

- early (12 years) onset of maturation in LO-SLR with variable total yellow eel habitat carrying capacity;
- late (17 years) onset of maturation in LO-SLR with variable total yellow eel habitat carrying capacity;
- early onset of maturation in LO-SLR with constant total yellow eel habitat carrying capacity;
- late onset of maturation in LO-SLR with constant total yellow eel habitat carrying capacity;
- early onset of maturation in LO-SLR with constant total yellow eel habitat carrying capacity and fixed leptocephalus and glass eel production; and
- late onset of maturation in LO-SLR with constant total yellow eel habitat carrying capacity and fixed leptocephalus and glass eel production.

These analyses generated plots of rank correlation coefficients as presented in Figures 4.1 to 4.6. See Appendix A for details on maturation schedules for LO-SLR. Notable consistent trends include high coefficients for the influence of glass eel production on abundance of silver eels and egg production. Glass eel production was less influential on the proportions of silver eels and eggs originating in the Lake Ontario sub-stock in runs with later onset of maturation of LO-SLR eels. Fixing production parameters for leptocephalus and glass eel stages had little influence on the ranking of sensitivities for other parameters. Variation in

production parameters generally influences the outcome of the model. Fishing mortality on yellow and silver eels in several sub-stocks, notably LO-SLR and SLR, also appear consistently among the most influential factors. Frequency distributions of results for these four cases, run over 1,000 trials, with associated descriptive statistics, are presented in Appendix B.

Table 4.2: Outcomes of model runs for selected forecasts of the model with early matuation of Lake Ontario eels, based on manipulations of single parameters, intermediate values of the parameter set, and high values for the parameter set. See Table 3.1 for model parameter designations.

Case	Parameter Set	Total N_{50}(silver)	Total N_{50}(egg)	Total N_{50}(silver)	Total N_{50}(silver)
	Base case	8.30E+11	3.7852E+05	0.1533	0.0961
	habitat = 0.67	5.65E+11	2.5629E+05	0.1504	0.0946
	F = 0.09	4.30E+11	2.3193E+05	0.1322	0.0769
Equal c	elver F = 0.05	8.24E+11	3.7394E+05	0.1542	0.0970
	dams = 2	4.62E+11	3.7520E+05	0.1509	0.0944
	h_{Ont} = 0.0001	6.95E+11	3.3960E+05	0.0000	0.0000
	Intermediate	1.91E+11	1.1885E+05	0.1801	0.1213
	High	5.69E+10	8.4655E+04	0.1616	0.1076
	Base case	8.30E+11	3.7852E+05	0.1533	0.0961
	habitat = 0.67	5.37E+11	2.1544E+05	0.2030	0.1446
	F = 0.09	3.69E+11	1.7418E+05	0.1931	0.1285
Unequal c	elver F = 0.05	7.75E+11	3.1112E+05	0.2102	0.1496
	dams = 2	4.32E+11	3.1023E+05	0.2051	0.1452
	h_{Ont} = 0.0001	6.29E+11	2.7186E+05	0.0000	0.0000
	Intermediate	1.91E+11	1.1885E+05	0.1801	0.1213
	High	5.69E+10	8.4655E+04	0.1616	0.1076

Table 4.3: Outcomes of model runs for selected forecasts of the model with late

matuation of Lake Ontario eels, based on manipulations of single parameters, intermediate values of the parameter set, and high values for the parameter set. See Table 3.1 for model parameter designations.

Case	Parameter Set	Total N_{50}(silver)	Total N_{50}(egg)	Total N_{50}(silver)	Total N_{50}(silver)
	Base case	7.47E+11	3.5451E+05	0.0595	0.0358
	habitat = 0.67	4.92E+11	2.3444E+05	0.0601	0.0361
	F = 0.09	3.92E+11	2.1992E+05	0.0338	0.0189
Equal c	elver F = 0.05	7.40E+11	3.4996E+05	0.0599	0.0362
	dams = 2	4.16E+11	3.5154E+05	0.0585	0.0352
	h_{Ont} = 0.0001	6.94E+11	3.3876E+05	0.0000	0.0000
	Intermediate	1.90E+11	1.4176E+05	0.0338	0.0189
	High	5.73E+10	1.0181E+05	0.0309	0.0173
	Base case	6.71E+11	2.8278E+05	0.0847	0.0575
	habitat = 0.67	4.58E+11	1.9208E+05	0.0829	0.0565
	F = 0.09	3.26E+11	1.6136E+05	0.0506	0.0322
Unequal c	elver F = 0.05	6.68E+11	2.8042E+05	0.0849	0.0578
	dams = 2	3.74E+11	2.8024E+05	0.0825	0.0559
	h_{Ont} = 0.0001	6.29E+11	2.7162E+05	0.0000	0.0000
	Intermediate	1.64E+11	1.0732E+05	0.0484	0.0310
	High	4.93E+10	7.6972E+04	0.0425	0.0270

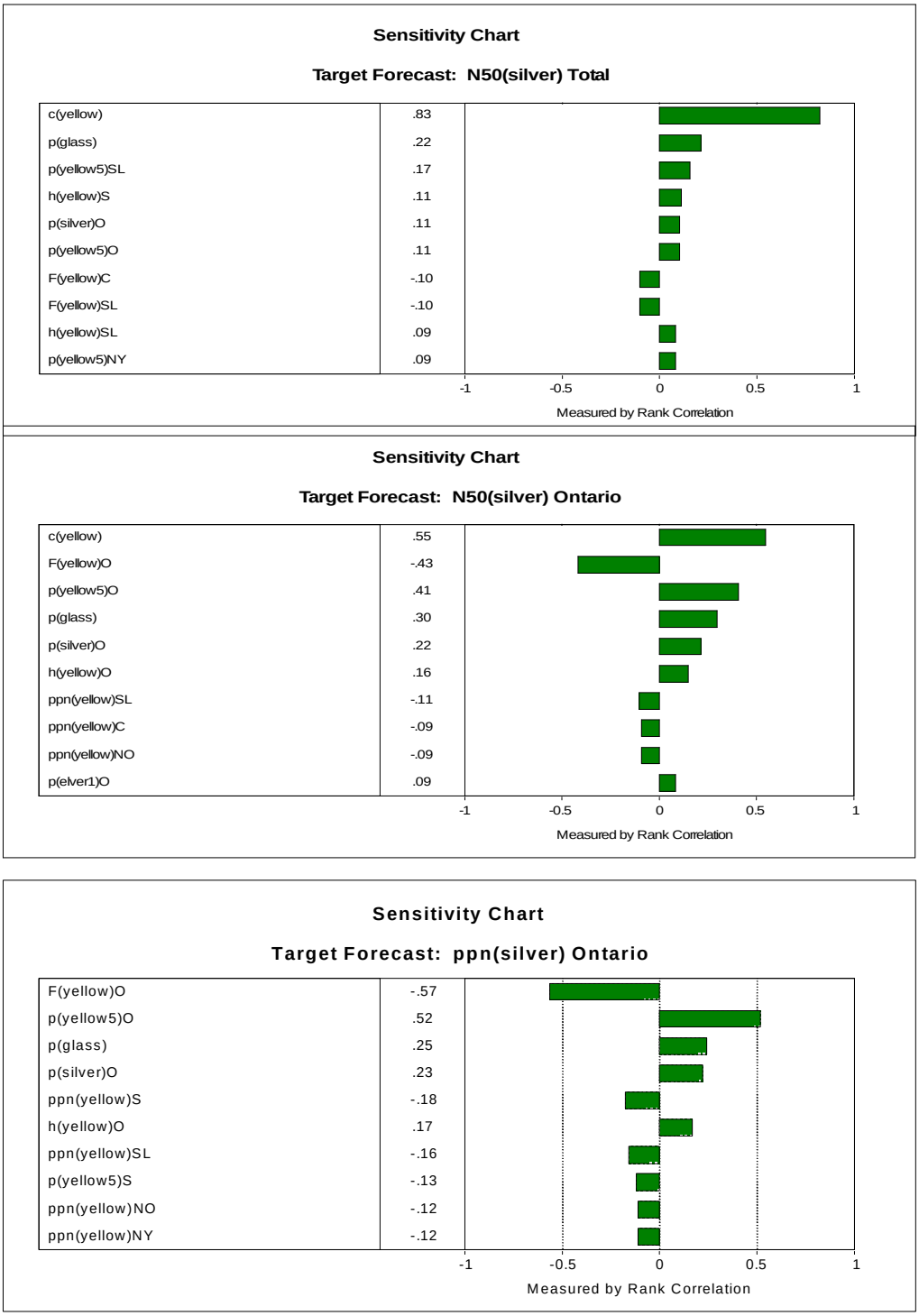
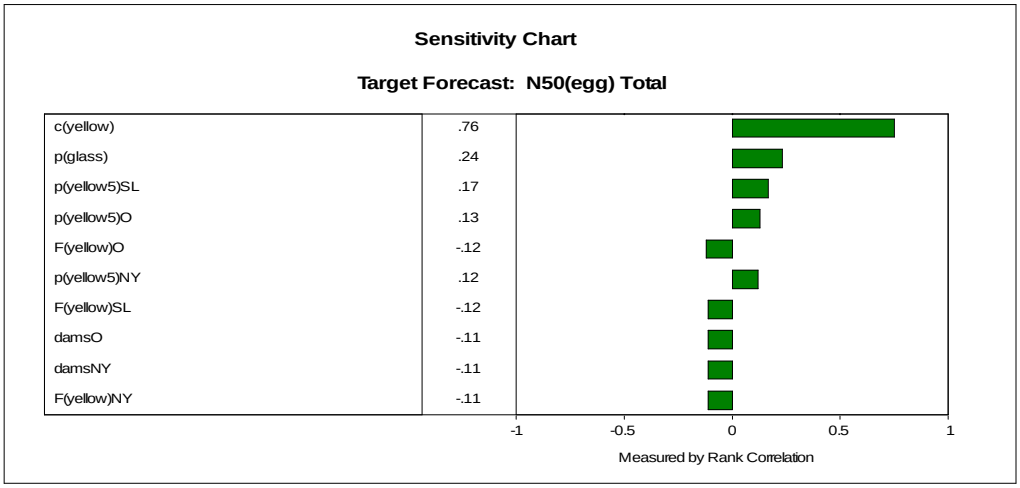
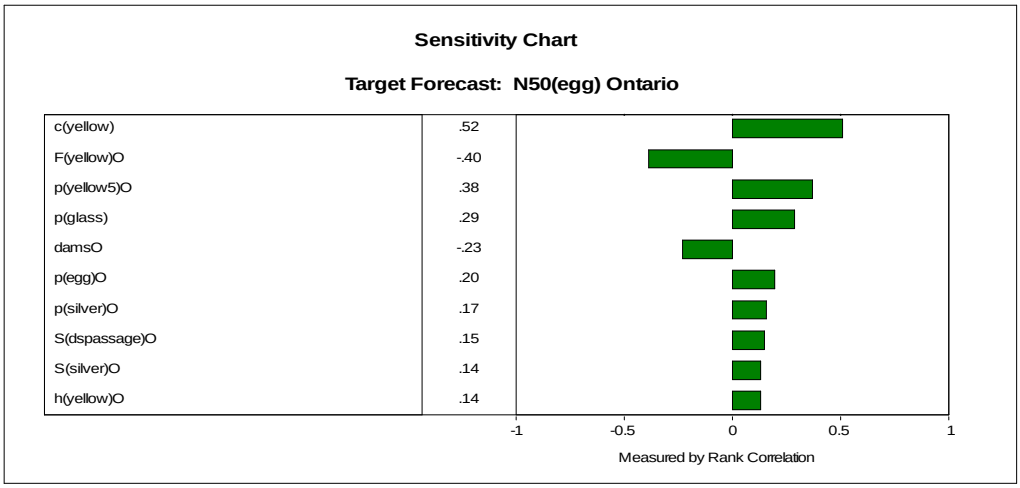


Figure 4.1. Model sensitivity analysis output for trials with variable total yellow eel capacity, and early maturation of LO-SLR eels. Values are rank correlations of the ten

coefficients of greatest magnitude influencing total silver eel abundance (N50(silver) Total), silver eel abundance prior to out-migration from Lake Ontario and the upper St. Lawrence (N50(silver)Ontario), and the proportion of total silver eel abundance represented by silver eels produced in Lake Ontario and the upper St. Lawrence (ppn(silver)Ontario), after 50 years. Model parameter designations are described in Table 3.1.





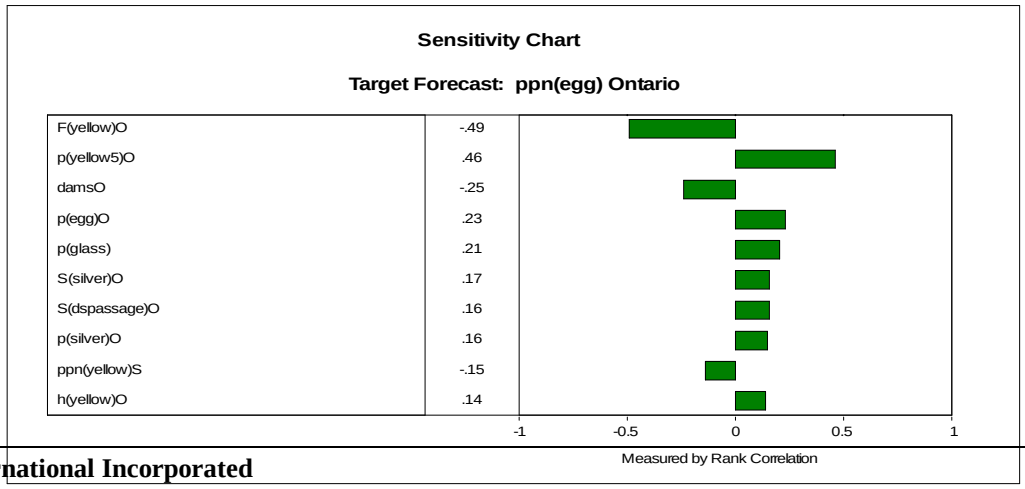


Figure 4.1. Model sensitivity analysis output for trials with variable total yellow eel capacity, and early maturation of LO-SLR eels. Values are rank correlations of the ten coefficients of greatest magnitude influencing total eel egg production (N50(egg)Total), eel egg production by eels originating in Lake Ontario and the upper St. Lawrence (N50(egg)Ontario)), and the proportion of total egg production represented by eggs produced by eels originating in Lake Ontario and the upper St. Lawrence (ppn(egg)Ontario)) after 50 years. Model parameter designations are described in Table 3.1.

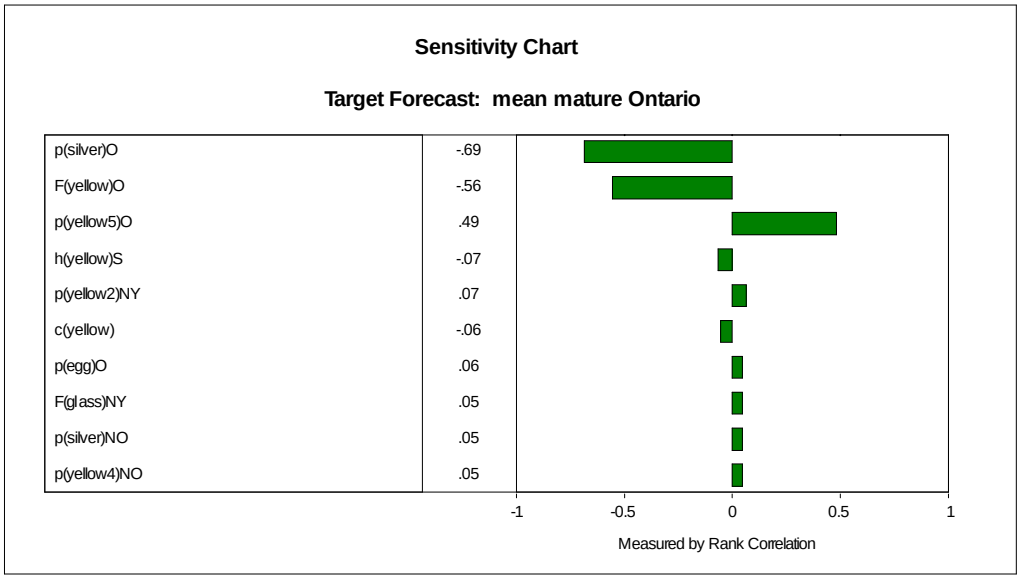
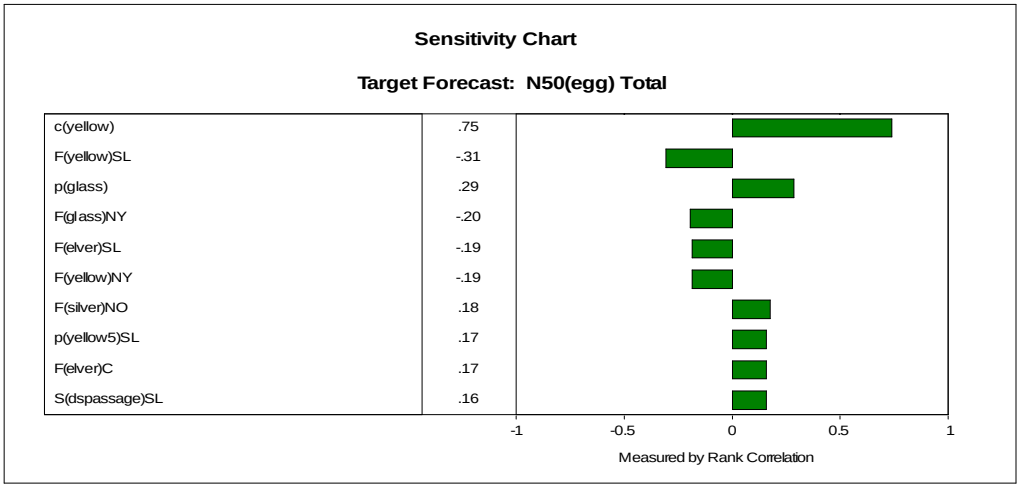
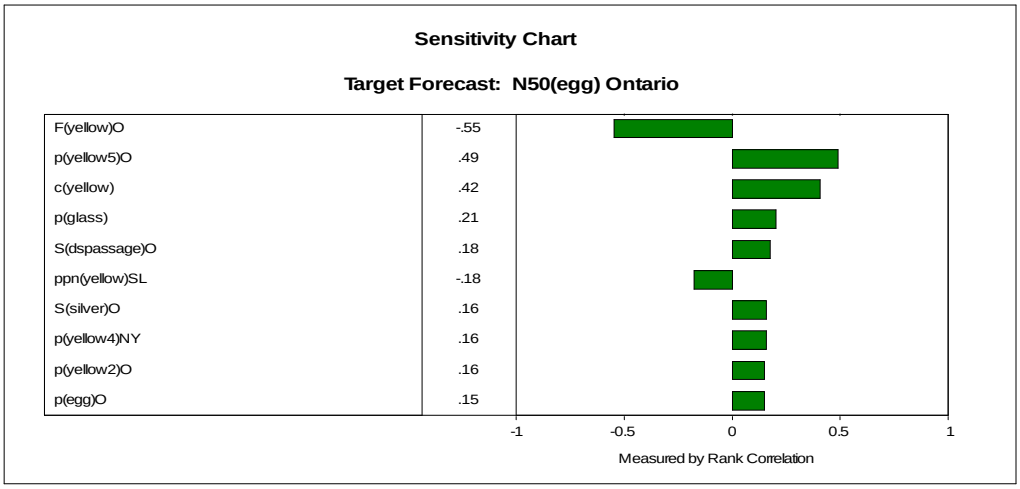


Figure 4.1. Model sensitivity analysis output for trials with variable total yellow eel capacity, and early maturation of LO-SLR eels. Values are rank correlations of the ten coefficients of greatest magnitude influencing maturation age of eels originating in Lake Ontario and the upper St. Lawrence, after 50 years. Model parameter designations are described in Table 3.1.





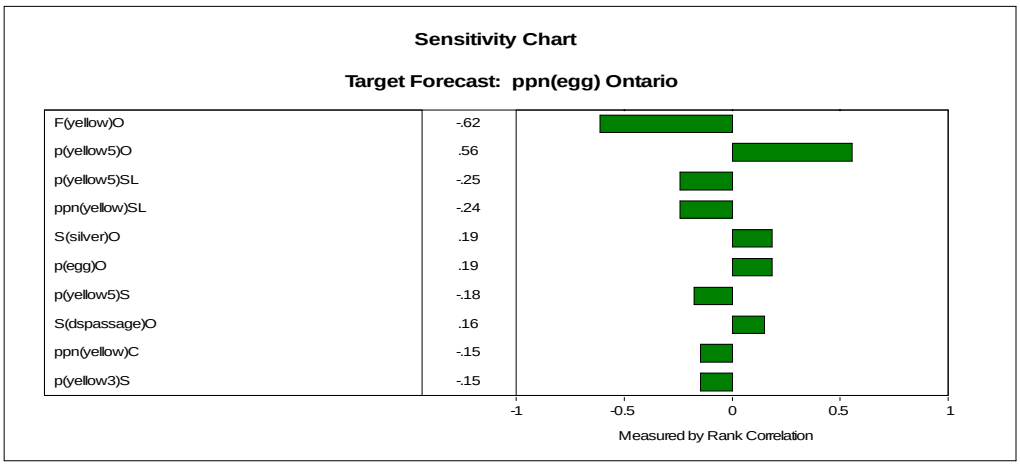
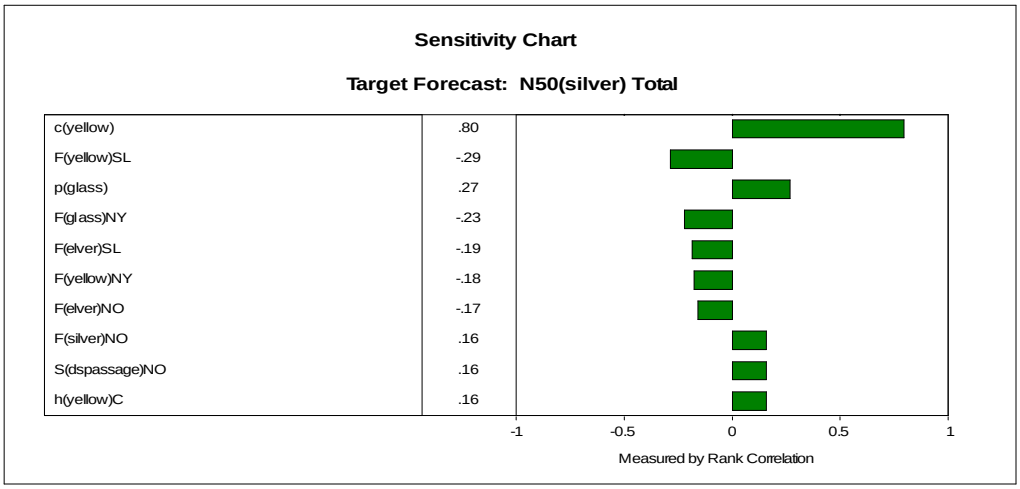
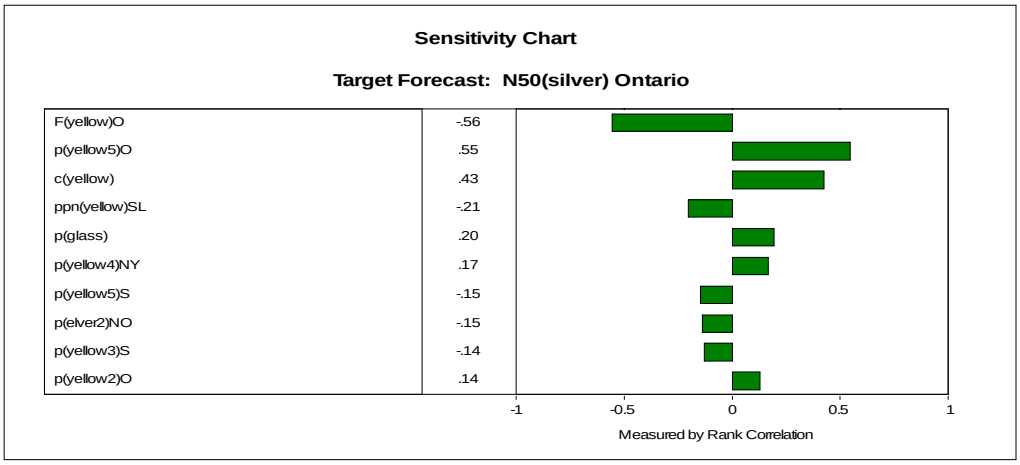


Figure 4.2. Model sensitivity analysis output for trials with variable total yellow eel capacity, and late maturation of LO-SLR eels. Values are rank correlations of the ten coefficients of greatest magnitude influencing total egg production (N50(egg)Total), egg production by eels originating in Lake Ontario and the upper St. Lawrence

(N50(egg)Ontario)), and the proportion of total egg production represented by eggs produced by eels originating in Lake Ontario and the upper St. Lawrence (ppn(egg)Ontario)) after 50 years. Model parameter designations are described in Table 3.1.





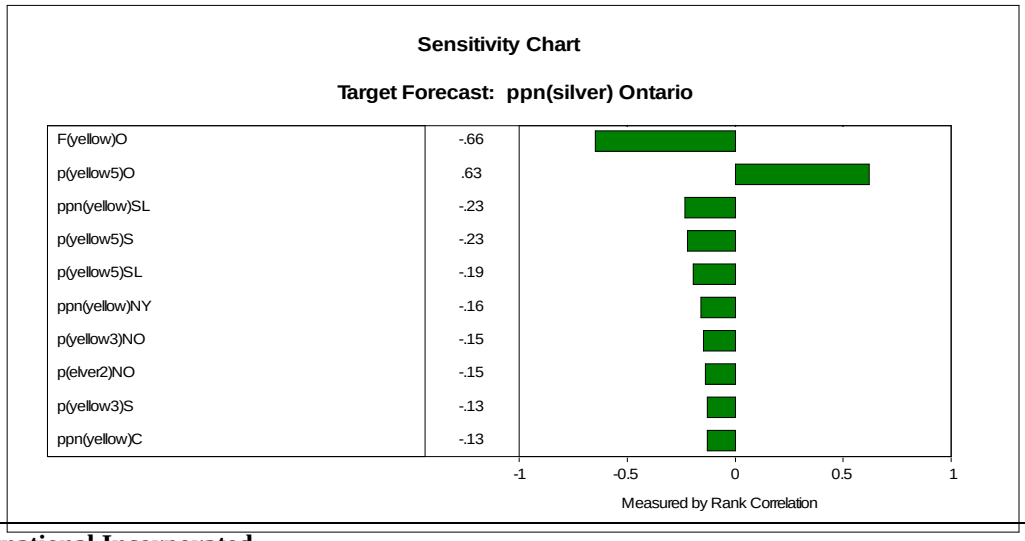


Figure 4.2. Model sensitivity analysis output for trials with variable total yellow eel capacity, and late maturation of LO-SLR eels. Values are rank correlations of the ten coefficients of greatest magnitude influencing total silver eel adundance (N50(silver) Total), silver eel abundance prior to migration in Lake Ontario and the upper St. Lawrence (N50(silver)Ontario), and the proportion of total silver eel abundance represented by silver eels produced in Lake Ontario and the upper St. Lawrence (ppn(silver)Ontario), after 50 years. Model parameter designations are described in Table 3.1.

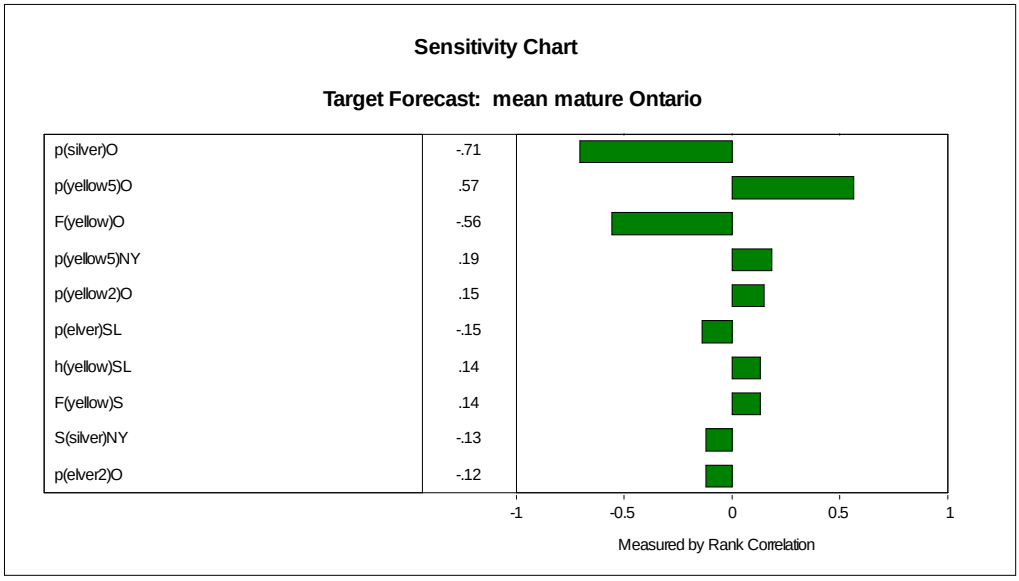
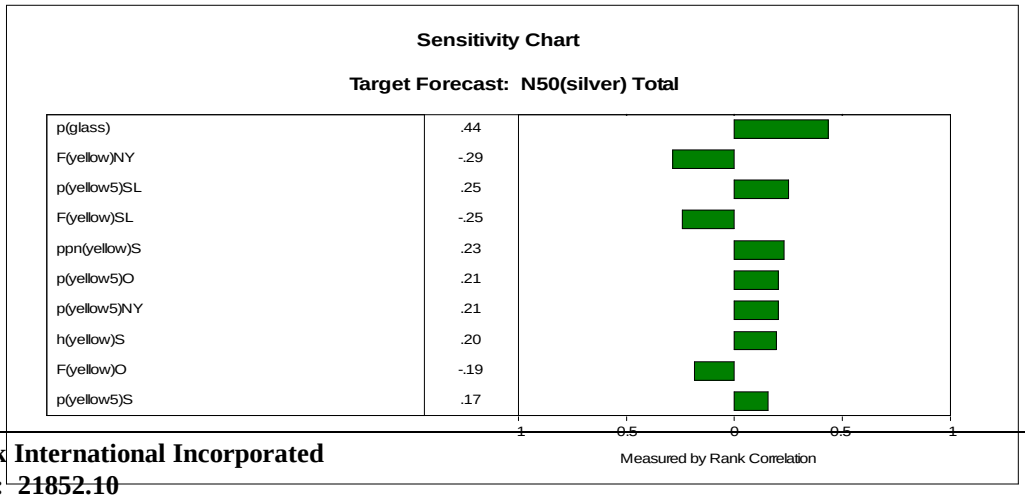


Figure 4.2. Model sensitivity analysis output for trials with variable total yellow eel capacity, and late maturation of LO-SLR eels. Values are rank correlations of the ten coefficients of greatest magnitude influencing mean maturation age of eels originating in Lake Ontario and the upper St. Lawrence after 50 years. Model parameter designations are described in Table 3.1.



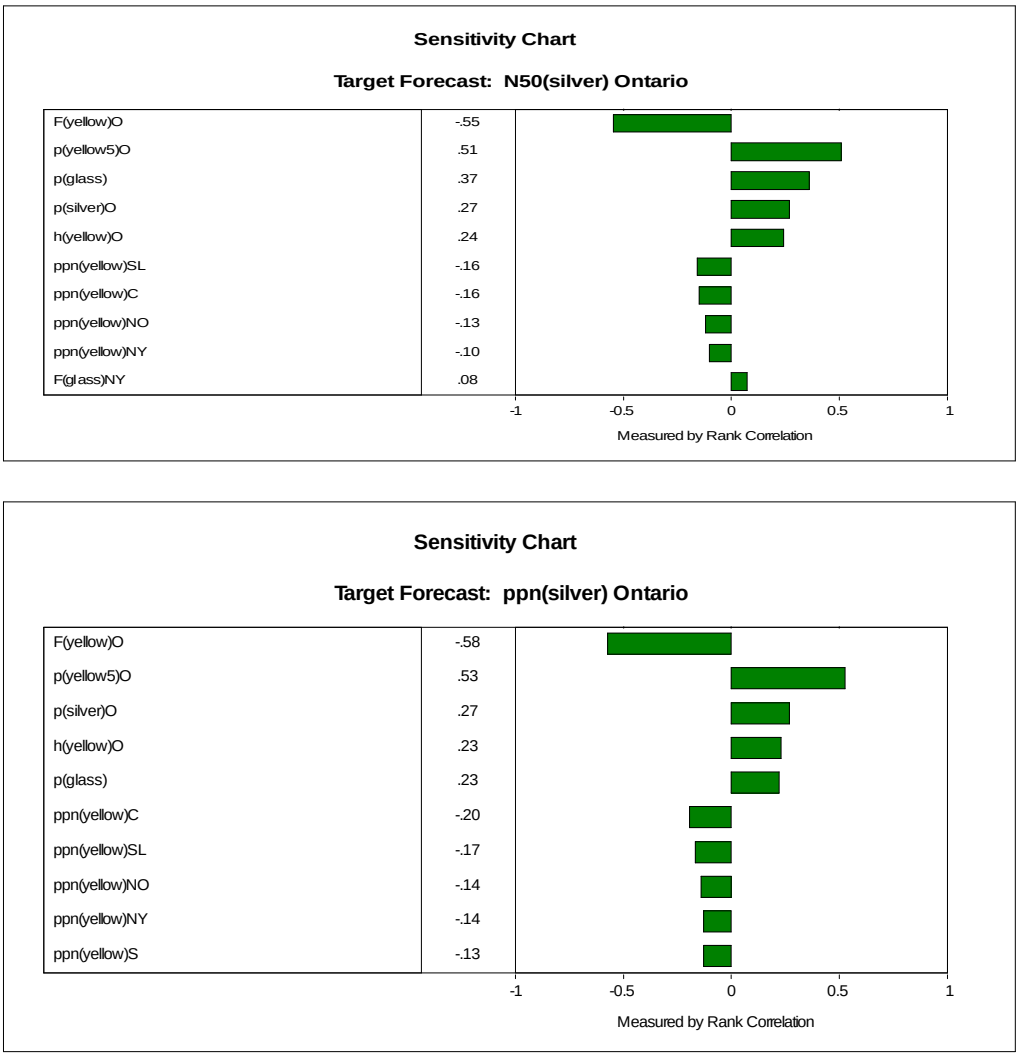
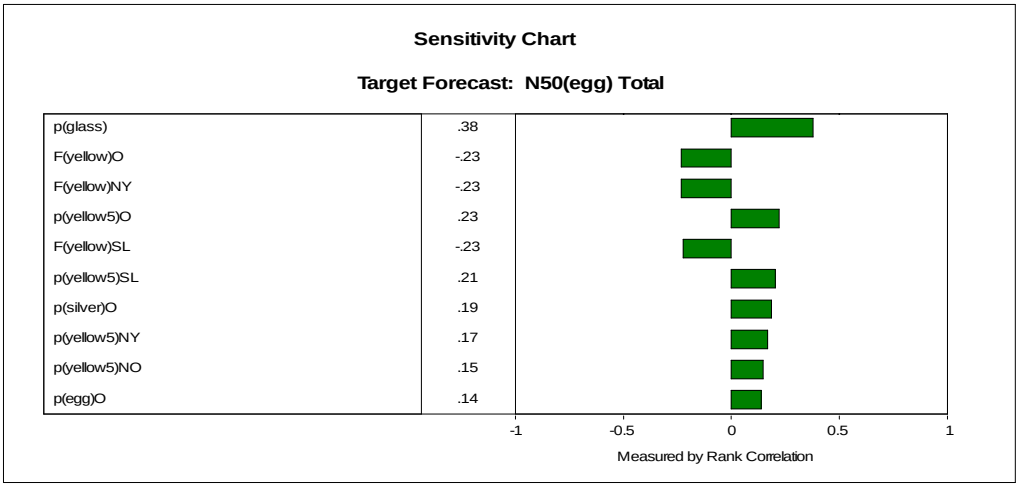
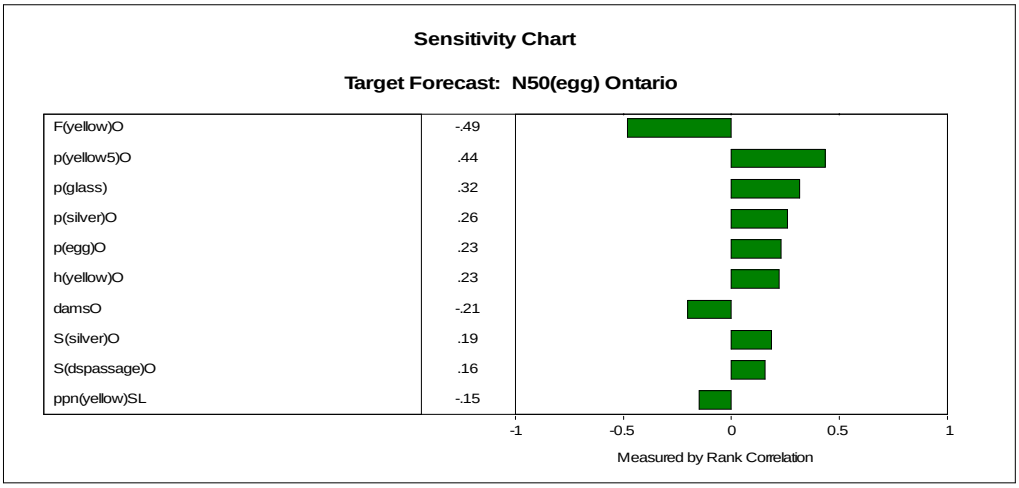


Figure 4.3. Model sensitivity analysis output for trials with constant total yellow eel capacity (c = 50 E+6), and early maturation of LO-SLR eels. Values are rank correlations of the ten coefficients of greatest magnitude influencing total silver eel adundance (N50(silver) Total), silver eel abundance prior to out-migration from Lake Ontario and the upper St. Lawrence (N50(silver)Ontario), and the proportion of total silver eel abundance represented by silver eels produced in Lake Ontario and the upper St. Lawrence (ppn(silver)Ontario), after 50 years. Model parameter designations are described in Table 3.1.


Sensitivity Chart
Target Forecast: N50(egg) Total
p(glass) .38
F(yellow)O -.23
F(yellow)NY -.23
p(yellow5)O .23
F(yellow)SL -.23
p(yellow5)SL .21
p(silver)O .19
p(yellow5)NY .17
p(yellow5)NO .15
p(egg)O .14
-1 -0.5 0 0.5 1
Measured by Rank Correlation


Sensitivity Chart
Target Forecast: N50(egg) Ontario
F(yellow)O -.49
p(yellow5)O .44
p(glass) .32
p(silver)O .26
p(egg)O .23
h(yellow)O .23
damsO -.21
S(silver)O .19
S(dspassage)O .16
ppn(yellow)SL -.15
-1 -0.5 0 0.5 1
Measured by Rank Correlation

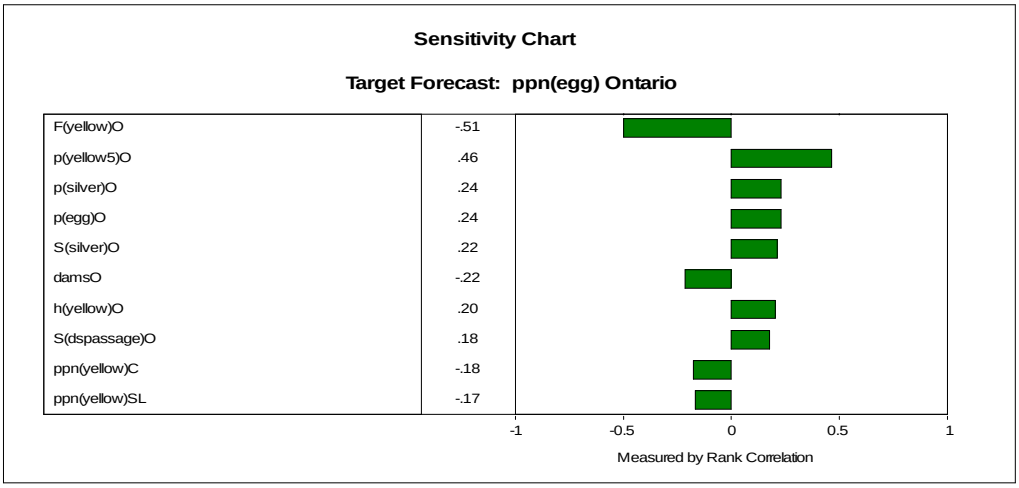
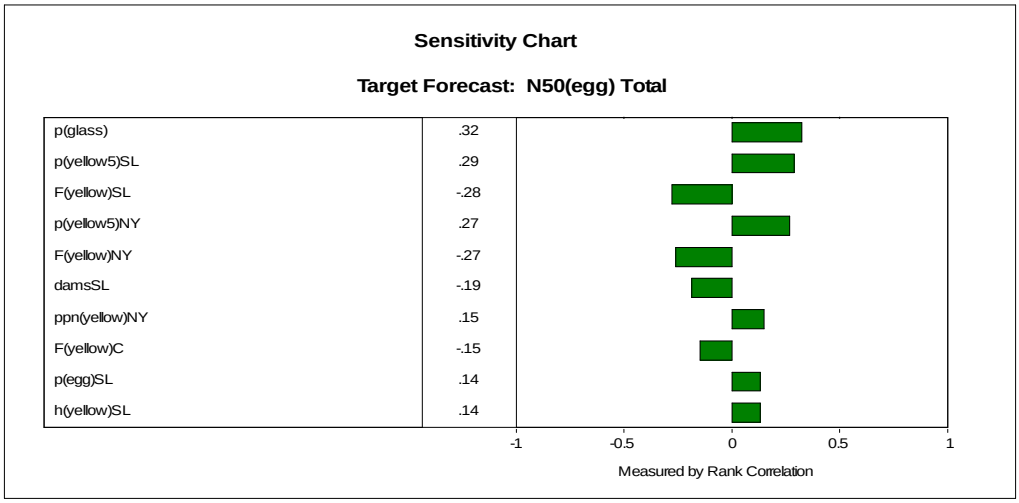
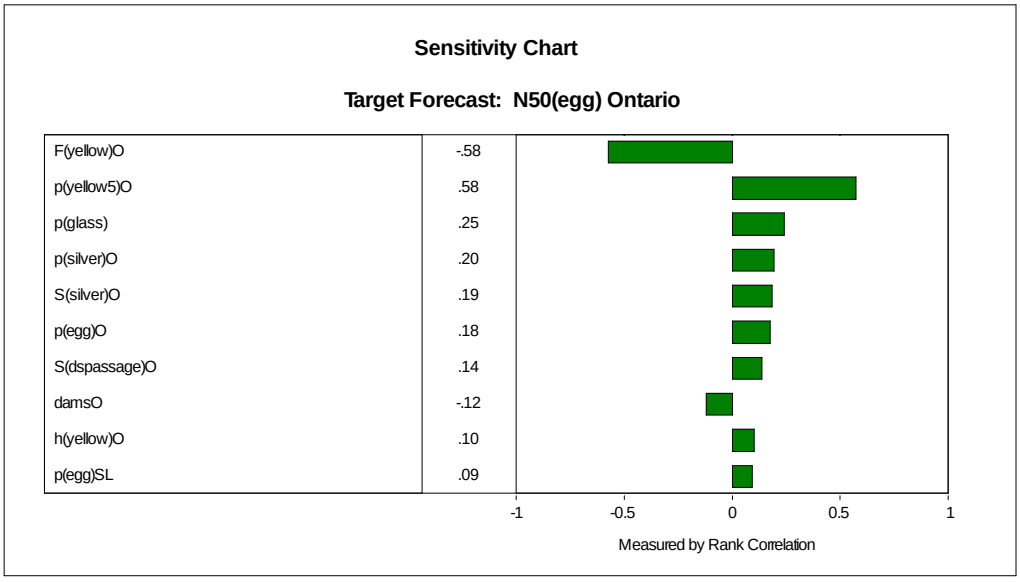

Sensitivity Chart
Target Forecast: ppn(egg) Ontario
F(yellow)O -.51
p(yellow5)O .46
p(silver)O .24
p(egg)O .24
S(silver)O .22
damsO -.22
h(yellow)O .20
S(dspassage)O .18
ppn(yellow)C -.18
ppn(yellow)SL -.17
-1 -0.5 0 0.5 1
Measured by Rank Correlation

Figure 4.3. Model sensitivity analysis output for trials with constant total yellow eel capacity (c = 50 E+6), and early maturation of LO-SLR eels. Values are rank correlations of the ten coefficients of greatest magnitude influencing total egg production (N50(egg)Total), egg production by eels originating in Lake Ontario and the upper St. Lawrence (N50(egg)Ontario)), and the proportion of total egg production represented by eggs produced by eels originating in Lake Ontario and the upper St. Lawrence (ppn(egg)Ontario)) after 50 years. Model parameter designations are described in Table 3.1..





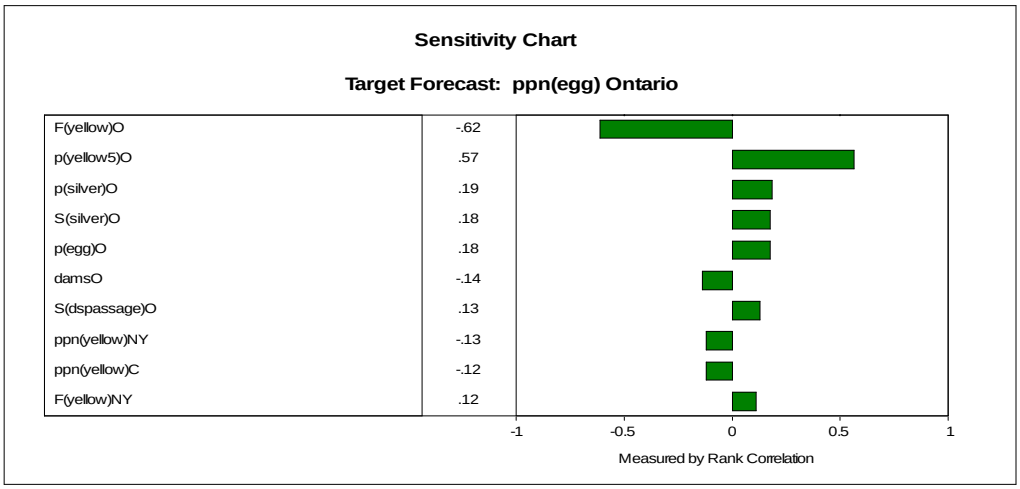


Figure 4.4. Model sensitivity analysis output for trials with constant total yellow eel capacity (c = 50 E+6), and late maturation of LO-SLR eels. Values are rank correlations of the ten coefficients of greatest magnitude influencing total egg production (N50(egg)Total), egg production by eels originating in Lake Ontario and the upper St. Lawrence (N50(egg)Ontario)), and the proportion of total egg production represented by eggs produced by eels originating in Lake Ontario and the upper St. Lawrence (ppn(egg)Ontario)) after 50 years. Model parameter designations are described in Table 3.1

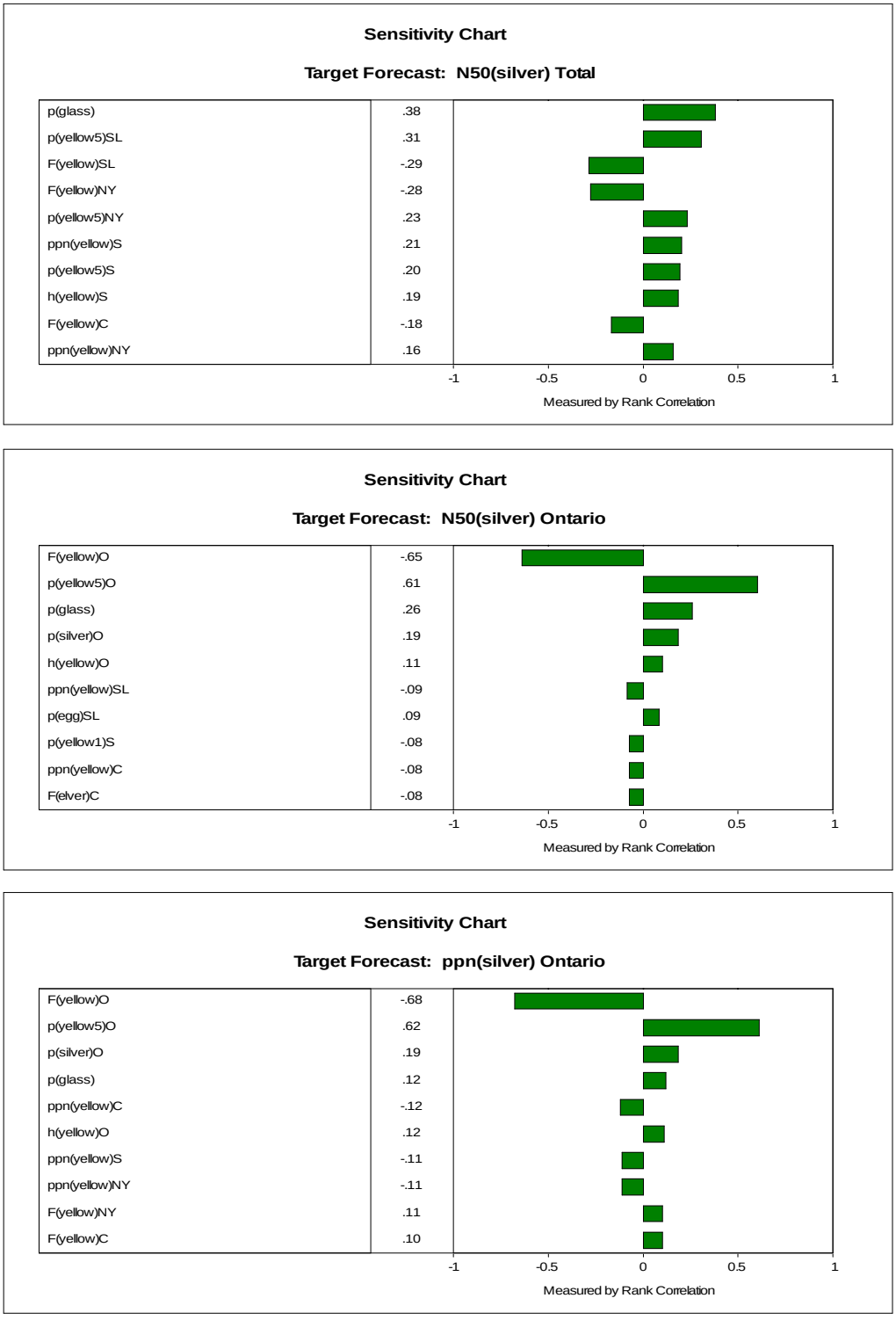


Figure 4.4. Model sensitivity analysis output for trials with constant total yellow eel capacity (c = 50 E+6), and late maturation of LO-SLR eels. Values are rank correlations of the ten coefficients of greatest magnitude influencing total silver eel adundance (N50(silver) Total), silver eel abundance prior to migration in Lake Ontario and the upper St. Lawrence (N50(silver)Ontario), and the proportion of total silver eel abundance represented by silver

eels produced in Lake Ontario and the upper St. Lawrence (ppn(silver)Ontario), after 50 years. . Model parameter designations are described in Table 3.1

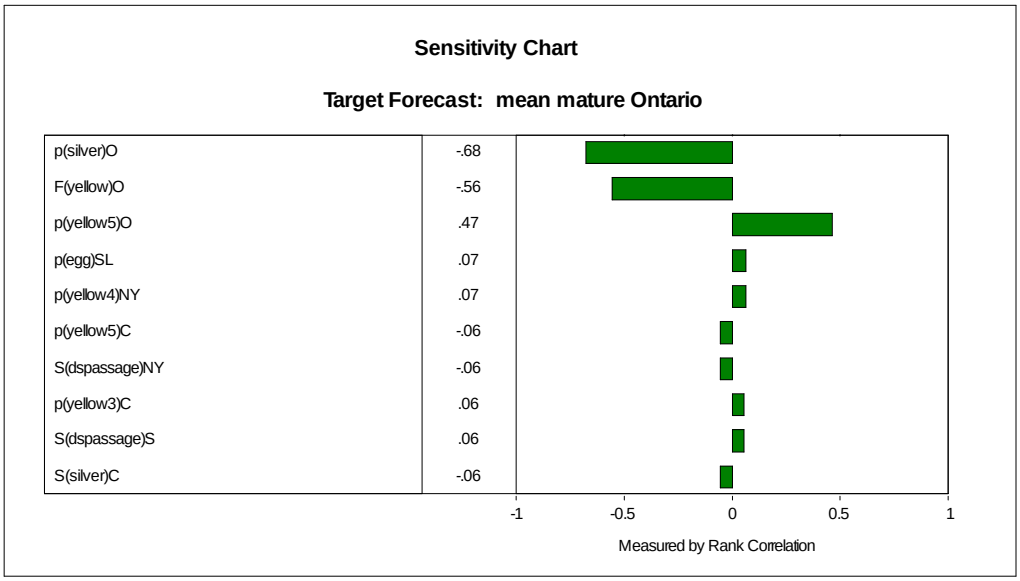


Figure 4.4. Model sensitivity analysis output for trials with constant total yellow eel capacity (c = 50 E+6), and late maturation of Lake Ontario eels. Values are rank correlations of the ten coefficients of greatest magnitude influencing maturation age of eels originating in Lake Ontario and the upper St. Lawrence after 50 years. Model parameter designations are described in Table 3.1

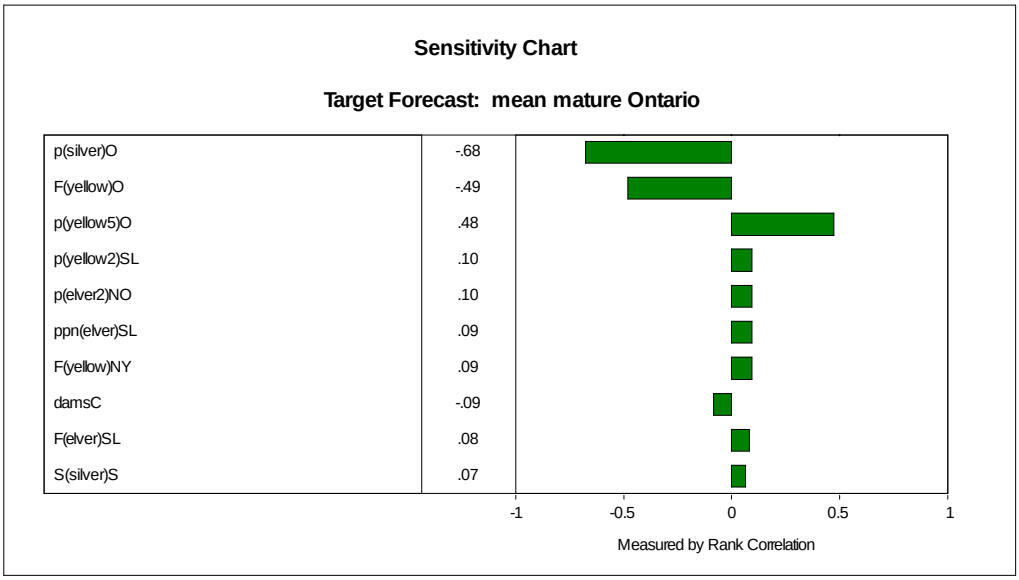
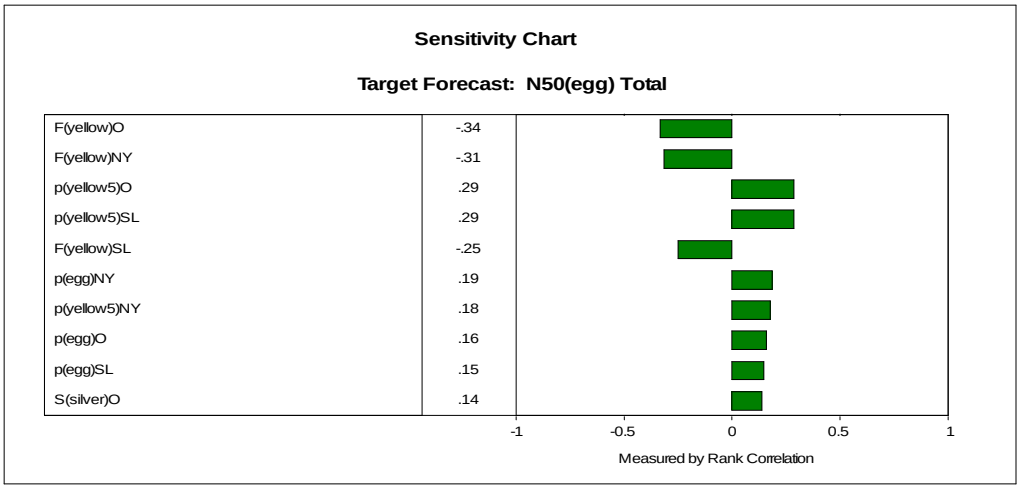
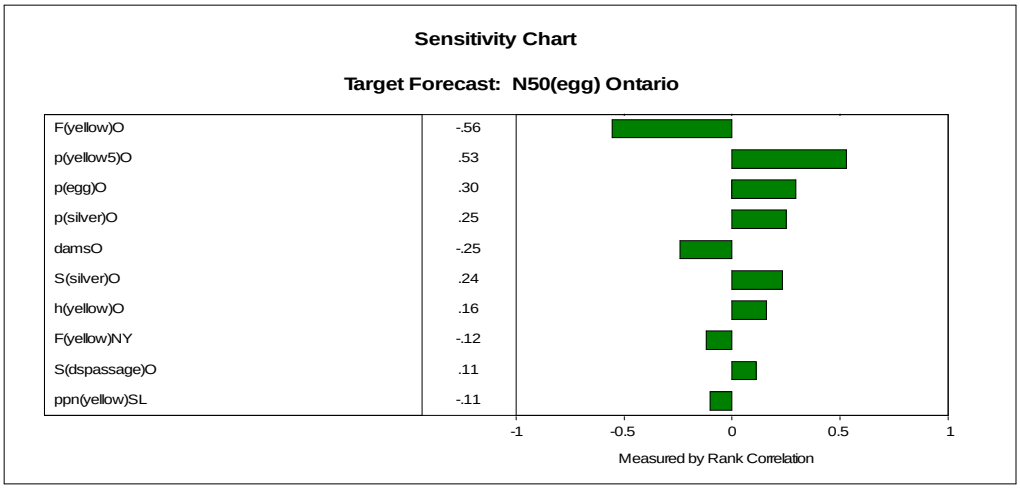


Figure 4.3. Model sensitivity analysis output for trials with constant total yellow eel capacity (c = 50 E+6), and early maturation of LO eels. Values are rank correlations of the ten coefficients of greatest magnitude influencing maturation age of eels originating in Lake Ontario and the upper St. Lawrence after 50 years. . Model parameter designations are described in Table 3.1.





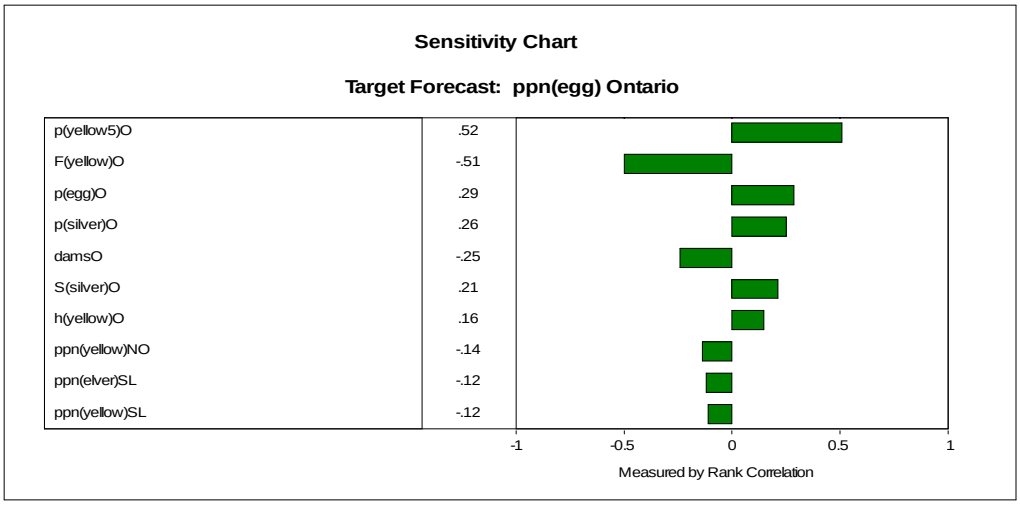
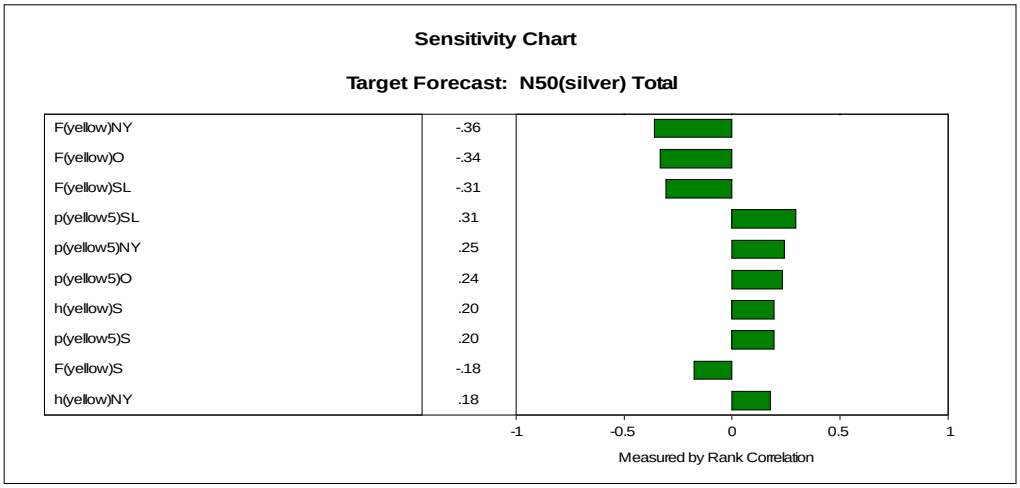
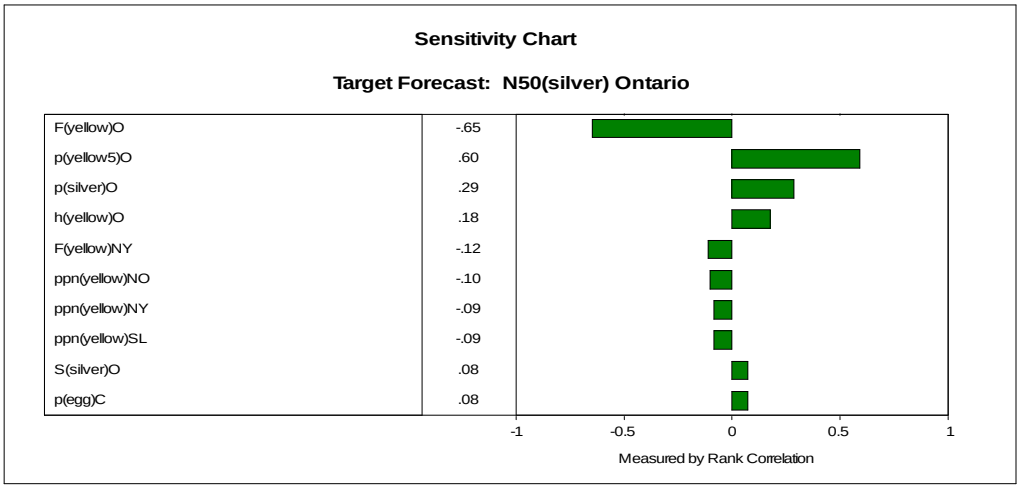


Figure 4.5. Model sensitivity analysis output for trials with constant total yellow eel capacity (c = 50 E+6), early maturation of LO-SLR eels, and fixed production of oceanic stages. Values are rank correlations of the ten coefficients of greatest magnitude influencing total egg production (N50(egg)Total), egg production by eels originating in Lake Ontario and the upper St. Lawrence (N50(egg)Ontario)), and the proportion of total egg production represented by eggs produced by eels originating in Lake Ontario and the upper St. Lawrence (ppn(egg)Ontario)) after 50 years. Model parameter designations are described in Table 3.1.





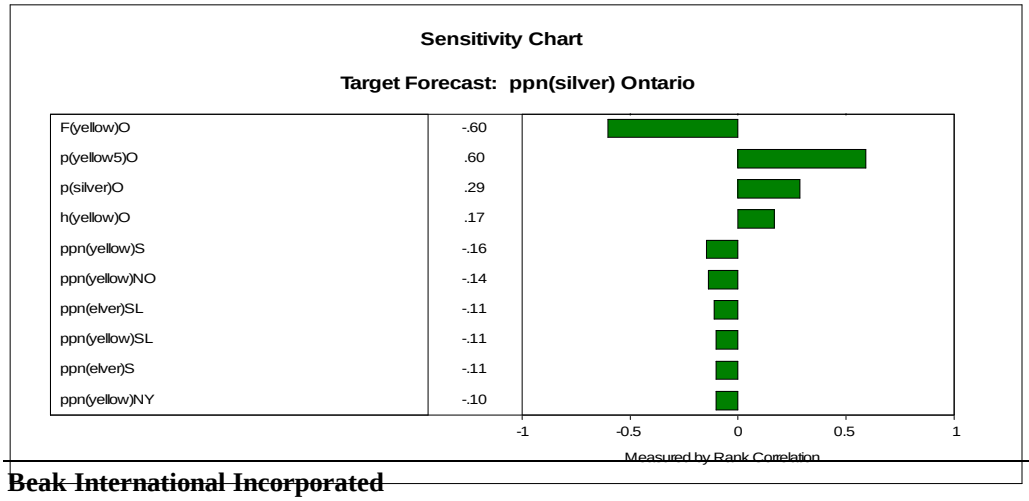


Figure 4.5. Model sensitivity analysis output for trials with constant total yellow eel capacity (c = 50 E+6), early maturation of LO-SLR eels, and fixed production of oceanic stages. Values are rank correlations of the ten coefficients of greatest magnitude influencing total silver eel adundance (N50(silver) Total), silver eel abundance prior to out-migration from Lake Ontario and the upper St. Lawrence (N50(silver)Ontario), and the proportion of total silver eel abundance represented by silver eels produced in Lake Ontario and the upper St. Lawrence (ppn(silver)Ontario), after 50 years. Model parameter designations are described in Table 3.1.

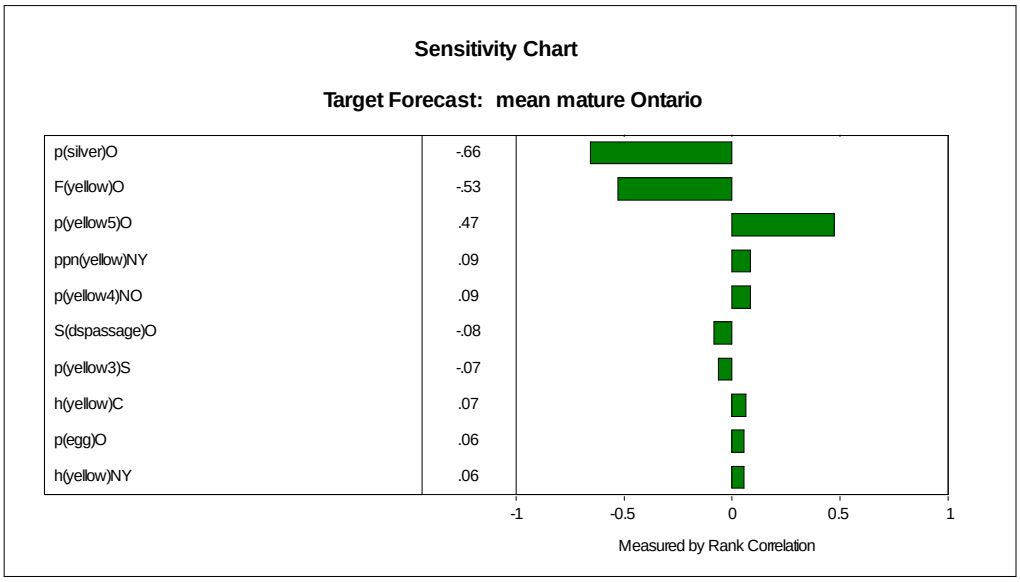
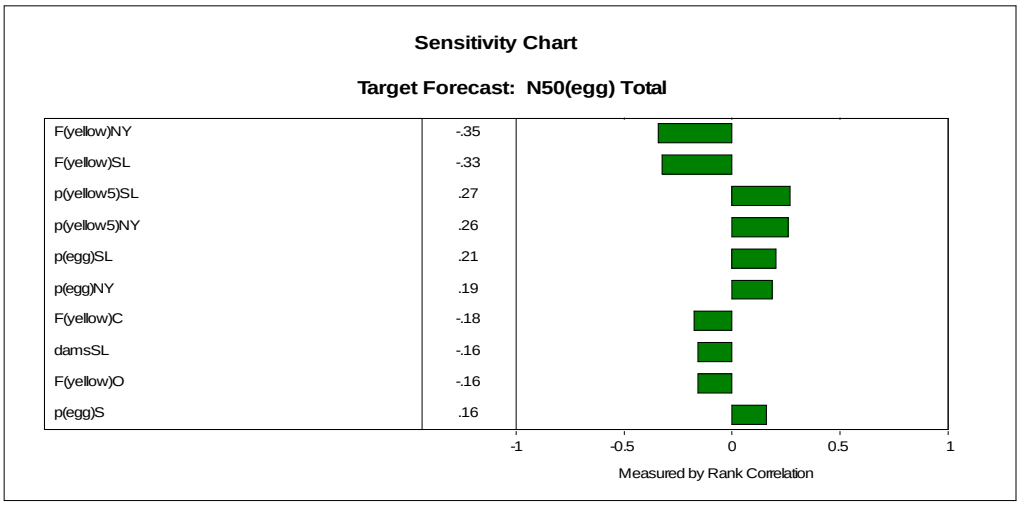
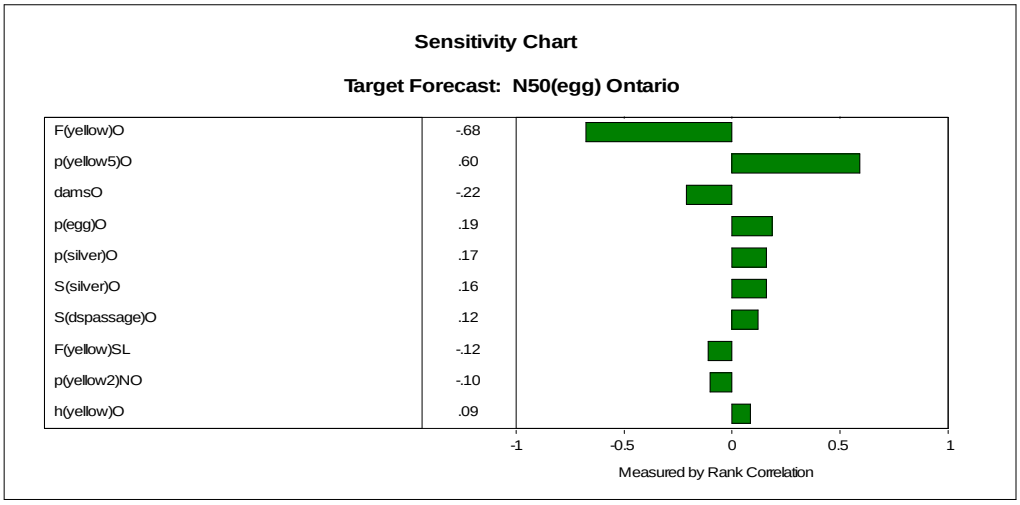


Figure 4.5. Model sensitivity analysis output for trials with constant total yellow eel capacity (c = 50 E+6), early maturation of LO eels, and fixed production of oceanic stages. Values are rank correlations of the ten coefficients of greatest magnitude influencing maturation age of eels originating in Lake Ontario and the upper St. Lawrence after 50 years. . Model parameter designations are described in Table 3.1.





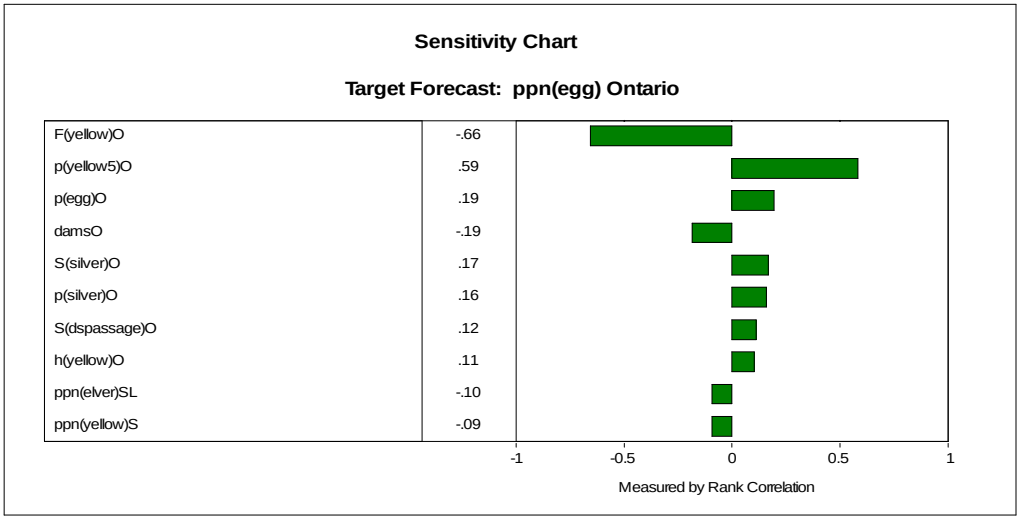


Figure 4.6. Model sensitivity analysis output for trials with constant total yellow eel capacity (c = 50 E+6), late maturation of LO-SLR eels, and fixed production of oceanic stages. Values are rank correlations of the ten coefficients of greatest magnitude influencing total egg production (N50(egg)Total), egg production by eels originating in Lake Ontario and the upper St. Lawrence (N50(egg)Ontario)), and the proportion of total egg production represented by eggs produced by eels originating in Lake Ontario and the upper St. Lawrence (ppn(egg)Ontario)) after 50 years. Model parameter designations are described in Table 3.1

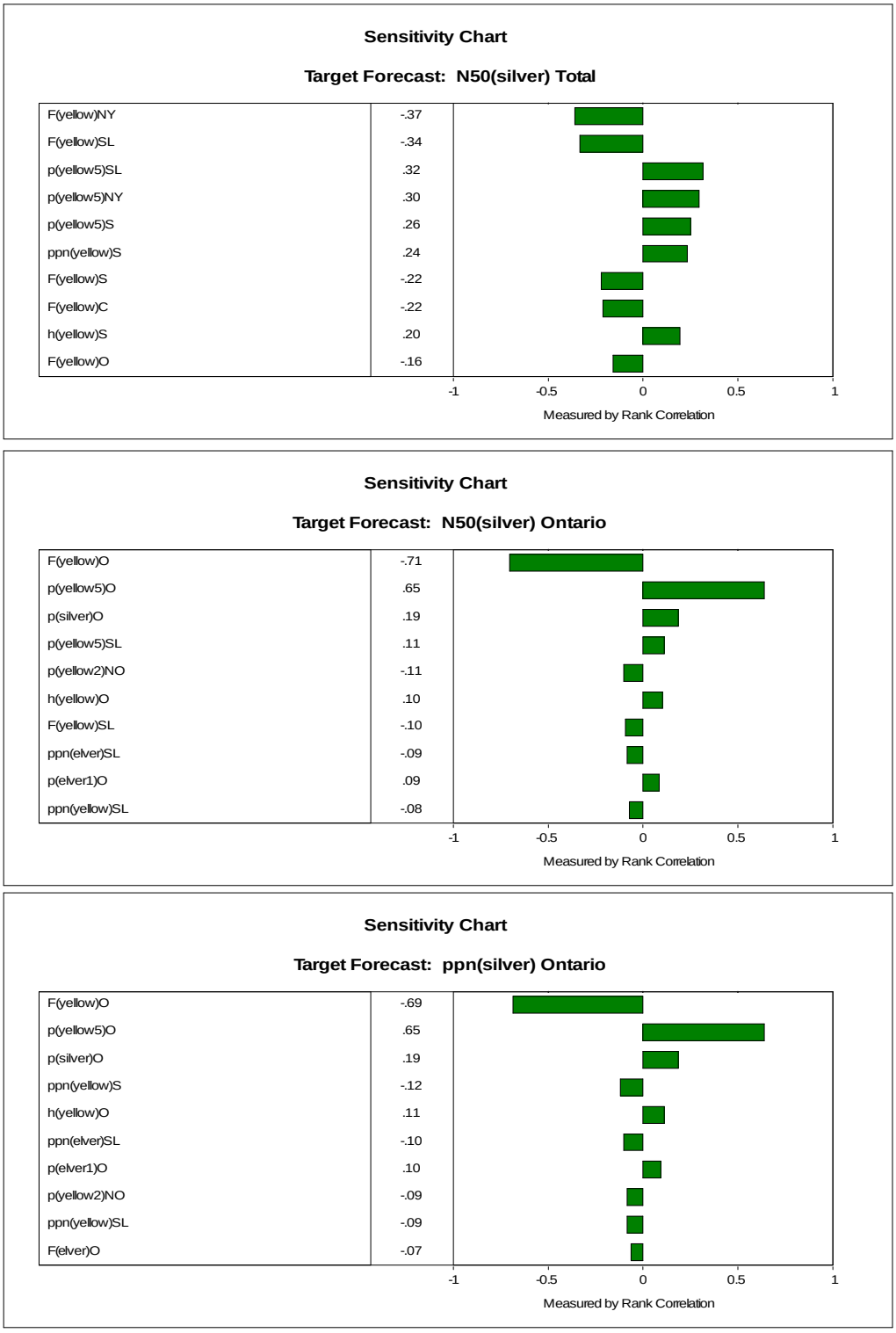


Figure 4.6. Model sensitivity analysis output for trials with constant total yellow eel capacity (c = 50 E+6), late maturation of LO-SLR eels, and fixed production of oceanic stages. Values are rank correlations of the ten coefficients of greatest magnitude influencing total

silver eel adundance (N50(silver) Total), silver eel abundance prior to migration in Lake Ontario and the upper St. Lawrence (N50(silver)Ontario), and the proportion of total silver eel abundance represented by silver eels produced in Lake Ontario and the upper St. Lawrence (ppn(silver)Ontario), after 50 years. Model parameter designations are described in Table 3.1

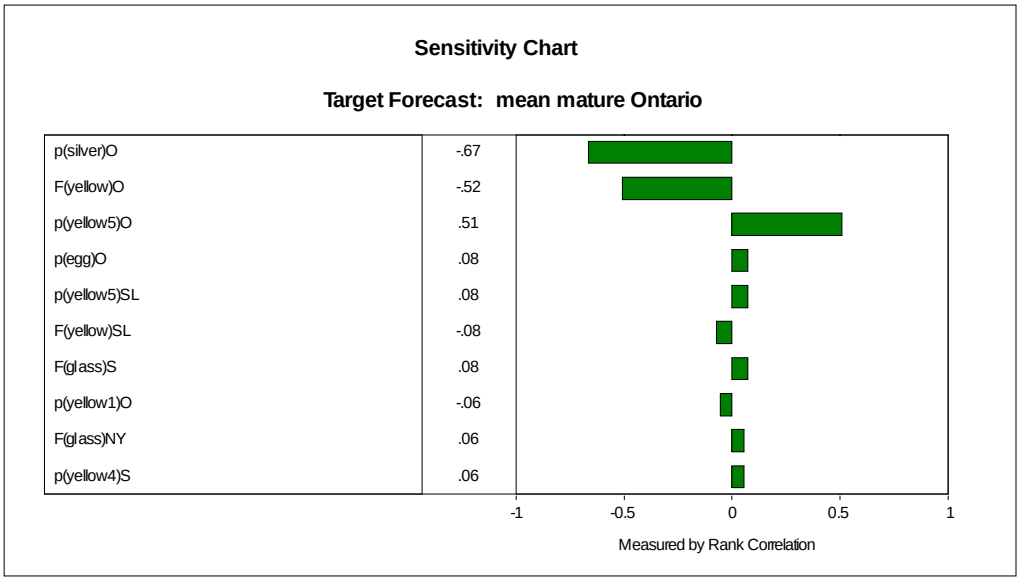


Figure 4.6. Model sensitivity analysis output for trials with constant total yellow eel capacity (c = 50 E+6), late maturation of Lake Ontario eels, and fixed production of oceanic stages. Values are rank correlations of the ten coefficients of greatest magnitude influencing maturation age of eels originating in Lake Ontario and the upper St. Lawrence after 50 years. Model parameter designations are described in Table 3.1

5.0 DISCUSSION

Any thought of attempting a rigorous statistical treatment of American eel population dynamics was abandoned early in the exercise when it became apparent that there was disagreement on virtually every quantitative aspect for which there were data. The disagreement is presumably only limited by the fact that there are no data whatsoever for many important life processes.

It must also be emphasized that the model presented here is not adequate as a management tool. It is intended to inform the process of setting priorities for further work by illuminating the most important aspects of system dynamics based on available information. The questions being asked are about how factors interact under various assumptions and the values employed are approximations based on a small amount of scientific information (itself usually hotly disputed) and anecdotal information from managers and eel researchers.

The model form was chosen because of its general acceptance in the fisheries management community and its tractability. Given sufficient effort to fill the gaps in data, the model, or something very much like it, might well form the basis of a useful management tool.

We abandoned efforts to explicitly model effects of contaminants, parasites or oceanic currents in any theoretically explicit manner. The discussion about factors acting to increase mortality generally will have application to questions about the possible effects of contaminants or parasites. The only effort made to peer into the murk of ocean currents as an issue was the variance of the relative proportion of recruitment to each subpopulation. This is crude, to say the least, but the absence of any information about how young eels get to their coastal destinations forced us to conclude that any such model would be pure artifice.

The first notable outcome of the modeling exercise is the observation that there is tight correspondence between the indications of the modeling exercise (Figures 4.1 to 4.6) and the opinion sample, with one notable exception (Table 4.1). The low importance attached to hypotheses related to oceanic processes, and the absence of any opinion whatsoever on the possible effects of harvesting sargassum, contrasts with the importance of glass eel production in the modeling exercise (Figures 4.1 to 4.6).

The influence of glass eel production on the outcome of several key indicators suggests that oceanic processes may well have an important effect on freshwater subpopulations. It must be acknowledged that this result is based on a range of production parameters that include a

very low assumed natural survivorship, the values all fall within the range of best guesses provided during the consultation process.

The opinion survey also could be interpreted to have rated downstream passage issues more strongly than the sensitivity analysis, although both number of dams and passage survivorship do appear among the ten most sensitive parameters in some forecasts (Figures 4.1 to 4.6).

The strong influence of parameters for which data are limited or nonexistent precludes any strict ranking of causes of the observed decline in recruitment of eels to the LO-SLR sub-stock. Given the caveat that the choice of parameter ranges will accept the outcome, it is possible to rank their plausibility as primary sources of declines of LO-SLR eel abundance.

Runs with Fixed Values

The individual model runs (Table 4.2 and 4.3) show that individual effects can have substantial effects on total eel abundance. In particular, it is clear that fishing mortality, habitat availability, and passage mortality can be significant factors contributing to declines within the range of values examined by the model. It is also clear at that the high end of effect ranges used in these models, acting in combination, can lead to a very large decline in egg production and mature eel abundance.

Sensitivity to Parameters

Life History Parameters

Production parameters figure among the top ten influences on outcomes throughout the sensitivity analyses, particularly for older stages. Gaps in understanding of fecundity and natural survivorship are therefore significant constraints on any further effort to describe the effects of other sources of mortality, limits on fecundity or effects on capacity.

The production parameters and capacities for oceanic stages (leptocephalus and glass eels) are not acted on by any other parameters. This was a consideration in setting relatively broad limits on the production parameters, as putative effects from the harvesting of *Sargassum* spp., marine pollutants, or other factors affecting survivorship in the ocean would act through them. Any changes in recruitment to oceanic stages will be passed on through the modeling of all sub-stocks. For these reasons, caution is advisable in dismissing consistent high sensitivity to the glass eel production parameter as an artifact of the choice of parameter values. It suggests that effects in the ocean could be critically important to recruitment to

later life stages and that a better understanding of what occurs there would significantly improve the ability to predict the effects of other variables.

Selecting appropriate values for egg production was complicated by substantial uncertainty regarding possible density dependent effects on sex ratios and the lack of estimates for mean gross fecundities. The model is exclusively concerned with female eels. If total recruitment in all sub-stocks is numerically biased towards males, the egg production parameters will be lower than if the ratio is balanced or female biased.

Recent work has suggested that large females may produce extremely large numbers of eggs. There are apparently no data on whether larger females also produce larger, more viable ova, as has been documented for other species in which females of many different sizes contribute to the spawning stock (Trippel, 1995). Such a phenomenon could presumably only be documented in the period immediately prior to spawning when ova are fully ripened, and we are not aware of any such studies. The effect of a relationship between females size and ovum size could be modelled through a weighted calculation of production variables for the leptocephalus stage, and perhaps other older stages, but such an effort would be complicated and speculative. A simpler approach would be to weight calculation of mean fecundity by female size, effectively treating ova from smaller females as less than an entire egg. At any rate, our estimates of ranges for mean fecundities for the sub-stocks are clearly subject to many caveats.

The question of a possible relationship between maternal size and egg size is also relevant to assumptions about the randomness of larval transport. If large females produce large offspring, and female size is markedly different among stocks as has been suggested, assumptions about the panmictic nature of the stock would have to be re-examined. The production parameters for older life history stages affect estimates of egg production and the list of parameters to which Lake Ontario silver eel and egg production are most sensitive includes both the 5+ yellow and silver stage production parameters. Varying the age structure of the Lake Ontario sub-stock affects the relative importance of the habitat loss parameter. Extending the residency period prior to onset of maturation by five years, from 12 to 17, slightly reduces its influence on production and proportion of eggs and silvers originating in Lake Ontario (Figures 4.3 and 4.4).

Habitat Capacity

There are local studies of resident eel habitat use (e.g. Bozeman *et al.* 1985). However, the highly imperfect understanding of habitat use, distribution, and abundance of American eels throughout their range makes assigning values for capacity difficult.

Additionally, the model addresses female population dynamics, and some of the proposed effects on eel abundance may interact with life history in poorly understood ways. The question of whether sex ratios are density dependent could affect outcomes in several ways. For example, reduction of available habitat would increase densities, all other things being equal, and could, in the short term, reduce the effective capacity for females by much more than a simple factor of the actual habitat loss. The effect is, in fact, largely conjecture, and there are no data available with which to attempt to model such effects.

It is not surprising that variation over an order of magnitude of the gross carrying capacity has a marked direct effect on egg production and less effect on the proportion of silver eel or egg production relative to the total. The relative effects of the other parameters (see Figures 4.1 to 4.6, and Appendix B) vary somewhat if capacity is allowed to vary in the trials. For the most part, however, the variation is seen in sensitive parameters of the sub-stocks with largest capacity (lower St. Lawrence and Nova Scotia-New York).

The effect of the habitat availability parameter on outcomes is obscured in runs with variable total capacity (Figures 4.1 and 4.2). Insofar as the habitat parameter acts through the capacity parameter, this is not surprising. The effect of Lake Ontario habitat loss on the production and proportion of silver eels and eggs originating in the Lake Ontario sub-stock is stronger in runs with assumed early onset of maturation in Lake Ontario eels. Total production shows some sensitivity to habitat effects in larger sub-stocks (Figures 4.3 and 4.5).

Oceanic Environment

Carrying capacities for all stages in the ocean environment are set at extremely high levels, given the nature of the life styles of the stages living there. Density dependent effects should not be a factor to any degree at any of these stages.

The order of magnitude range on the bounds on glass eel production notwithstanding, the influence of glass eel production on the model (Figures 4.1 to 4.6), speaks to the potential importance of oceanic processes on the status of all sub-stocks. Natural mortality of the youngest stages is certainly very high – that is the norm for young, small, unprotected animals generally. If even one one-thousandth of the egg production of a single large female producing 20 million eggs survives to glass eel stage, twenty thousand of her progeny will leave the Gulf Stream and head for shore. The effect on recruitment to older stages of increasing mortality at the youngest stages through harvesting of *Sargassum*, global warming, marine pollution or changes to the Gulf Stream appears to matter, within the range of parameter values proposed in this model.

The hypothesized effect of changes in the Gulf Stream on larval transport and recruitment to more northerly stocks (e.g., Castonguay, 1994b) has not been properly investigated. The fact that the proportion of elver production recruiting to more southerly sub-stocks registers as a correlate of the proportion of eggs and silver eels (Figures 4.1 to 4.2) is not entirely convincing because of the fact that Lake Ontario elver recruitment is calculated as a function of recruitment to other sub-stocks. It does indicate, however, that the relationship is not entirely swamped by other factors.

Elver and glass eel fisheries register as correlates of silver eel production in the model run with variable total capacity and early onset of maturation in the Lake Ontario sub-stock (Figure 4.1). In the variable capacity run with late maturation (Figure 4.2), parameters associated with silver eel production in Lake Ontario are more important and these fisheries drop out of the top ten influences. This presumably reflects limits on total production by early life history mortality at very high capacities.

Mortality on Resident Eels

Although the F parameter is designated as fishing mortality in the model, it is more appropriate to think of it as a generic increase in mortality above historical natural mortality related to any of several factors. Because data on fishing rates are imprecise, and information

on other sources of mortality such as chemical contaminants or exotic diseases such as swimbladder nematode infestation is entirely lacking, a single general parameter is all that can realistically be accommodated.

As indicated in Figures 4.3 and 4.4 and also in Figures 4.5 and 4.6, increased mortality on resident eels through the fishing parameter has a strong influence on Lake Ontario production of eggs and silver eels. While this stems in part from the use of 0 as the lower bound on the simulation range, this is also true for other parameters subject to management, on the grounds that elimination of fishing, dams, or habitat impairment are at least hypothetically management options. The significance of F is undoubtedly its repeated application over the life of each age class. The strength of its effect on egg production relative to mortality on silver eels, in spite the fact that silver eel mortality acts immediately on the egg production parameter, is consistent with concerns raised from several sources that the resident eel fishery's repeated effect on individual age classes can yield substantial effects (Richkus and Whalen, 1999; ASMFC, 1999).

That the effect of F on total egg production in model implementations with early onset of maturation (Figures 4.3 and 4.5) is greater than on those with late maturation (Figures 4.4 and 4.6) presumably reflects the reduction in proportion of overall silver eel production from the Lake Ontario sub-stock resulting from additional years of natural mortality acting on recruitment to the sub-stock.

The mechanism by which eel maturation is triggered is obscure and the methods employed in these models to simulate the process are simplistic. Simulation results produce plausible distributions of mature eel abundances (see Appendix B), but the possible interactions of age, size, fecundity, and gamete viability discussed in other sections argue strongly for more detailed studies of this question.

Outmigration

Effects on silver eels are modelled with more complexity than other stages. Where effects on the production parameter are modelled as a single effect acting through F for younger stages, silver eel effects include number of dams, dam passage mortality rate, fishing, and natural survivorship. The natural survivorship parameter is, in technical terms, a dodge to permit use of fecundity as the production parameter, but compartmentalization of additional effects at the silver eel stage serves to mask the combined importance of total mortality at this stage. Nonetheless, passage survival, dam number, and natural survivorship are among the most

sensitive variables for egg production from the Lake Ontario sub-stock, generally superceded by only production parameters and the fishery on resident eels in the Lake Ontario sub-stock. Infestations of swimbladder nematode and mobilization of fat-soluble contaminants along with fat reserves and other tissues during the migration may be sources of additional mortality. As with other stages, these may be viewed as contributing to the silver eel fishing mortality parameter. The silver eel fishing mortality parameter does not figure as a primary correlate of either total egg production or of Lake Ontario egg production in any of the four cases, although like fishing mortality on yellow eels, it has a lower bound of 0.

Summary of Model Finding

The ranking, from greatest to least influence, of the top five plausible factors for the entire population in terms of model sensitivity would (with some room for argument) be:

- oceanic effects;
- cumulative effects of fishing (and other anthropogenic mortality) on resident eels;
- dam passage effects;
- habitat effects (blockage or impedance of upstream passage and/or habitat destruction) throughout the entire range; and
- habitat effects in the Lake Ontario/ upper St. Lawrence sub-stock.

The caveat that must be attached to this ranking concerns the previously stated fact that the degree of uncertainty within the oceanic effects component of the model is part of what has driven it to the top of the list.

The ranking, from greatest to least influence, of plausible factors for the Lake Ontario / upper St. Lawrence River contribution to total reproduction, in terms of model sensitivity would (with some room for argument) be:

- cumulative effects of fishing (and other anthropogenic mortality) on resident eels;
- oceanic effects;
- dam passage effects;
- habitat effects in the Lake Ontario/upper St. Lawrence sub-stock; and
- habitat effects throughout the entire range.

These rankings could change substantially if the precision and accuracy of estimates were improved.

Data Gaps and Research Priorities

The most obvious gap in knowledge is the life history of oceanic stages. Although the model output for both total eel and egg production and production in the LO-SLR sub-stock is sensitive to assumptions about production in the oceanic environment, virtually nothing is known about what habitats, if any, are critical to spawning success, hatching, or recruitment to the leptocephalus and glass eel stages. Understanding at least the basics of these issues will lead to a significantly better understanding of how other factors contribute to distribution and abundance of American eels throughout their range. Indeed, these results indicate that a proper understanding of overall trends will not be possible without some new insights into oceanic life history and environmental influences, and that such research should be a priority. Intensive (and expensive) field research is the only option for such study.

The basic ecology of sub-stocks is also poorly understood. These animals do not exhibit simple population dynamics based on straightforward equations. Standard fishery production models are wholly inadequate for their study. Improvement in data regarding the age structure, growth, survivorship, maturation, and fecundity of eels from all habitat components is required. At present, most studies have been fragmentary. Although some recent work has been more focused on answering fundamental life history questions, more such work is needed. Structured research programs investigating basic biology and ecology of American eels in representative habitats within sub-stocks are clearly required. Juvenile natural mortality schedules and the nature of density dependence are critical components of any analytical framework through which effects might fruitfully be evaluated, and they are not adequately understood.

Most fishing mortality data for North American eels stocks do not include dependable estimates of effort and are therefore inadequate as an index of abundance, or measure of fishing rate. Standardized collection of fishing effort data throughout the range of American eels would help elucidate both stock abundance and fishing mortality. As mentioned previously, fishing mortality is one component of the cumulative anthropogenic mortality potentially inflicted on immature, resident eels. The effects of other contributing factors such as microcontaminant toxicity and introduced pathogens are not readily tractable to field study and will probably require laboratory study.

The fact that dam number and passage mortality both figure in egg production results, even when treated as separate variables, is an indication that turbine mortality is important. The

sensitivity analyses are supported by results from deterministic runs in which turbine mortality through two dams with seventy-five percent survivorship had a comparable effect on the base case egg production to an annual silver and yellow eel fishing mortality of nine percent. The actual effect of turbine-induced mortality, both immediate and latent, on silver eels needs to be quantified and measures of the proportion of silver eel production affected by downstream passage effects are needed. Tagging studies would seem to be the most plausible option for such work. Quantification of the efficacy of downstream passage mitigation measures would be a corollary to any such research.

Accurate estimates of habitat capacity for eel production is also needed. Some good work has been done to identify obstacles to migration, but the implications are poorly understood. The apparent importance of density dependence in eel life history means that the capacity of posited sub-stocks – those used in this model or others agreed upon by the research community – needs clarification. Any effort to comprehend the effect of channel obstructions and habitat modification will require some estimation of historical habitat capacity. This will require a combination of historical research and theoretical extrapolation.

A related issue is the question of how obstacles affect upstream passage of early life stage eels. That smaller dams can be passed is known, but whether or to what extent the upstream recruitment of eels is affected by such structures is not. Such studies would be relatively inexpensive and straightforward if structures can be found with readily manipulated stop log structures or other such mechanisms for controlling height. Quantification of the efficacy of upstream passage devices would be a corollary to any such research.

Potential for Mitigation

Although the model makes clear that conclusions about the potential for mitigative measures must be treated with caution, it is possible to make some general comments about the likely effect of specific measures, as indicated by the model. The model is sensitive to the effects of sources of mortality characterized in the model as fishing mortality. A substantial reduction in such mortality in the LO-SLR sub-stock would have a reasonable expectation of improving egg production both from the sub-stock and in total.

The model is relatively insensitive to the effects of silver eel mortality, although the natural survivorship term for silvers is among the most sensitive for LO-SLR egg production. Because the real natural survivorship of silver eels during migration is not known, and because model sensitivity to the yellow eel fishing mortality parameter in LO-SLR is so much

greater than sensitivity to silver eel fishing mortality, it is unlikely that elimination of silver eel fisheries would confer the same benefits as the same measures directed on yellow eel fisheries.

Substantial (close to 100%) removal of barriers to migration, or the provision of high efficiency upstream passage facilities, can also be expected to confer substantial benefits on egg production from the LO-SLR sub-stock. Upstream passage was treated as an either/or proposition in the model. In such an instance, which approximates some hypotheses related to lock function in the seaway, removal of the obstacle would be a basis for all mitigative measures. Without efficient upstream passage, eliminating the fishery or other sources of mortality would be moot.

Mitigation of downstream passage could have substantial benefits to egg production from the LO-SLR sub-stock. All silver eels above Saunders dam must pass through a minimum of two dams (not the maximum of two posited in the sensitivity runs) so it has especially strong implications for that component of the sub-stock. Depending on assumptions about the nature and extent of resident eel habitat above that barrier, this alone could have substantial implications for the total sub-stock, comparable to the effect of the fishery.

General Conclusions

Any effort to provide a formal framework for decisions regarding American eel management in the Saint Lawrence and Lake Ontario is fraught with difficulties ranging from poor data to the highly unusual life history of the subject species. Modeling of the stock and its interactions with the rest of the American eel population would be helpful in structuring debates about the state of both the stock and the total eel population.

The modeling exercise we have undertaken is well short of what would be needed to conclude specifics about sub-stock abundance. It is, we believe, a first step toward structuring discussion of actual relationships in the eel life-history, gaps in understanding, and the likely effects of posited effects.

Doubtless there are many elements of the model that could have been estimated more finely if certain assumptions were made. More resources would have permitted use of statistical distributions for trials with fewer implications for the sensitivity of some parameters. However, certain patterns do emerge. It appears that what happens in the oceanic environment is of material importance to resolving questions about recruitment to coastal and

freshwater habitat. Fisheries on younger, migratory ages and mature fish appear less important than those on resident immature eels. Habitat exclusion and passage mortality can make a difference. Taken together, the effects can be very substantial.

Given the well-documented nature of the dramatic decline in abundance observed in the LO-SLR sub-stock, it would be advisable to immediately initiate research/monitoring efforts that would help to fill the more critical data gaps as determined by this analysis. These are:

- fishing and natural mortality rates for resident immature eels in a range of representative areas, e.g., eastern Lake Ontario, Lac St. Francis, Lac St. Pierre;
- accurate estimates of historical and current habitat capacity for resident immature eels, and the effects of dams on density in upstream habitats; and
- accurate estimates of downstream migrant (adult) mortality including natural mortality, direct and latent turbine passage mortality, and mortality in the Quebec silver eel fishery.

These data would be especially useful in the refinement of the model and could considerably reduce uncertainty regarding the management of the LO-SLR sub-stock.

Finally, we re-emphasize that this effort is intended as a first and tentative step toward an adaptive management approach to dealing with the uncertainties that complicate American eel management. It is not intended to form a basis for management of the sub-stock, but as a tool to guide investigations that might improve management and help to preserve this valuable and unique resource.

6.0 REFERENCES

Atlantic States Marine Fisheries Commission (ASMFC). 1999. Interstate Fishery Management Plan for American Eel (*Anguilla rostrata*). pp. 79.

Avise, J.C., G.S. Helfman, N.C. Saunders and L.S. Hales. 1986. Mitochondrial DNA differentiation in North Atlantic eels: population genetic consequences of an unusual life history pattern. Proc. Natl. Acad. Sci. USA 83:4350-4354.

Avise, J.C., W.S. Nelson, J. Arnold, R.K. Kohen, G.C. Williams, and V. Thorsteinsson. 1990. The evolutionary genetic status of Icelandic eels. Evolution 44:1254-1262.

Barse, A. and D.H. Secor. 1999. A exotic nematode parasite of American eel. Fisheries 24(2): 6-10.

Beverton, R.J.H. and S.J. Holt. 1957. On the dynamics of exploited fish populations. Chapman and Hall. London. 533 pp. + app.

Bond, C.E. 1979. Biology of Fishes. W.B. Saunders Co. Philadelphia. 514 pp.

Bozeman, E.L, G.S. Helfman and T. Richardson. 1985. Population size and home range of American eels in a Georgia tidal creek. Trans. Amer. Fish. Soc. 114: 821-825.

Caron and G. Verreault. 1997. *In:* R.H. Petersen (Ed.). The American eel in Eastern Canada: Stock Status and Management Strategies. Proceedings of Eel Workshop, January 13-14, 1997, Quebec City, QC. Biological Station, St. Andrews, NB. Can Tech. Rep. Fish. Aquat. Sci. No. 2196. 74 pp.

Casselman, J.M., L.A. Marcogliese, T. Stewart and P.V. Hodson. 1997a. Status of the upper St. Lawrence River and Lake Ontario American eel – 1996, pp. 106-120. *In:* R.H. Petersen (Ed.). The American eel in Eastern Canada: Stock Status and Management Strategies. Proceedings of Eel Workshop, January 13-14, 1997, Quebec City, QC. Biological Station, St. Andrews, NB. Can Tech. Rep. of Fish. Aquat. Sci. No. 2196. 174 pp.

Casselman, J.M., L.A. Marcogliese and P.V. Hodson. 1997b. Recruitment index for the upper St. Lawrence River and Lake Ontario eel stock: a re-examination of eel passage at the R.H. Saunders hydroelectric generating station at Cornwall, Ontario 1974-1995, pp. 161-169. *In:* R.H. Petersen (Ed.). The American eel in Eastern Canada: Stock Status and Management Strategies. Proceedings of Eel Workshop, January 13-14, 1997, Quebec City, QC. Biological Station, St. Andrews, NB. Can Tech. Rep. of Fish. Aquat. Sci. No. 2196. 174 pp.

Castonguay, M., P.V. Hodson, C.M. Coulliard, M.J. Eckersley, J.D., Dutil, and G. Verreault. 1994a. Why is recruitment of American eel declining in the St. Lawrence River and Gulf. Can J. Fish Aquat. Sci. 51: 479-488.

Castonguay, M., P.V. Hodson, C. Moriarty, K.F. Drinkwater, and B.M. Jessop. 1994b. Is there a role of ocean environment in American and European eel decline? Fish. Oceanogr.3(3):197-203.

De Charleroy, D., L. Grisez, K. Thomas, C. Belpaire and F. Ollivier. 1990. The life cycle of *Anguillicola crassus*. Dis. Aquat. Org. 8:77-84.

De Leo, G.A., and M. Gatto . 1995. A size and age-structured model of the European eel (*Anguilla anguilla* L.). Can. J. Fish. Aquat. Sci. 25:1351-1367.

Dutil, J-D., M. Besner and S.D. McCormick. 1987. Osmoregulatory and ionregulatory changes and associated mortalities during the transition of maturing American eels to a marine environment. Am. Fish. Soc. Symp. 1:175-190.

Eales, J.G. 1968. The eel fisheries of eastern Canada. Fish Res. Board. Can. Bull. 166. 79 pp.

Facey, D.E. and M.J. Van Den Avyle. 1987. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (North Atlantic) –American eel. US Fish Wildl. Ser. Biological Report 82(11.74) U.S. Army Corps of Engineers, TR EL-82-4. 28 pp.

Fahay, M.P. 1978. Biological and fisheries data on American eel, *Anguilla rostrata* (LeSuer). U.S. Sept. Commer. Natl. Mar. Serv. Tech. Rep. No. 17, Northeast Fisheries Center, Highlands, N.J> 82p. *In* Anon. 1991. Chesapeake Bay American Eel Fishery Management Plan. Chesapeake Bay Program. Agreement Commitment Report 1991. U.S. Environmental Protection Agency. 26 pp.

Giesy, J.P., J. Newsted and D.L. Garling. 1986. Relationships between chlorinated hydrocarbon concentrations and rearing mortality of Chinook salmon (*Oncorhynchus tshawytscha*) eggs from Lake Michigan J. Great Lakes Res. 12:82-98

Greatbatch, R.J., A.F. Faning, A.D. Goulding and L. Levitus. 1991. A diagnosis of interpentadal circulation changes in the North Atlantic. J. Geophys. Res. 96(C):22,009-22,023.

Hadderingh, R.H. 1990. Eel mortality at hydro-power stations and possible solutions for this problem. N.V. KEMA. Envir. Res. Dept. The Netherlands.

Haro, A.J. and W.H. Kreuger. 1991. Pigmentation, otolith rings, and upstream migration of Juvenile American eel (*Anguilla rostrata*) in a coastal Rhode Island stream. Can. J. Zool. 69:812:814.

Haro, A., W. Richkus, K. Whalen, A. Hoar, W. Dieter-Busch, S. Lary, T. Brush and D. Dixon. 2000. Population decline of the American eel: Implications for research and management. Fisheries 25(9): 7-16.

Helfman, G.S., D.E. Facey, L.S. Hales, Jr. and E.L. Bozeman, Jr. 1987. Reproductive ecology of the American eel. Am. Fish. Soc. Symp. 1:42-56.

Hilborn, R. and C.J. Walters. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall. New York. 570 pp.

Hodson, P.V., C. Desjardins, E. Pelletier, M. Castonguay and C.M. Couillard. 1992. Decrease in chemical contamination of American eels (*Angullia rostrata*) captured in the estuary of the St. Lawrence River. Can. Tech. Rep. Fish. Aquat. Sci. 1876. 57 pp.

Höglund, J. and K. Thomas. 1992. The black goby *Gobius niger* as a potential paratenic host for the parasitic nematode *Anguillicola crassus* in a thermal effluent of the Baltic. Dis. aquat. Org. 13: 175-180.

Jessop, B.M. 1987. Migrating American eels in Nova Scotia. Trans Amer. Fish. Soc. 116:161-170.

Jessop, B.M. 1997. An overview of European and American eel stocks, fisheries and management issues, pp. 6-20. *In:* R.H. Petersen (Ed.). The American eel in Eastern Canada: Stock Status and Management Strategies. Proceedings of Eel Workshop, January 13-14, 1997, Quebec City, QC. Biological Station, St. Andrews, NB. Can Tech. Rep. Of Fish. Aquat. Sci. No. 2196. 174 pp.

Jessop, B.M. 1998. Geographical and seasonal variation in biological characteristics of American eel elvers in the Fundy area and on the Atlantic coast of Nova Scotia. Can. J. Zool. 76:2172-2185.

Kirk, Lewis and Kennedy. 2000. Parasitology 120:289-295.

Kleckner, R.C. 1980. Swimbladder wall guanine enhancement related to migratory depth in silver phase *Anguilla rostrata*. Comp. Bioch. Physiol. 65A:351 –354.

Kleckner, R.C. and W.H. Krueger. 1981. Changes in swim bladder retial morphology in *Angullia rostrata* during premigration metamorphosis. J. Fish Biol. 18:569-577.

Kleckner, R.C. and J.D. McCleave. 1982. Entry of migrating American eel leptocephali into the Gulf Stream system. Helgo. Wiss. Meersunters. 35:329-339.

Kleckner, R.C., J.D. McCleave and G.S. Wippelhauser. 1983. Spawning of American eel, *Angullia rostrata*, relative to thermal fronts in the Sargasso Sea. Environ. Biol. Fishes 9:289-293.

Knopf *et al*. 1998. Dis. Aquat. Org. 33: 143-149.

Krueger and Oliviera. 1999. Evidence for environmental sex determination in the American eel (*Angullia rostrata*). Environ. Biol. Fishes 55:381-389.

Lary, S.J. and W.–D.N. Busch. 1997. American eel (*Angullia rostrata*) in Lake Ontario and it's tributaries: distribution, abundance essential habitat restoration and restoration requirements. Administrative Report No 97-01, U.S. Department of the Interior, Fish and Wildlife Service, Lower Great Lakes Fishery Resource Office, Amherst, NY. 27 pp.

Liew, P.K.L. 1982. Impact of the eel ladder on the upstream migrating eel (*Angullia rostrata*) population in the St. Lawrence River at Cornwall:1974-1978, pp. 17-22. *In* K.H. Loftus (ed.) Proceedings of the 1980 North American Eel Conference. 1982. Ont. Fish. Tech. Rep. Ser. No. 4. 97 p.

Marcogliese, L.A., J.M. Casselman and P.V. Hodson. 1997. Dramatic declines in recruitment of American eel (*Anguilla rostrata*) entering Lake Ontario – long-term trends, causes and effects. Plenary presentation to the 3rd National Environmental Monitoring and Assessment Network Meeting, Saskatoon, Saskatchewan, 22 January 1997. http://www.cciw-temp/reports/publications/nm97_eel/intro.html.

Mousalli, E. and R. Hilborn. 1986. Optimal stock size and harvest rate in multi-stage life history models. Can. J. Fish. Aquat. Sci. 43:135-141.

McCleave, J.D. 1987. Migration of *Anguilla* in the ocean: signposts for adults/signposts for leptocephali, pp. 243-273. *In:* W.F. Herrakind and A.B. Thistle. (Eds.) Signposts in the Sea. Tallahassee, FL, Florida State University.

McCleave, J.D. and R.C. Kleckner. 1985. Oceanic migrations of Atlantic eel (*Anguillia* spp.): adults and their offspring. Contrib. Mar. Sci. 27:316-337.

McCleave, J.D., R.C. Kleckner and M. Castonguay. 1987. Reproductive sympatry of American and European eel and implications for migration and taxonomy. Am. Fish. Soc. Symp. 1:268-297.

Moravec, F. and R. Konecny. 1994. Some new data on the intermediate and paratenic hosts of the nematode *Anguillicola crassus* Kuwahara, Niimi and Itagaki, 1974 (Dracunculoidea), a swimbladder parasite of eels. Folia Parasitologica 41:65-70.

Moravec and Skoríková . 1998. Dis. Aquat. Org. 34: 217-222.

Pankhurst, N.W. 1982. Relation of visual changes to the onset of sexual maturation in the European eel *Anguilla anguilla* (L.) Journal of Fish Biol. 21: 127-140.

Pankhurst, N.W. 1984. Artificial maturation as a technique for investigating adaptations for migration in the European eel, *Anguilla anguilla* (L.). *In:* Mechanisms of migration in fishes. *Edited by* J.D. McCleave, G.P. Arnold, J.J. Dodson, and W.H. Neill. Plenum Press, New York. pp. 143 – 157.

Pankhurst, N.W. and J.N. Lythgoe. 1982. Structure and colour of the integument of the European eel *Anguilla anguilla* (L.). J. Fish Biol. 21: 279-296.

Power, J.H. and J.D. McCleave. 1983. Simulation of the North Atlantic ocean drift of *Anguilla* leptocephali. U.S. Natl. Mar. Fish. Serv. Bull. 81:483-500.

Reimer, L.W., A. Hildebrand, D. Scharberth and U. Walter. 1994. *Anguillicola crassus* in the Baltic Sea: field data supporting transmission in brackish waters. Dis. Aquat. Org. 18: 77-79.

Richkus, W.A. and K.G. Whalen. 1999. American Eel (*Anguilla rostrata*) Scoping Study Report. Final Report, March 1999 by Versar Inc., prepared for Electric Power Research Institute.

Schmidt, J. 1925. The breeding places of the eel. Smithson. Inst. Annu. Rep. 1924:279-316.

Sorensen and Pankhurst. 1988. Histological changes in gonad, skin, intestine, and olfactory epithelium of artificially matured American eels. J. Fish Biol. 32: 297-307.

Stasko, A.B. and S.A. Rommel, Jr. 1977. Ultrasonic tracking of Atlantic salmon and eels. Rapp. P.-V. Reun. Cons. Int. Explor. Mer. 179:36-40.

Taylor, B.L. 1993. "Best" abundance estimates and best management: why they are not the same. NOAA Technical Memorandum. NOAA-TM-NMFS-SWFSC-188.

Taylor, B.L. and T. Gerrodette. 1993. The uses of statistical power in conservation biology: the vaquita and northern spotted owl. Conservation Biology 7: 489-500.

Taylor, B.L., P.R. Wade, D.P.De Master and J. Barlow. 2000. Incorporating uncertainty into management models for marine mammals. Conservation Biology 14(5): 1243 – 1252.

Tesch, F.W. 1977. The Eel. J. Greenwood, translator. Chapman and Hall, London. 422 pp.

Tesch, F.W. 1991. Anguillidae. *In:* The freshwater fishes of Europe V.2: Clupeidae, Anguillidae. *Ed.* Hoestlandt.. AULA-Verlag. Wiesbaden pp. 388 – 437.

Thomas and Ollevier. 1992. Population biology of *Anguillicola crassus* in the final host *Anguilla anguilla*. Dis. Aquat. Org. 14:163-170.

Trippel, E.A. 1995. Age at maturity as a stress indicator in fisheries. BioScience 45(11): 759-771.

Wade, P.R. 2000. Bayesian methods in conservation biology. Conservation Biology 14(5): 1308–1316.

Wainwright, E. 1998. Crystal Ball Version 4.0g Pro. Decisioneering Inc. Denver.

Wenner, C.A. 1973. Occurrence of American eels, *Anguilla rostrata*, in water overlying the eastern North American Continental Shelf. J. Fish. Res. Board Can. 30:1752-1755.

Wenner, C.A. and J.A. Musick. 1974. Fecundity and gonadal observation of the American eel, *Anguilla rostrata*, migrating from Chesapeake Bay, Virginia. J. Fish. Res. Board Can. 31:1387-1391.

Würtz and Taraschewski. 2000. Dis. Aquat. Org. 39: 121-134.