Ecological Applications, 7(3), 1997, pp. 991–1001

PISCIVORES, PREDATION, AND PCBs IN LAKE ONTARIO'S PELAGIC FOOD WEB

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Abstract. PCB concentrations in Great Lakes sport fishes continue to concern managers. Proposed reductions in consumption advisories, if adopted, would increase pressure to further reduce contaminant concentrations. However, management of Great Lakes pelagic food webs for minimum PCB concentrations and maximum sustainability represents a potential conflict. Here I use a detailed age-structured chinook salmon–alewife model to examine the potential for changes in stocking rates to further reduce contaminant concentrations in Lake Ontario's chinook salmon. Uncertainty surrounding recruitment of alewife, the principal prey of all stocked salmonids, is considered, and sustainability of alewife is cast in probabilistic terms. The interaction between size-selective predation and chinook salmon growth rates leads to a relatively narrow range of chinook salmon stocking that should keep the alewife eaten small (thus having relatively low PCB concentrations) but not reduce the age structure of the alewife population to few reproductive individuals. Stocking rates necessary to achieve PCB consumption advisories $\leq$0.5 mg/kg fish mass carry $\approx$90% probability of an alewife population crash. Modest increases (25%) in current stocking rates would decrease PCB concentrations of chinook salmon without a large increase in the probability that the alewife population would crash. These results are applicable to other salmonids (coho salmon and lake, rainbow, and brown trout), because they too exhibit size selective predation, and their recruitment is largely determined by stocking.

Key words: alewife; Alosa pseudoharengus; *chinook salmon; ecosystem model; fisheries management; Great Lakes;* Oncorhynchus tshawytscha; *PCBs; predator–prey interaction.*

INTRODUCTION

History of the Lake Ontario offshore fishery

The Lake Ontario fishery has experienced some impressive changes over the last century. The offshore pelagic fish community was historically dominated by lake trout (*Salvelinus namaycush*), Atlantic salmon (*Salmo salar*), and burbot (*Lota lota*). Alewife (*Alosa pseudoharengus*) appeared during the late 1800s, and in the absence of abundant piscivores the alewife population exploded (Christie 1974). Rainbow smelt (*Osmerus mordax*) were first noticed in 1929; they too proliferated and were implicated in the collapse of the native herring stocks (Christie 1974). Sea lamprey (*Petromyzon marinus*) numbers rose in the early 1900s coincident with the highest yields of lake trout. The combined effects of sea lamprey predation and overfishing (Christie 1974) led to the elimination of the lake trout (Baldwin and Saalfeld 1962) and Atlantic salmon (Jones et al. 1993) from Lake Ontario by $\approx$1960. Burbot abundance had also been reduced, and the pelagic food web lacked a top predator. In 1968 a salmonid stocking program began that was intended to reestablish the lake trout and produce an economically important sport fishing industry. Sport fish predators stocked included Pacific salmonids (chinook salmon, *Oncorhynchus tshawytscha,* and coho salmon, *O. kisutch*), rainbow trout (*O. mykiss*), brown trout (*Salmo trutta*), and the native lake trout and Atlantic salmon.

Between 1968 and the late 1980s stocking rates of sport fishes rose steadily to $>8 \times 10^6$ individuals/yr in 1986 (Jones et al. 1993). The stocking program transformed a "dwindling" (Kitchell 1991) resource to a 10^9 US$/yr industry (Talhelm 1987). Great Lakes sport fisheries became so successful that Gale (1987) referred to them as a "resource miracle." Shoreline communities revitalized their waterfronts and local economies benefitted (Kitchell 1991) as use of the resource grew. Over this same period phosphorus loadings to the lake declined by $\approx$80% (International Joint Commission 1978). By 1990 the combined effects of high rates of salmonid stocking and decreased phosphorus loading began to appear as signs of stress in Lake Ontario's pelagic food web. For example, increases in dying salmon in bottom trawls, decreases in the size of salmon returning to spawn, and reduced angler harvest rates had been noticed (Great Lakes Fishery Commission 1992). Growth of stocked salmonids is currently sustained principally by alewife, and to a minor degree by rainbow smelt and slimy sculpin (*Cottus cognatus*). Concerns were raised that the supply of prey fishes was no longer able to meet the demands of stocked sport fish (Jones et al. 1993). Two exceedingly poor year

Manuscript received 11 April 1996; revised 27 September 1996; accepted 6 October 1996.

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classes of alewife suggested that salmonid predation was so excessive that the alewife population had been reduced to nearly all pre-reproductive individuals. In response to concerns of an impending prey fish collapse, stocking rates of all salmonids were reduced by ≈55% between 1991 and 1994 (Great Lakes Fishery Commission 1994).

Polychlorinated biphenyls (PCBs) in the Great Lakes, and fisheries management

PCB production was banned in the United States in the mid-1970s. Soon thereafter, PCB concentrations in Great lakes sport fish declined, but they have remained fairly stable since 1985 (Borgmann and Whittle 1991, Stow et al. 1995*a*). Despite substantial progress made in reducing PCB concentrations of Great Lakes sport fish, organochlorines continue to concern those who manage the Great Lakes. For example, a recent ranking of toxic chemicals in the Great Lakes began with eight organochlorine compounds (Bicknell 1992). Some contaminants are believed to impair successful reproduction of sport fish (Kubiak et al. 1989) and present a hurdle for the restoration of species that were once major players in Great Lakes food webs. There are continuing health concerns for humans who consume Great lakes fishes (Evans 1988).

Sources of PCBs to Great Lakes food webs include the atmosphere (Swackhamer and Armstrong 1986, Sweet et al. 1993), resuspension from sediments (Swackhamer and Armstrong 1988, Hermanson et al. 1991), and local areas of elevated concentrations such as landfill and industrial waste sites. Around the five Great Lakes there are 43 local areas of high concentration that are currently proposed for cleanup (Hartig and Zarull 1992). However, there is no technically or financially feasible way to clean up atmospheric and sediment PCB sources to the Great Lakes.

If adopted, proposed reductions in the sport fish PCB consumption advisory from 2.0 mg/kg fish biomass either to 0.1 mg/kg (International Joint Commission 1978) or to doses related to consumption frequency (e.g., 0.22 mg/kg for 1 meal/wk or 0.95 mg/kg for 1 meal/mo) (Great Lakes Sport Fish Advisory Task Force [GLSFATF] in Anderson et al. [1993]) would almost certainly lead to public anxiety and would result in a major challenge to managers who are charged with reducing contaminant levels in Great Lakes fishes. Organochlorine contaminant concentrations in Great Lakes fishes vary widely among species, even when corrected for size and age (Jensen et al. 1982, Masnado 1987, Thomann 1989). Variation in growth rates and diets is partly responsible for these differences (Weininger 1978, Jude et al. 1987). The alteration of sport fish stocking rates has been suggested as a means by which PCB concentrations in stocked sport fish might be altered (Stow and Carpenter 1994, Stow et al. 1995*b*, Jackson 1996*a*). Because natural reproduction of exotic salmonids and lake trout is low (Jones et al. 1993), recruitment of these predators is largely the result of hatchery plantings. This affords the opportunity to regulate salmonid predation by controlling the number and species of salmonids stocked.

PCBs and the Lake Ontario sport fishery: a conflict of goals?

It is highly likely that management of the Lake Ontario fishery for maximum sustainability and minimum PCB concentrations constitutes a contradiction of goals (Jackson 1996*a*). Changes in salmonid stocking should affect prey fish contaminant dynamics because salmonid predation influences prey fish size structure and possibly prey fish growth rates. The prey fish response feeds back to affect salmonid diets, growth, and their contaminant burdens because trophic transfer is the major pathway for organochlorine contaminant accumulation in salmonids (Thomann and Connolly 1989, Rasmussen et al. 1990, Rowan and Rasmussen 1992, Madenjian and Carpenter 1993). Stocking fewer salmonids should decrease predation on prey fishes and therefore increase prey fish survival, which should, in turn, lead to prey fish populations containing older, more contaminated individuals (Fig. 1). Reduced stocking should therefore offer better prospects for a sustainable fishery. Alternatively, stocking more salmonids should increase predation, decrease prey fish survival, and lead to prey populations of younger, less contaminated individuals (Fig. 1). However, increased predation rates will drive the system farther from a situation where prey supply can sustain predator demand. Clearly, there is a potential trade-off between acceptable PCB concentrations and sustainability of the salmonid fishery. However, it is not known what stocking rate is most likely to lead to the best compromise between PCB concentration and fishery sustainability goals.

Lake Ontario is one example where only a simulation model will allow analyses to be performed at temporal and spatial scales that are relevant to the ecosystem scale, and modeling carries the benefit of allowing synthesis of empirical data from many sources. Synthesis papers emphasize and call for management of the Great Lakes with an ecosystem perspective (Spangler et al. 1987, Steedman and Regier 1987, Stewart and Ibarra 1991, Jones et al. 1993), yet there are currently no programs that survey PCBs in the entire Lake Ontario pelagic food web. A lack of whole-system analyses represents a substantial hurdle to reaching an ecosystem perspective (Leach et al. 1987, Lewis et al. 1987). I used simulation modeling to examine the potential to alter chinook salmon PCB concentrations by altering their stocking rates. I considered the possible tradeoffs between lower salmonid PCB concentrations and sustainability of the pelagic food web. My approach was to first use a detailed age-structured chinook salmon–alewife model to examine how different stocking scenarios alter chinook salmon PCB concentrations. I did this with deterministic simulations that ignored pa-

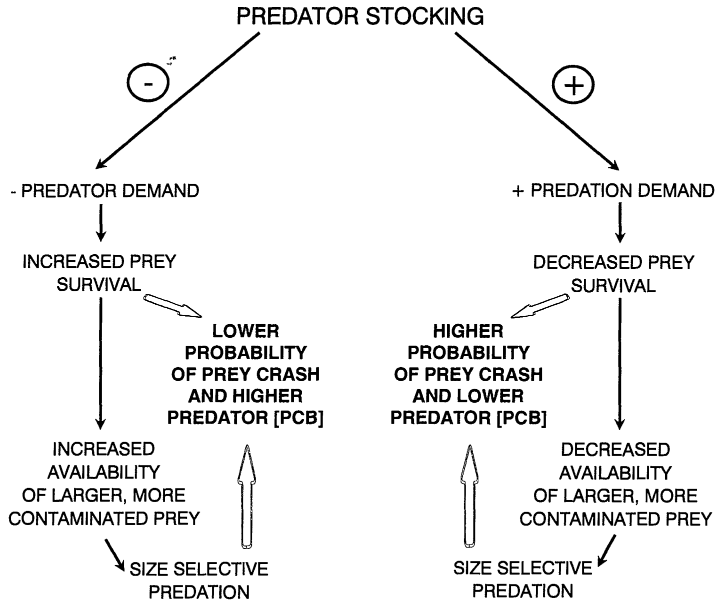

FIG. 1. Flow chart illustrating the dichotomy of prey and predator responses to changes in stocking rates of the predator salmon *Oncorhynchus tshawytscha* in Lake Ontario. Size selective predation by salmonids is for the largest available alewife (*Alosa pseudoharengus*) (Stewart and Ibarra 1991).

rameter uncertainty, but explored model behavior. Then I estimated the uncertainty in my predictions that was due to potential errors in the alewife stock–recruitment function. The results showed that at high stocking rates, PCB concentrations in chinook salmon were minimized, but there was a high probability that alewife supply could not meet chinook salmon demand. At low stocking rates, increased survival of alewife led to an alewife population containing older, larger, more contaminated individuals that fed back to produce relatively high levels of PCBs in the chinook salmon.

THE MODELS

A predator–prey example from Lake Ontario

I developed a detailed age-structured chinook salmon–alewife model that was based on a six-species pelagic food web model previously developed for Lake Ontario (Jackson 1996*b*). Both the earlier and the present models begin in 1971 with the same initial conditions for alewife and chinook salmon, and use the same chinook salmon stocking, mortality, and sport fish harvest rates, bioenergetics, and alewife mortality rates and stock–recruitment function. Similar alewife and chinook salmon dynamics occur for the two models. In the previous, six-species model chinook salmon consumed an average individual from the entire alewife population, while in this age-structured model chinook salmon consume individuals from specific age classes. Full details of the six-species Lake Ontario pelagic food web model, including parameters, model calibration, and sensitivity analysis, have been presented elsewhere (Jackson 1996*b*). In this model inclusion of detailed alewife age structure was necessary to account for higher PCB concentrations in larger alewife (Jackson and Carpenter 1995) because Great Lakes salmonids prefer the largest prey available (Stewart and Ibarra 1991). I chose to model chinook salmon because they accounted for ≈60% of total predation on alewife in 1990 (Jones et al. 1993), and alewife because they are the principal prey of all stocked salmonids in Lake Ontario (Stewart and Ibarra 1991). Below I note the principal differences between the two models.

The major differences between the six-species model of the pelagic food web and the present two-species chinook salmon–alewife model is that the two-species model includes detailed age structure and PCB concentration with size for alewife. These distinctions were made for two reasons. First, I wanted to incorporate increasing PCB concentrations with size for the alewife, rather than treating them as a homogeneous pool with an average PCB concentration. Second, I wanted to incorporate size selective predation by chinook salmon on alewife, in accordance with the findings of Stewart and Ibarra (1991).

The functional response that describes the amount of predation on alewife age class i by age class j chinook salmon (γ_{ij}) is the asymptotic formulation of DeAngelis et al. (1975):

$$\gamma_{ij} = \frac{\mathrm{Cmax}_j \times B_j \times B_i \times S_{ij}}{B_j + \sum_{i=1}^{k} (B_i \times S_{ij})} \qquad (1)$$

where Cmax is the maximum potential consumption rate for chinook salmon age class j calculated from bioenergetics (Hewett and Johnson 1992), B is the biomass of an age class, k is an index over alewife age classes, and S is the selectivity of chinook age class j for alewife age class i. Selectivities for the functional response (Table 1) were set to range from 0.2 for the youngest alewife (age class 2+) to 1.0 for the oldest

TABLE 1. Selectivity coefficients for the asymptotic functional response (DeAngelis et al. 1975) describing chinook salmon consumption of alewife. Coefficients are assumed to be independent of chinook salmon age class.

Alewife age class (yr)	Selectivity coefficient
2+	0.2
3+	0.4
4+	0.6
5+	0.8
6+	0.9
7+	1.0

alewife (age class 7+). These values were chosen to span the range of possible values for the five age classes of alewife. Therefore, for equivalent biomasses of alewife age classes, a chinook salmon age class would consume five times more biomass of age class 7+ than age class 2+ alewife.

Alewife PCB concentrations and time trend

There is a paucity of PCB concentration data for Lake Ontario alewives. Thus little is known regarding temporal trends or how PCB concentration varies with size for this species. I previously estimated (Jackson 1996*b*) the PCB concentration of the average alewife consumed that would have been necessary to lead to measured PCB concentrations in Lake Ontario lake trout (Borgmann and Whittle 1991). In that analysis, I made no assumptions regarding the age/size structure of the average alewife eaten by Lake Ontario sport fish over time and therefore assumed that the sport fish ate individuals representing the average for the entire adult population. However, in the current analysis changes in stocking rates are assumed to cause changes in the alewife age/size structure. For each year of the simulation I assumed the previously estimated PCB concentration time trend represented concentrations for age class 3+ alewife. I then used a Lake Michigan alewife PCB accumulation model, calibrated to the available empirical size and PCB concentration data for Lake Ontario (Rowan and Rasmussen 1992; D. M. Whittle, Fisheries and Oceans Canada, Burlington, Ontario, *unpublished data* for 45 fish sampled during 1992 and 1993), to estimate PCB concentration of the average individual of each size class of the alewife population. From 1993 onward I assumed the PCB concentration–size relationship remained constant.

Deterministic simulations

Simulations were performed to examine the response of chinook salmon PCB concentrations to changes in chinook salmon stocking rates. These simulations ignore parameter uncertainty, yet are useful because they easily identify model behavior because complications due to noise are removed. 1994 stocking rates were the baseline to which changes were compared. Alewife and chinook salmon biomass dynamics were calibrated to match those of the aggregated six-species pelagic food web model. To account for predation by all stocked sport fish, I multiplied chinook salmon consumption by 1.67. I examined the response of chinook salmon PCB concentrations to changes in 1994 stocking rates (1.45×10^6 individuals) of −25%, −50%, +25% and +50%, and assumed that chinook salmon always accounted for 60% of the total alewife consumption. Alewife recruitment was predicted from adult biomass with the Shepherd function with the parameters calculated by Jones et al. (1993).

Incorporating uncertainty into alewife stock–recruitment relations

I estimated the uncertainty in my predictions that was due to potential errors in the alewife stock–recruitment relationship by bootstrapping by observations (Efron and Tibshirani 1993) 14 yr (1978–1991) of alewife stock–recruit data (Jones et al. 1993) for Lake Ontario. I used two different recruitment models. One model was a density-dependent relationship (Shepherd 1982) with the parameters calculated by Jones et al. (1993):

$$R = \frac{\alpha \times P}{1 + (P/K)^{\beta}} \quad (2)$$

where P is adult alewife biomass, and α, K, and β are fitted parameters. The second model used the average recruitment over the 14-yr period:

$$R = \lambda \quad (3)$$

where λ is the average recruitment. I drew, at random with replacement, 200 sets of 14 observations, and fitted either the density-dependent model to these groups of observations with a non-linear curve fitting procedure (SAS Institute 1987), or calculated mean recruitment. This procedure therefore generated either 200 parameter estimates (Table 2), or 200 mean values, which were then used in successive model runs. I ran the model as per baseline conditions until 1995, then used one set of bootstrapped parameter estimates or a mean recruitment to complete the simulation. This was repeated for each chinook salmon stocking rate considered. I therefore evaluated: (1) the density-dependent stock–recruitment relationship (Shepherd 1982) that has formed the basis for alewife recruitment in previous simulations (Jones et al. 1993, Jackson 1996*a*, *b*), and (2) the 14-yr average recruitment. The latter

TABLE 2. Summary statistics of one set of 200 bootstrapped parameter estimates for the density-dependent stock–recruitment relationship (Shepherd 1982). The parameter notation follows that of Jones et al. 1993.

Parameter	Mean	Standard error
α	0.02103	0.00128
β	5.29	0.33
K	0.00002124	0.00000097

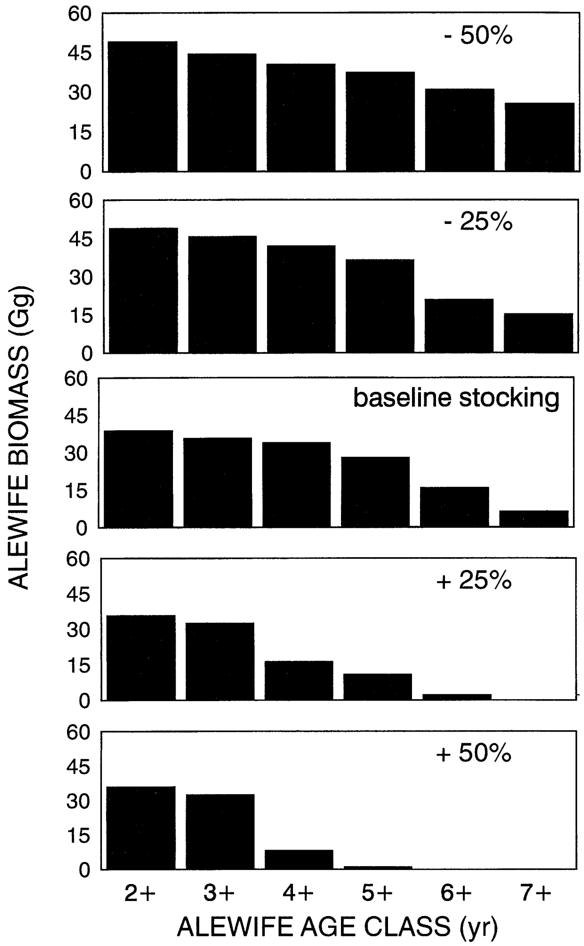

FIG. 2. Remaining biomass of alewife age classes for year 2005, 10 yr into the deterministic simulations of predator–prey relations between two fish species in Lake Ontario. Percentage changes in stocking rate are relative to the baseline, which is the 1994 rate (1.45×10^6 chinook salmon annually).

scenario does not necessarily mean there is no relationship between adult stock size and subsequent recruitment; rather, it assumes that measures of adult stock size and next year's yearling abundance are sufficiently poor as to not provide a meaningful relationship. The model updated annually the biomass of each alewife age class. If at any time there were no reproductive (age classes 3+ and older) alewife remaining, the population was considered to have crashed and the model run ended. The probability of a population crash was simply the proportion of model runs, for a given chinook salmon stocking rate, that resulted in no reproductive alewife by year 2015.

RESULTS

Changes in stocking rates and chinook salmon PCBs: deterministic simulations

Reductions to chinook salmon stocking rates led to changes in the age structure of the alewife population (Fig. 2). Increasing stocking by 50% led to no 6+ or 7+ alewife and reduced biomass in the age classes that remained by 2005. Decreased stocking rate scenarios led to more biomass in predominantly the older alewife age classes (Fig. 2).

Cuts to 1994 stocking rates were predicted to lead to increases in the PCB concentration of all age classes of chinook salmon (Fig. 3). The trend in PCB concentration was similar for each age class but the 4+ yr and 2+ yr fish were consistently the most and least contaminated, respectively. There was a greater predicted increase in contaminant level for the first 25% decrease in stocking (baseline–25%) than for the second 25% decrease (25%–50% decrease). Deviations in PCB concentrations between the three stocking rate scenarios were predicted to occur only after ≈2002. By 2015 chinook salmon PCB concentrations were predicted to rise by 20–22% if stocking was reduced by 25%, and by 29–31% is stocking was reduced by 50%. Lower chinook salmon stocking rates were predicted to result in higher alewife standing stocks; for example, 25% and 50% cuts in stocking were predicted to lead to higher alewife standing stocks of ≈200 Gg and 210 Gg, respectively, by 2015.

Increased stocking rates were predicted to lead to decreased chinook salmon PCB concentrations (Fig. 4). Increasing stocking by 50% was predicted to double the decrease in chinook salmon PCB concentrations

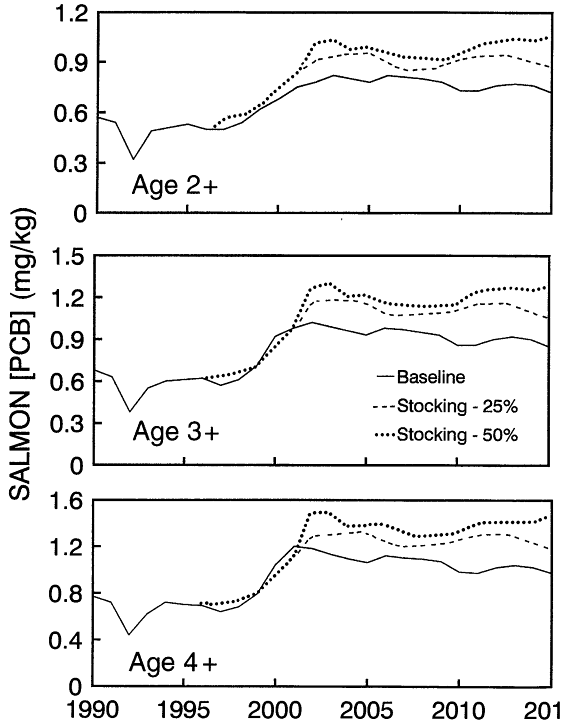

FIG. 3. Deterministic simulations of the change in PCB concentrations of three age classes of chinook salmon in response to decreased rates of stocking. Baseline stocking is identical to that of Fig. 2.

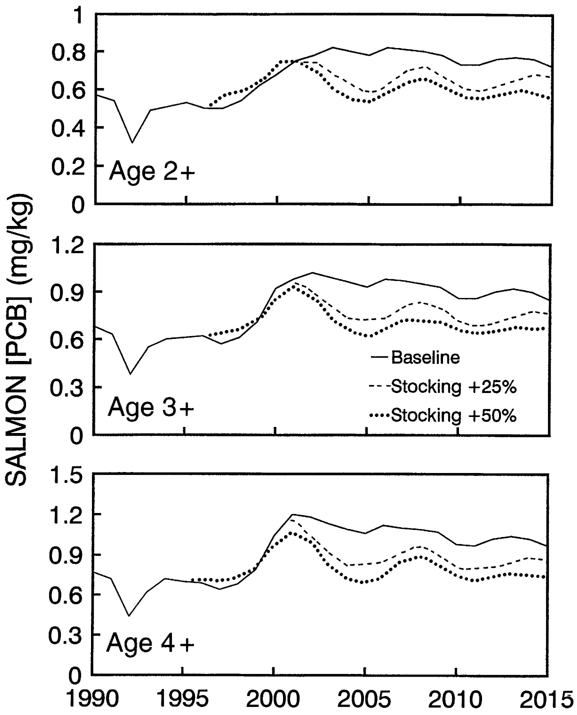

FIG. 4. Deterministic simulations of the change in PCB concentrations of three age classes of chinook salmon in response to increased rates of stocking. Baseline stocking is identical to that of Fig. 2.

compared to a stocking cut of 25% for all age classes. For example, PCB concentrations were predicted to decrease by ≈10% and ≈18% for the 25% and 50% increased stocking scenarios, respectively by 2015. As for the decreased stocking scenarios, visually observable differences in PCB concentrations of chinook salmon would not be apparent until ≈2005, and the 4+ and 2+ fish were the most and least contaminated, respectively. Adult alewife biomass was predicted to lower with successive increases in stocking rate by ≈16 and ≈24 Gg with 25% and 50% increases in stocking, respectively.

Incorporating uncertainty in alewife stock–recruitment relations

Density-dependent stock–recruitment function.—Current chinook salmon stocking levels result in age 4+ PCB concentrations below the FDA action level, but well above the proposed GLSFATF 1 meal/wk and Great Lakes water quality agreement levels (Fig. 5A). Decreasing stocking would have little effect on the probability of an alewife population crash, but PCB concentrations would increase to unacceptable levels if stocking was reduced by 50%. To achieve a 0.5 mg/kg target concentration, stocking rates would have to be doubled over current rates.

At current stocking rates, the probability of an alewife population crash is very low but increases rapidly and non-linearly with stocking increases of ≥25% (Fig. 5A). At stocking rates necessary to achieve the GLSFATF 1 meal/wk target level, there was ≈90% chance that alewife supply could not meet sport fish demand. Age class 4+ chinook salmon PCB concentrations can not be reduced to the 0.1 mg/kg level through altered stocking because their concentrations appear to level off at ≈ 0.4 mg/kg, and further increases in stocking rates pose an exceedingly high risk of an alewife population crash.

Constant recruitment (1978–1991).—Setting alewife recruitment to the long-term average produced general predictions the same as that of recruitment determined with the Shepherd function, with two notable exceptions. PCB concentrations of age class 4+ chinook salmon were consistently lower at all levels of stocking (Fig. 5B). At the highest stocking levels, age class 4+ PCB concentrations were predicted to be ≈0.3 mg/kg.

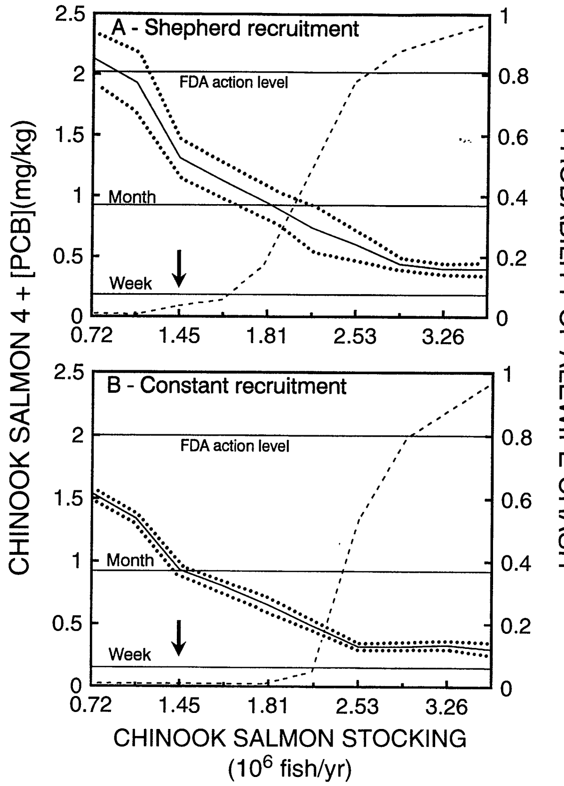

FIG. 5. PCB concentrations (solid line) of age class 4+ chinook salmon and the probability of an alewife population crash (line of large dashes) for chinook salmon stocking rates with (A) Shepherd (1982) stock–recruitment relationship and (B) average recruitment from a 14-yr record (Jones et al. 1993). PCB concentrations are the result of 200 model runs to year 2015, at each stocking rate, based on bootstrapped estimates of the Shepherd stock–recruitment relationship or mean annual recruitment. The arrow indicates 1994 stocking rate. The dotted lines around the chinook salmon PCB concentrations represent ±2 SE. The week and month levels are Great Lakes Sport Fish Advisory Task Force (Anderson 1993) targets for 1 meal per week and month, respectively. The 0.1 mg/kg consumption level given in the Great Lakes water quality agreement has been omitted for clarity.

Following a 50% decrease in current stocking rates age class 4+ PCB concentrations remained well below the FDA action level. With constant recruitment, the probability of an alewife crash remained very low for stocking rate increases of up to 50% above today's rates. The increase in probability of a crash was greater for constant recruitment than with the Shepherd function, but at the highest stocking rates simulated the probability of an alewife crash was similar for both alewife recruitment methods. Variability in predicted PCB concentrations was much lower for the constant recruitment.

Discussion

Prey PCB concentrations have been shown to be more important than predator growth rates in determining predator PCB concentrations (Jackson and Schindler 1996). As consumption approaches the level that is necessary to balance metabolic requirements, i.e., as growth rates approach zero, predator PCB concentrations increase rapidly. This occurs because consumption is a source of PCBs to the predator, but most of the mass consumed is lost to metabolism. Thus, the PCB content of the organism continues to increase, and PCB concentration rises at a much faster rate than mass (Jackson 1996*c*). However, across a range of growth rates, the principal determinant of predator PCB concentrations is prey PCB concentration. This implies that management actions that change the PCB concentration of prey should be more effective than those actions that affect predator growth rates.

In reality, stocking rates, and thus predation, affect the size structure and PCB concentration of the prey by selectively removing the largest available prey (Stewart and Ibarra 1991). The number of sport fishes stocked influences the total predatory demand. Changes in predator demand should affect the amount of prey available to predators, and thus predator growth rates. High rates of stocking should increase predator demand and consumption of larger individuals. This should result in a prey population that contains few, relatively small prey. Small prey should have low PCB concentrations and their consumption by predators should tend to decrease predator PCB concentrations. However, because there is less available prey, predator growth rates should decrease, and predator PCB concentrations should tend to increase. Alternatively, low rates of stocking should decrease predation and increase survival of larger, more contaminated prey. Predators would then consume individuals that have higher PCB concentrations, which should increase predator PCB concentrations. However, increased survival of prey should result in more available prey and higher growth rates of the predator, and this should tend to decrease their PCB concentrations. Clearly, evaluations of changes in stocking rates on predator PCB concentrations need to simultaneously consider the combined effects of changes in prey PCB concentration and predator growth rates.

The deterministic simulations I performed coupled the effects of changes in alewife PCB concentrations and chinook salmon growth rates on chinook salmon PCB concentrations. Increased stocking was predicted to lead to decreased salmonid PCB concentrations because increased predation led to an alewife population with smaller, less contaminated individuals which, in turn, resulted in lower salmonid PCB concentrations. Reduced chinook salmon PCB concentrations due to consumption of prey with lower PCB concentrations is consistent with models of contaminant accumulation (e.g., Thomann 1989, Madenjian et al. 1993, Stow and Carpenter 1994, Jackson 1996*c*). The decrease in the alewife population age structure was roughly equal for each 25% cut in salmonid stocking rates, and thus the reduction in chinook salmon PCB concentration was approximately double for the 50% decreased stocking scenario compared to the 25% decreased stocking scenario. Continued increases in stocking rates should lead to a progressive culling of the alewife population, and at some rate, stocking should lead to sufficient predatory demand to reduce the alewife population to only pre-reproductive individuals. This of course would lead to failed year classes and ultimately the inability of alewife supply to meet salmonid predation demand. Jones et al. (1993) suggested that the whole-lake alewife biomass below which prey supply was unlikely to meet salmonid demand was 70–90 Gg. The alewife in Lake Ontario are currently below this 70–90 Gg window, and appear to be more resilient than earlier thought (Rudstam et al. 1996).

Because reduced stocking led to an alewife population that contained larger, more contaminated individuals (Fig. 2), decreased stocking was predicted to lead to increased chinook salmon PCB concentrations. The largest decrease in chinook salmon PCB concentrations was predicted to occur for the first 25% decrease in stocking rates. This resulted because the first 25% decrease in stocking led to a larger change in the size of alewife consumed by the chinook salmon. For example, following a 25% stocking reduction, chinook salmon were predicted to consume primarily age classes 5+, 6+, and 7+ alewife. A 50% stocking reduction led primarily to consumption of age classes 6+ and 7+ alewife. These simulations demonstrated that when both factors were considered simultaneously, alewife PCB concentrations and not chinook salmon growth rates, had the largest effect on chinook salmon PCB concentrations.

Deterministic simulations reveal model behavior but do not include the reality that processes and parameters are not known with certainty. One of the most difficult fisheries relationships to quantify is that between adult stock and recruitment, yet this relationship is perhaps the most important in the assessment of a fishery (Hilborn and Walters 1992). Alewife are clearly an important species in the flow of energy and materials through the Lake Ontario pelagic food web. Alewife are the principal prey for all stocked salmonids and are therefore the primary link in PCB flow from lower trophic levels to the salmonids. Alewife also support the salmonid production that is enjoyed by recreational fishers. It would seem prudent then that predictions of the pelagic food web to fisheries management actions should consider uncertainty in alewife dynamics.

A consideration of PCB concentrations of age class 4+ chinook salmon and the probability of an alewife population crash given current stocking levels indicated that the Lake Ontario pelagic food web should satisfy FDA consumption advisories and exist in a state where alewife supply could meet salmonid demand (Fig. 5A). Stocking rates in excess of $\approx 2.2 \times 10^6$ chinook salmon annually were predicted to yield diminishing returns in the form of lowered PCB concentrations in the age class 4+ fish. At stocking rates $>2.8 \times 10^6$ fish annually there was no benefit to the fishery because PCB concentrations were predicted to remain unchanged but the probability of an alewife crash increased. An interesting feature of the predictions was that sustainability of the alewife population decreased rapidly and non-linearly with increasing stocking rates. Indeed, there appeared to be a narrow margin for error, as the probability of a crash escalated from $\approx 20\%$ to $\approx 80\%$ with a mere 25% increase in stocking. My analysis suggested that stocking levels that would achieve a 0.5 mg/kg consumption advisory (for age class 4+ chinook salmon) would carry a very high risk ($\approx 90\%$) of an alewife population crash (Fig. 5A). Note that the current simulations did not include scenarios of a severe alewife winter mortality, decreased lake productivity, or decreased alewife growth rates as have been considered in a previous analysis (Jackson 1996*a*).

Reductions in stocking rates below current levels would not benefit the Lake Ontario pelagic food web because a reduction in the probability of an alewife crash would be minimal, and PCB concentrations would increase relatively rapidly. In fact, stocking reductions by as little as 25% were predicted to put age class 4+ chinook salmon close to the FDA 2 mg/kg action level (Fig. 4). Younger fish (e.g., age classes 2+ and 3+) would remain below the action guideline.

Management of Lake Ontario would not differ greatly depending on whether the Shepherd stock–recruitment relationship or the 14-yr average recruitment was assumed for driving predictions of alewife recruitment. The pattern of PCB concentrations and probability of an alewife population crash was similar for both recruitment dynamics (Fig. 5A, B). The constant recruitment scenario predicted lower PCB concentrations at all stocking levels, and much less variability (Fig. 5B). This resulted because the bootstrapped parameters of the Shepherd stock–recruitment relationship led to more variable recruitment than the bootstrapped mean recruitment. This resulted in less variability in predicted PCB concentrations and a sharper delineation in the predicted stocking rate above which alewife supply could not meet stocked sport fish demands. The probability of an alewife crash was not a significant factor until stocking was $>2.2 \times 10^6$ chinook salmon annually. Stocking levels greater than $\approx 2.2 \times 10^6$ chinook salmon, the stocking level necessary to achieve a 0.5 mg/kg consumption advisory level, would carry a high probability of an alewife population crash. In this respect the two recruitment mechanisms predicted similar dynamics.

Implications for fisheries management

This analysis illustrates the potential effect that predator–prey interactions and size-selective predation play in modifying the flow of PCBs through the pelagic food web. The most important message from this analysis is that changes in salmonid stocking rates led to a tradeoff between PCB concentrations in the salmon and the probability of salmonid demand not being met by alewife supply. Thus, it would not be possible to manage the fishery for maximum sustainability and minimum PCB concentrations in stocked salmonids. However, this analysis did suggest that stocking levels between ≈ 1.5 and 2.2×10^6 chinook salmon annually offered the greatest probability of maintaining low salmonid PCB concentrations and a low probability of an alewife population crash. The validity of this prediction depends of course on the model and the assumptions contained therein. The value of the predictions therefore lies more in the ideas and general patterns rather than the specific numbers. The message to fisheries managers is that they will have to decide which of these two goals takes priority, and adjust stocking rates accordingly.

My analyses represent conservative estimates on the effect of changes in stocking rates because I have not explicitly included density-dependent changes in alewife growth rates. Increased alewife survival might lead to increased competition for food, lower alewife growth rates, and an increase in alewife PCB concentrations. Alternatively, decreased alewife survival might lead to less competition for food, higher alewife growth rates, and growth dilution (Thomann 1989) of alewife PCB concentrations. Thus, there might be two factors contributing to a change in alewife PCB concentrations of salmonid prey as a function of changes in salmonid stocking rates: one change due to an alteration of the resulting size structure of the alewife population, and a second change, in the same direction, due to changes in alewife growth rates. Diet shifts (Hewett and Stewart 1989, Mills et al. 1992, Mills et al. 1995) have led to changes in length–mass relationships for Lake Ontario alewife (Mills et al. 1992). However, the effect of diet changes on alewife contaminant accumulation is not known.

In the early 1990s stocking rates of chinook salmon were as high as 3.4×10^6 juveniles (Great Lakes Fishery Commission 1993). The predation pressure generated by this stocking rate plus stocking of other salmonids manifested itself as signs of stress in the Lake Ontario pelagic food web (Great Lakes Fishery Commission 1992). In fact, there were two essentially failed year classes of alewife during the early 1990s. My stocking scenarios were consistent with these empirical findings as my model predicted high probability of an alewife population crash at stocking levels of the early 1990s. A population crash was the combined result of excessive consumption of alewife coupled to a reduction in the age structure of the alewife to prereproductive individuals.

The results of these analyses, while considering only chinook salmon and alewife, are still applicable to the entire Lake Ontario pelagic food web because I have scaled chinook salmon predation to include predation by other stocked salmonids. Reductions in alewife biomass would likely lead to more heavy reliance on alternative prey fishes like rainbow smelt (*Osmerus mordax*) and slimy sculpin (*Cottus cognatus*). However, rainbow smelt have not achieved the high lake-wide biomass of alewife (Jones et al. 1993), and slimy sculpin appear to be important diet items for young lake trout only (Elrod and O'Gorman 1991). Thus, it is unlikely that poor recruitment of alewife could be directly compensated for by reliance on alternative prey fishes.

A previous analysis (Stow and Carpenter 1994) showed that chinook salmon PCB concentrations should decrease if their growth rates increase. This might appear to contradict results of the present analysis. However, because Stow and Carpenter (1994) assumed invariant prey PCB concentrations, they did not account for any feedback that might include changes in the PCB concentration of the prey. Subsequent papers (Stow et al. 1995*b*, Jackson 1996*a*) have suggested that altering stocking rates might generate a prey feedback whereby the age structure of the prey fishes might be affected by changes in predation rates. My analysis shows that a prey feedback is likely to occur, and that changes in prey PCB concentrations, rather than changes in salmonid growth rates, are likely to exert the greatest effect on salmonid PCB concentrations. We do not know the alewife PCB concentration allometry for the Lake Ontario population or its variance, but these population attributes are easy to measure and, from a management point of view, important to know. This analysis assumed that the ratio of predation on alewife would remain the same, i.e., chinook salmon 60% and other salmonids combined 40%. Additional fisheries management actions, such as stocking larger fish (Madenjian and Carpenter 1993), or stocking those species whose physiology and ecology lead to lower contaminant concentrations (e.g., steelhead [*Oncorhynchus mykiss*]), Stow et al. 1995*b*), should also be considered.

Hilborn and Walters (1992) suggest that as much as 60% of the world's major fish stocks are overexploited. Maximizing, or at least sustaining, harvest often presents trade-offs for fisheries managers. After fishing had provided food and income for >350 yr, in 1992 a moratorium was imposed on the largest Atlantic cod (*Gadus morhua*) fishery in the northwest Atlantic (Trippel 1995). Cod fishing represented a conflict between jobs and the fishery. Kitchell et al. (1997) identified a trade-off between maximizing harvest and preserving biodiversity in Lake Victoria, a lake in which conservation biologists argue for the preservation of endemic species, yet the social and economic benefits to an area of high unemployment are undeniable (Greboval 1990). The yellowfin tuna (*Thunnus albacares*) is often found associated with various species of dolphins (National Research Council 1992). Fishers set nets around herds of dolphins and take advantage of this association, but many dolphins are caught as bycatch and killed (Alverson et al. 1994). Here the trade-off is between locating and catching the yellowfin tuna, and death of many dolphins as bycatch. My analysis illustrates the trade-off between low PCB concentrations in sport fish consumed by wildlife and humans, and sustainability of a 10^9 US$/yr sport fishery. Fisheries managers are faced with the prospect of having to satisfy multiple interest groups. Analyses such as the present one should help identify management avenues that might lead to compromise between groups that appear to have opposite goals.

Acknowledgments

I thank Daniel Schindler, Steve Carpenter, and Craig Stow for discussing ideas in this paper. I thank Daniel Schindler, Craig Stow, Tim Johnson, Steve Carpenter, Lars Rudstam, and an anonymous reviewer for offering valuable suggestions that improved this manuscript. This research was supported by the University of Wisconsin Sea Grant Institute under grants from the National Sea Grant College Program, National Oceanic and Atmospheric Administration, U.S. Department of Commerce, and from the State of Wisconsin. Federal Grant NA90AA-D-SG469, project R/MW-41.

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