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Diet and Prey Selection by Lake Superior Lake Trout during Spring, 1986–2001

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ABSTRACT. *We describe the diet and prey selectivity of lean* (Salvelinus namaycush namaycush) *and siscowet lake trout (S. n. siscowet) collected during spring (April–June) from Lake Superior during 1986–2001. We estimated prey selectivity by comparing prey numerical abundance estimates from spring bottom trawl surveys and lake trout diet information in similar areas from spring gill net surveys conducted annually in Lake Superior. Rainbow smelt* (Osmerus mordax) *was the most common prey and was positively selected by both lean and siscowet lake trout throughout the study. Selection by lean lake trout*

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*for coregonine (*Coregonus *spp.) prey increased after 1991 and corresponded with a slight decrease in selection for rainbow smelt. Siscowet positively selected for rainbow smelt after 1998, a change that was coincident with the decrease in selection for this prey item by lean lake trout. However, diet overlap between lean and siscowet lake trout was not strong and did not change significantly over the study period. Rainbow smelt remains an important prey species for lake trout in Lake Superior despite declines in abundance.*

INDEX WORDS: *Lake trout, diet, Lake Superior, prey selectivity, siscowet.*

INTRODUCTION

Lake trout (*Salvelinus namaycush*) is the most abundant predator in Lake Superior (Kitchell *et al.* 2000, Bronte *et al.* 2003). Overfishing and predation by sea lamprey (*Petromyzon marinus*), however, caused significant declines in lake trout populations in Lake Superior during the 1950s (Lawrie and Rahrar 1973, Pycha and King 1975, Hansen *et al.* 1995, Hansen 1999). Management agencies on Lake Superior endeavored to restore the native fish community to abundances observed prior to sea lamprey colonization (Busiahn 1990, Horns *et al.* 2003). Efforts to restore lake trout populations in Lake Superior included sea lamprey control, conservative fishery regulations, and stocking of hatchery-reared lake trout (Pycha and King 1975, Hansen *et al.* 1995). Lake trout natural reproduction increased in response to these efforts (Selgeby 1995, Hansen *et al.* 1995), and Lake Superior now supports wild lake trout populations that have reached or exceeded historic levels in some locations (Wilberg *et al.* 2003).

There are three documented phenotypes of lake trout in Lake Superior (Lawrie and Rahrer 1973, Moore and Bronte 2001), although anecdotal accounts suggest additional phenotypes. The two most abundant phenotypes are siscowet lake trout (*S. namaycush siscowet*) and lean lake trout (*S. namaycush namaycush*). The siscowet, which lives primarily in deep water (> 80 m), is more abundant than the lean lake trout and may be increasing in abundance more rapidly than lean lake trout (Bronte *et al.* 2003). Siscowet expansion may also be placing an increasing demand on prey fish resources (Harvey *et al.* 2003). The lean lake trout is the preferred phenotype in commercial and recreational fisheries and typically inhabits near shore waters < 80 m deep and have increased in abundance over the last 20 years (Bronte *et al.* 2003, Wilberg *et al.* 2003). Because of the increased abundance of siscowet, fishery managers have initiated efforts to estimate their demand on prey fish in Lake Superior.

Historically, native coregonines (*Coregonus* spp.) were the principal prey of lake trout (Dryer *et al.* 1965). The collapse of cisco (*Coregonus artedii)* stocks (Selgeby 1982) in the late 1950s caused a shift in the pelagic prey fish abundance from coregonines to one dominated by higher proportions of the exotic rainbow smelt (*Osmerus mordax)* (Dryer and Beil 1964, Dryer *et al.* 1965, Selgeby 1982, Conner *et al.* 1993). Over the past 20 years coregonines have increased in abundance and have become the most abundant planktivore in most locations in Lake Superior (Selgeby *et al.* 1994, Bronte *et al.* 2003). Despite the resurgence of coregonines, and the decline in rainbow smelt abundance, the latter species continued to compose up to 90% of lake trout diets, suggesting lake trout continue to feed disproportionately higher on rainbow smelt (Conner *et al.* 1993).

Siscowet is the most abundant predator in Lake Superior (Ebener 1995, Bronte *et al.* 2003), but does not have much commercial or recreational value due to its high fat content (Eschmeyer and Phillips 1965). Siscowet generally inhabit waters deeper than 80 m (Bronte *et al.* 2003) and feed primarily on deepwater coregonines (*Coregonus hoyi* and *C. kiyi*) and deepwater sculpin (*Myoxocephalus thompsonii*) (Conner *et al.* 1993, Kitchell *et al.* 2000, Harvey and Kitchell 2000). Stomach contents indicated siscowet sometimes feed in near shore waters typically inhabited by lean lake trout (Bronte *et al.* 2003, Harvey *et al.* 2003), and may compete with lean lake trout if food resources are limited. Given simultaneous increase in abundances of both phenotypes over the last 20 years (Bronte *et al.* 2003), it is important to describe their diets, identify trends in prey selection, and determine dietary overlap over time.

A temporal analysis of the diet characteristics of lean lake trout and siscowet required a pooling of existing data cooperatively collected by fishery management and research agencies on Lake Superior. The objectives of this study were to: 1) determine prey selectivity of Lake Superior lake trout by coupling available data on prey fish abundance with

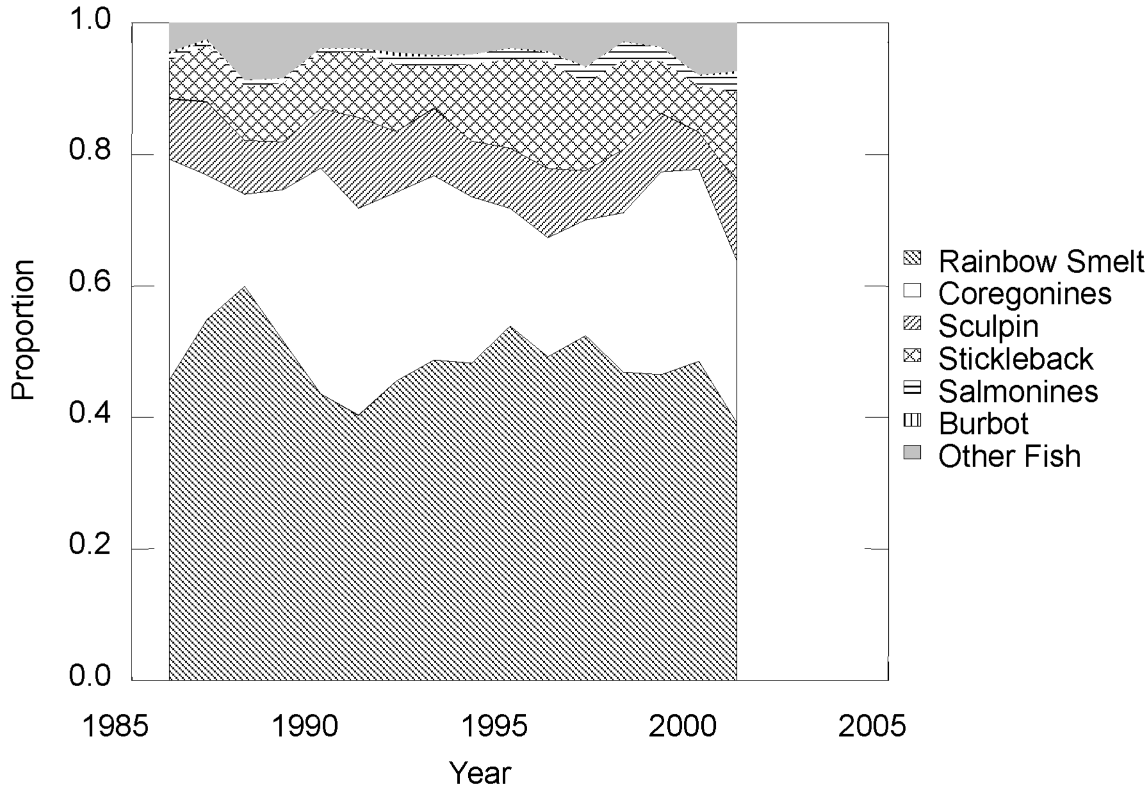

FIG. 1. Proportional abundance of major Lake Superior prey fishes from 1986–2001 determined by USGS spring bottom trawl surveys.

predator diet data collected at common sites; 2) assess dietary overlap between lean and siscowet lake trout; and 3) identify temporal changes in prey selection since 1986. We used spatially explicit data sets of prey fish composition from trawl surveys and lake trout diet data compiled annually during 1986-2001 to address these objectives.

METHODS

Field Surveys

Lake trout were caught yearly from 1986 to 2001 by tribal, provincial, and state agencies around Lake Superior in spring (April–June) gill net surveys conducted annually to assess the status of lake trout populations. Lake trout were caught using 114 mm stretch-measure, 210/2 multifilament nylon twine, 18 meshes deep, bottom set gillnets fished at depths between 18 m to 108 m for a duration of 1 to 3 nights (Hansen *et al.* 1995, Hansen 1996, Schram *et al.* 2004).

Prey fish abundance was estimated using bottom trawls at consistently sampled locations around Lake Superior during late April through June from 1986 to 2001 (Bronte *et al.* 1991, Bronte *et al.* 2003). The United States Geological Survey's Lake Superior Biological Station conducts this survey at 51 to 87 locations using a 12-m bottom trawl towed cross contour starting at depths < 15 m at nearshore and ending at a depth of 100 m offshore (Gorman *et al.* 2004). This data set was also used to estimate prey selectivity by linking to the gillnet data at the grid cell level. Figure 1 shows the proportional numerical abundance of prey fish caught in the bottom trawl during 1986-2001. The mean size of rainbow smelt in the trawl catches throughout the study was 91 mm and ranged from 10 mm to 261 mm. Coregonines caught in the trawl ranged from 20 mm to 760 mm with a mean length of 165 mm. Initial evaluations of prey lengths in the diet indicated no significant relationships of prey length and selectivity; therefore, all lengths of prey were pooled in the analyses.

Laboratory Processing of Stomachs

A total of 30,866 lean and siscowet lake trout stomachs were removed and either examined imme-

TABLE 1. Number of stomachs examined from lean and siscowet lake trout from spring surveys in Lake Superior during 1986–2001.

	Lean Lake Trout		Siscowet	
Year	With food	Total	With food	Total
1986	380	638	—	—
1987	583	828	—	—
1988	600	803	—	—
1989	706	1,039	—	—
1990	376	748	1	1
1991	1,105	1,406	7	8
1992	1,003	1,420	13	18
1993	1,106	1,507	33	124
1994	961	1,412	22	37
1995	1,553	1,868	67	80
1996	1,106	1,315	229	257
1997	1,346	2,801	173	541
1998	663	2,522	111	318
1999	1,172	2,974	163	242
2000	2,544	4,774	258	554
2001	869	2,150	257	479
totals	16,073	28,207	1,334	2,659

diately or frozen for later examination. In total, 18,035 contained food (Table 1). For each stomach, date, location of capture, the predator length, and the length and number of each prey fish item were recorded. The prey items were grouped into seven categories that included burbot (*Lota lota*); coregonines; rainbow smelt; salmonines; sculpins (*Myoxocephalus thompsonii, Cottus cognatus,* and *C. ricei*); sticklebacks (*Pungitius pungitius* and *Gasterosteus aculeatus*); and other fish (alewife (*Alosa pseudoharengus*), suckers (*Catostomus commersoni* and *C. catostomus*), yellow perch (*Perca flavescens*), minnows (*Cyprinidae*), bass (*Micropterus dolomieui* and *M. salmoides*), and walleye (*Sander vitreum*)). Unidentified and non-fish prey items were omitted due to the inability to determine selectivity with the bottom trawl data.

Data Analysis

We used the numerical proportion of each prey category in lake trout diets to estimate prey selectivity by calculating Chesson's index of prey selection, α (Chesson 1983):

$$\alpha_i = \frac{(r_i / n_i)}{\sum_{j=1}^{m}(r_j / n_j)} \tag{1}$$

where r_i is the proportion of prey species i in a predator diet, n_i is the proportion of prey species i in the environment, α_i is the Chesson's index of prey selection for prey species i, and m is the number of prey categories. These values were compared to 1/m to determine selection. Values of α greater than 1/m indicate positive selection and means that the predator was eating the prey item in greater proportion than it was found in the environment. Values of α less than 1/m indicate negative selection for the prey item and α equal to 1/m indicate neutral selection. Proportion of each prey species in the environment was calculated from the bottom trawl catch data. We calculated prey selectivities for lean lake trout for each year during 1986–2001. Because either no samples were obtained or sample sizes were low for years 1986–1991, prey selectivities for siscowet were calculated for each year during 1992-2001. We calculated 95% confidence intervals for selectivity of each prey. To determine whether prey selectivity for a particular prey taxon exhibited a significant linear trend over time, we applied simple linear regression analysis. This trend analysis was performed for each combination of prey taxon and lake trout subspecies.

We estimated the extent of dietary overlap between lake trout phenotypes using Schoener's (1970) index C_{xy}:

$$C_{xy} = 1 - 0.5 * \sum_{i=1}^{m} \left| p_{xi} - p_{yi} \right| \tag{2}$$

where p_{xi} is the proportional abundance of species i in the diet of lean lake trout, and p_{yi} is the proportional abundance of species i in the diet of siscowet. When C_{xy} equals 1 there is 100% diet overlap between the two phenotypes and when C_{xy} equals 0 there is no overlap; a value of 0.6 is considered ecologically significant (Wallace 1981). Diet overlap was estimated in all years when the sample size exceeded 10 individuals for each lake trout phenotype. To determine if diet overlap exhibited a significant linear trend over time, we applied simple linear regression anaylsis. In the diet overlap analyses, years prior to 1992 were not used because of insufficient samples of siscowet.

RESULTS

Lean lake trout composed 91% of all lake trout stomach samples collected between 1986 and 2001 and more than 50% of all stomach samples contained food (Table 1). Siscowet sample sizes were

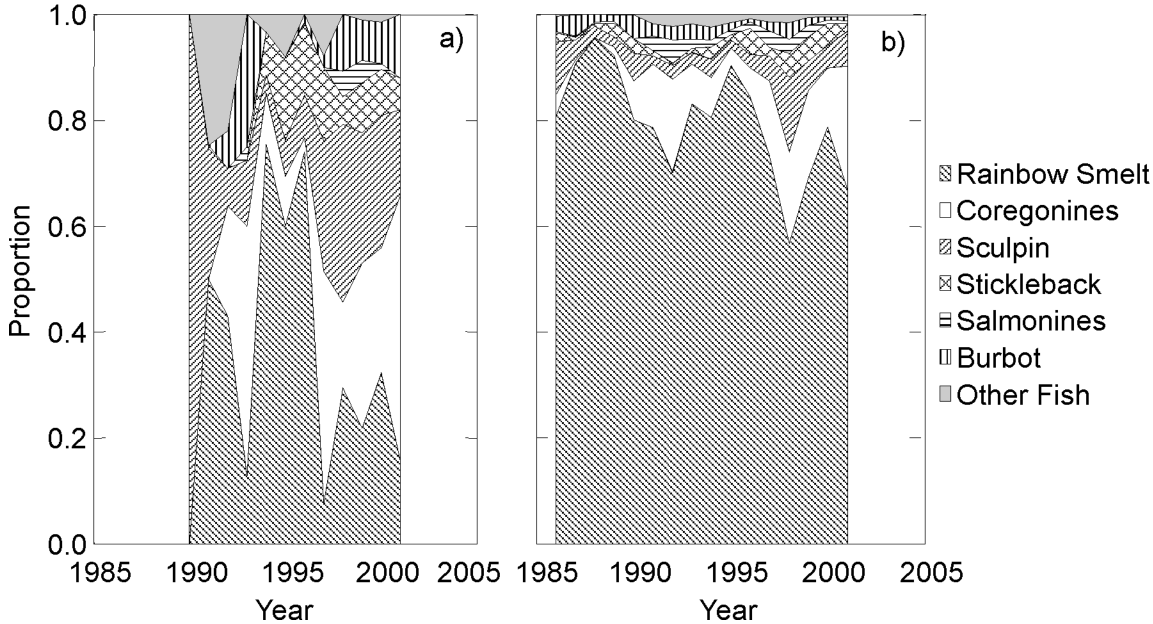

FIG. 2. Proportional abundance of prey items in siscowet (a) and lean lake trout (b) diets in Lake Superior during 1986–2001.

relatively low prior to 1996 and were absent from samples prior to 1990. Rainbow smelt made up most of the spring diet of lean lake trout in Lake Superior (Fig. 2). Coregonines, sculpin, and sticklebacks were also frequently found in predator diets (Fig. 2). Siscowet diets during the study averaged 29% rainbow smelt, 27% coregonines, 22% sculpin and 11% stickleback (Table 2), while lean lake trout diets were much less diverse and were dominated by rainbow smelt (80%). Coregonines (9%), sculpin (4%), and stickleback (3%) were much less important in diets of lean lake trout than in siscowet (Table 2). Salmonines, burbot, and other fish contributed minimally to siscowet and lean lake trout diets. Further, there was high variation in the diet composition of siscowet among years than those of lean lake trout (Fig 2).

There were no temporal trends in selectivity for rainbow smelt by lean lake trout during 1986-2001; however, selectivity appeared to decline late in the time series (Table 3; Fig. 3a). Furthermore, selection for coregonines increased from negative selection in 1986 to neutral selection by 2001 (Table 3; Fig. 3b). Lean lake trout had negative selection for sculpin, sticklebacks, salmonines, and burbot (Fig 3).

Selection for rainbow smelt by siscowet was variable during 1986–2001 but with no significant trend (Table 3; Fig. 4a). Siscowet selection for

TABLE 2. Percent composition of prey fish in the spring diet of lean and siscowet lake trout in Lake Superior averaged across 1986–2001.

Prey Item	Lean Lake Trout	Siscowet
Rainbow Smelt	80	29
Coregonines	9	27
Sculpin	4	22
Stickleback	3	11
Salmonines	< 1	< 1
Burbot	1	3
Other	2	6

TABLE 3. Simple linear regression slopes and P-values for lean lake trout and siscowet prey selectivity during 1986–2001. Bold values indicate a statistically significant trend.

	Lean Lake Trout		Siscowet	
Prey Item	Slope	P-value	Slope	P-value
Rainbow Smelt	–0.005	0.399	0.027	0.357
Coregonines	**0.010**	**0.001**	–0.004	0.830
Sculpin	–0.002	0.363	–0.047	0.119
Stickleback	**0.005**	**0.012**	0.020	0.379
Salmonines	0.001	0.231	0.008	0.426
Burbot	–0.005	0.11	NA	NA

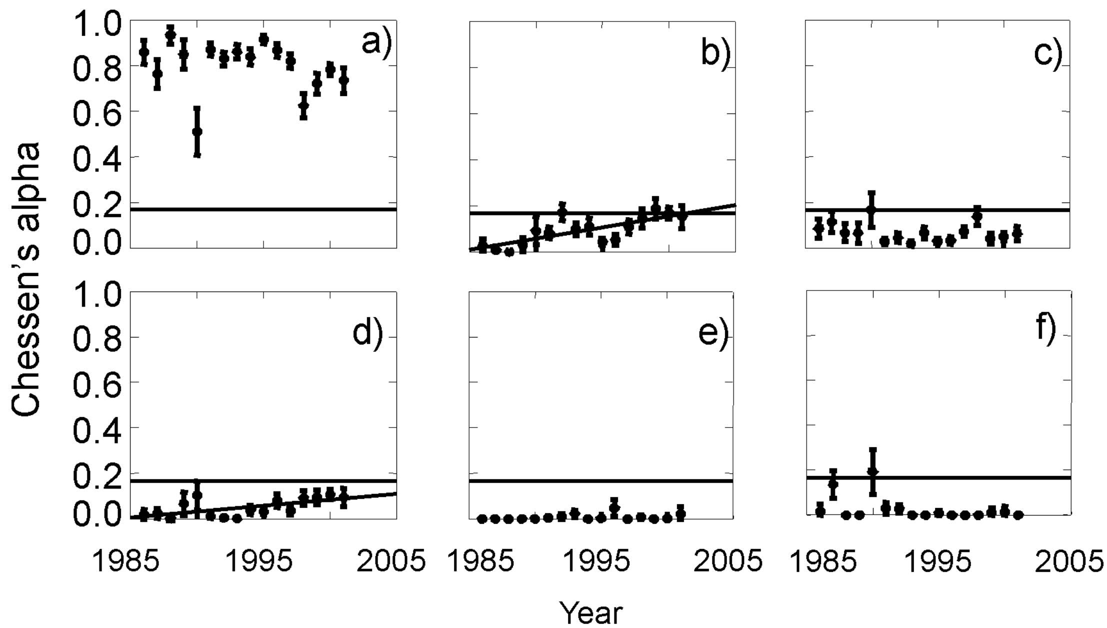

FIG. 3. Annual estimates of prey selection by lean lake trout for a) rainbow smelt, b) coregonines, c) sculpin, d) sticklebacks, e) salmonines, and f) burbot in Lake Superior during 1986–2001. Error bars represent 95% confidence intervals for the mean.

sculpin declined from strong positive selection in 1994 to neutral selection in 2001 (Table 3; Fig. 4c). Selection for coregonines and sticklebacks did not differ significantly from neutral selection during the time period (Fig. 4). Similar to lean lake trout, siscowet had neutral or negative selection for salmonines and burbot (Fig. 4).

Diet overlap between lean lake trout and siscowet

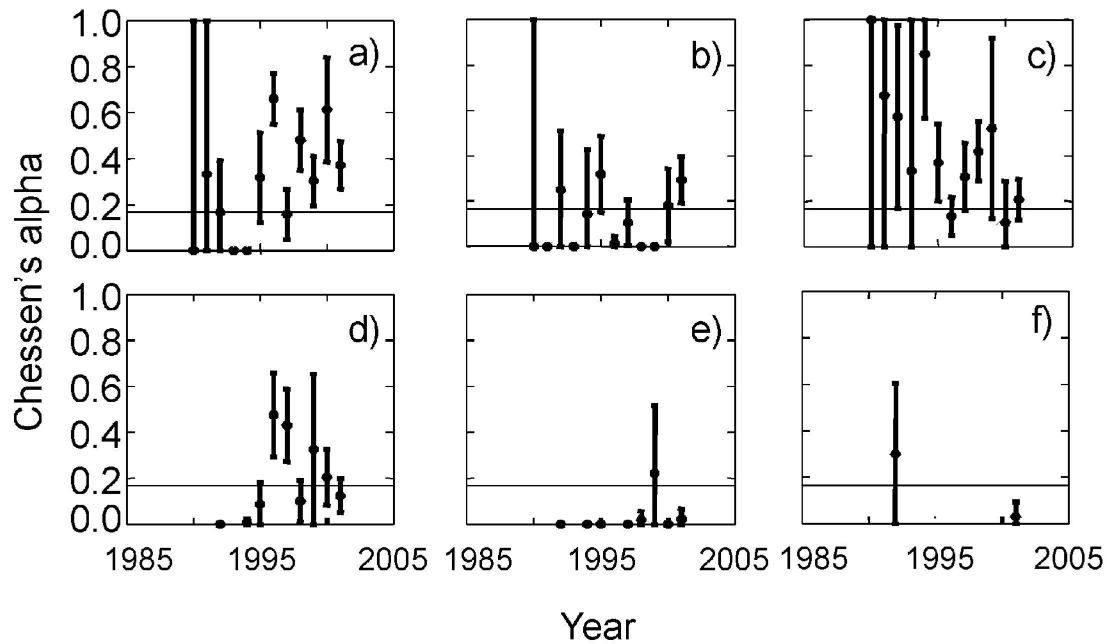

FIG. 4. Annual estimates of prey selection by siscowets for a) rainbow smelt, b) coregonines, c) sculpin, d) sticklebacks, e) salmonines, and f) burbot in Lake Superior during 1986-2001. Error bars represent 95% confidence intervals for the mean.

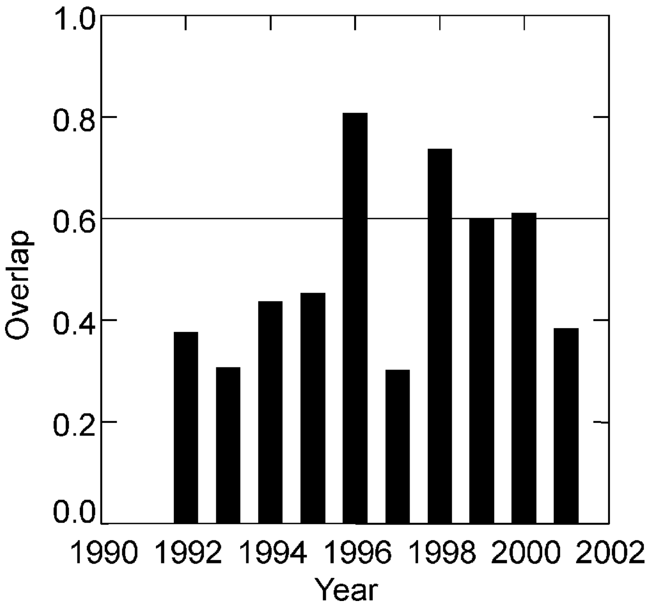

FIG. 5. Dietary overlap between lean lake trout and siscowet lake trout during 1992–2001. Line represents minimum value for ecological significance of dietary overlap (0.6).

averaged approximately 50% on a lake wide basis over all years of the study. Diet overlap showed no significant temporal trend during 1992–2001 (slope = 0.020; P = 0.327; Fig. 5). Only in 1996, 1998, and 2000 was the overlap considered to be ecologically significant.

DISCUSSION

The spring diets of Lake Superior lean lake trout were dominated by rainbow smelt throughout the study period, while the diets of siscowets were more diverse. Conner *et al.* (1993) also found that rainbow smelt dominated the diets of Lake Superior lean lake trout and other salmonine predators during the 1980s. Disproportionate consumption of rainbow smelt by lake trout has likely resulted in high mortality of rainbow smelt and may have contributed to the decline of rainbow smelt in Lake Superior (Bronte *et al.* 2003). Although lean lake trout and siscowet continue to show positive selection for rainbow smelt, lean lake trout selection for coregonines has increased. Furthermore, selection for rainbow smelt appeared to slightly decline since the mid-1990s, corresponding with declines in rainbow smelt abundance (Bronte *et al.* 2003).

Differential apical sizes, behavior, and seasonal aggregations may explain higher selection for rainbow smelt by lake trout. Apical lengths of rainbow smelt rarely exceed 250 mm and are generally smaller and slimmer than coregonines, which commonly exceed 250 mm. Hence smaller lake trout may have difficulty consuming larger coregonines, which results in less selection. Lake trout did not show positive selection for coregonines, although lean lake trout > 400 mm total length did consume large coregonines (Mason *et al.* 1998). Coregonine avoidance by lake trout, a product of both species evolving together may also influence lake trout diet selection (Conner *et al.* 1993, Mason *et al.* 1998). In the laboratory, coregonines were able to avoid capture by predators about 60% of the time but rainbow smelt are captured with ease once detected (Savitz and Bardygula 1989). Further, coregonines are active swimmers unlike rainbow smelt that often remain motionless in the water, (Savitz and Bardygula 1989), which increases their probability of capture. This might allow lake trout to feed more effectively on this less abundant prey item thereby explaining the positive selection we observed. While coregonines are more abundant in the lake, the lower selection of this species by lake trout may be associated with reduced capture rates as a consequence of their larger size and speed as well as rainbow smelt being congregated in the spring during spawning. Behavioral segregation by coregonines may also contribute to the lower selection by predatory species.

Siscowet showed positive selection for sculpin and rainbow smelt. Ostazeski *et al.* (1999) found that siscowet utilized sculpin more than lean lake trout. However, selection for sculpin by siscowet has declined since 1986, and may be related to the decline in sculpin biomass in U.S. waters since 1982 and Canadian waters since 1999 (Bronte *et al.* 2003) and the observed increased selection for rainbow smelt. Siscowet showed an increase in selection for rainbow smelt over a period where selection by lean lake trout appeared to decline. This shift from neutral selection to positive selection of rainbow smelt may be related to the increased siscowet population size (Kitchell *et al.* 2000, Bronte *et al.* 2003). Furthermore, this change may be the result of increased demand on prey resources associated with some siscowets moving into shallow water to feed (Harvey *et al.* 2003). The observation of the increasing number of siscowets in lean lake trout habitat may indicate density-dependent effects in deepwater areas. However, the observed differences in prey selection between siscowet and lean lake trout are consistent with their bathymetric habitat with siscowets distributed in deeper water compared to lean lake trout (Ostazeski *et al.* 1999, Moore and Bronte 2001, Bronte *et al.* 2003). If siscowet populations continue to increase, there may be more demand placed on the near shore prey resources used by lean lake trout.

Trends in prey selection by lake trout in Lake Superior may be associated with an overall decrease in abundance of preferred prey in the later years of our study. Rainbow smelt abundance in Lake Superior began to decline by 1978 (Bronte *et al.* 2003). While coregonine abundance also decreased since 1990 due largely to recruitment failure, the decline was less severe than that observed for rainbow smelt. This decrease in prey abundance may not have immediately affected lake trout consumption rates, as seen in the functional response for lake trout in other Laurentian Great Lakes (Eby *et al.* 1995). However, Stewart and Ibarra (1991) showed that the decline of the principal prey of Lake Michigan salmonines (alewives) caused a 25% decline in the average weight of sport caught fish. Lake Superior lake trout exhibit the lowest growth rate and experience the lowest prey densities of all the Laurentian Great Lakes (Martin and Olver 1980, Eby *et al.* 1995, Madenjian *et al.* 1998). Further decreases in prey fish abundance may exacerbate the decline in lake trout growth rates that has been observed since the 1970s (Hansen 1994, Sitar and He 2006). Detailed analyses of prey supply relative to demand by predators over this time period are needed to determine the sustainability of all salmonine predators.

Prey fish abundance estimates computed with bottom trawl samples must be interpreted with caution; therefore our selectivity indices need to be interpreted cautiously. Availability of species to the bottom trawl depends on their preferred habitat. Rainbow smelt and coregonines are less susceptible to the bottom trawl because some of the population is found higher in the water column than that fished by the bottom trawl hence their abundances are underestimated (Argyle 1982, Fabrizio *et al.* 1997, Mason *et al.* 2005, Stockwell *et al.* 2006). Species associated with the bottom such as sculpin are less problematic. Further, rainbow smelt densities were much greater using mid water trawl estimates linked with acoustic estimates at night in Lake Superior than bottom trawl estimates during the day in spring 2005 (Jason Stockwell, USGS-Lake Superior biological station, personal communication) which could indicate that the positive selection for rainbow smelt is not as strong as we indicate. Additionally, as lake herring mature they become more pelagic making adults less susceptible to bottom trawl surveys (Stockwell *et al.* 2006) which could indicate the selection of coregonines by lake trout was actually neutral or negative.

Overall, rainbow smelt has remained the predominant portion of lean lake trout diet despite the substantial decline in rainbow smelt abundance during the 1980s and diet overlap between lean and siscowet lake trout has not been strong during 1986-2001. Other studies have indicated that dietary overlap between siscowets and lean lake trout may not be ecologically significant (e.g., Harvey and Kitchell 2000, Bronte *et al.* 2003, Harvey *et al.* 2003). However, recent increases in siscowet abundance (Bronte *et al.* 2003), and the observed trend of increasing positive selection for rainbow smelt by siscowet may raise the potential for resource competition between lean lake trout and siscowet.

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