Fishing down Canadian aquatic food webs[1]

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Abstract: The mean trophic level (TL) of fish landed in fisheries on the east and west coasts of Canada is declining by 0.03–0.10·decade^{-1}, similar to global trends. This finding is based on data from United Nations Food and Agriculture Organization and the Canadian Department of Fisheries and Oceans and other Canadian sources for the period 1873–1997. Significant rates of decline in mean TL were obtained even when key species — Atlantic cod (*Gadus morhua*) on the east coast and Pacific herring (*Clupea pallasi*) and Pacific hake (*Merluccius productus*) on the west coast — were omitted from the analysis. Fish taken in inland water fisheries did not exhibit a decline in mean TL. Two models were developed, based on length and age, respectively, for correcting TL estimates of individual species for the effects of changes in body size due to changes in fishing mortality. Both produced corrections that were small relative to changes in mean TL that resulted from changes in species composition of the catch over time. Overall, these results suggest that the mean TL of fish landed can be used as an index of sustainability in multispecies fisheries and that its reliability will depend on the quality of the data and length of the time series available for analysis.

Résumé : Le niveau trophique (NT) moyen des poissons débarqués dans les pêches des côtes est et ouest du Canada baisse de 0,03 à 0,10 par décennie, comme c'est le cas dans les tendances mondiales. Ce constat se fonde sur des données de l'Organisation des Nations Unies pour l'alimentation et l'agriculture (FAO), du ministère des Pêches et des Océans du Canada et d'autres sources canadiennes, pour la période allant de 1873 à 1997. Des taux significatifs de déclin du NT moyen ont été obtenus même lorsque des espèces clés — morue franche sur la côte atlantique, hareng et merlu sur la côte pacifique — étaient omises dans l'analyse. Les poissons capturés dans les eaux intérieures ne présentaient pas de baisse du NT moyen. Deux modèles ont été construits, basés respectivement sur la longueur et sur l'âge, pour corriger les estimations du NT de chaque espèce de façon à tenir compte des effets des changements de la taille corporelle dus à des changements dans la mortalité par pêche. Les deux modèles ont produit des corrections qui étaient petites par rapport aux changements dans le NT moyen dus à des modifications de la composition spécifique des captures au fil du temps. Globalement, ces résultats permettent de penser que le NT moyen des poissons débarqués peut être utilisé comme un indice de durabilité dans les pêches plurispécifiques, et que sa fiabilité dépendra de la qualité des données et de la longueur des séries chronologiques disponibles pour les analyses.

[Traduit par la Rédaction]

Introduction

There is broad agreement in the literature that fisheries affect not only target and bycatch species but also the ecosystems in which these species are embedded (Parsons 1996; National Research Council 1999). The resulting calls for ecosystem-based management are more controversial. One

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reason is because there is at present no consensus on possible ecosystem "reference points" analogous to those used for single-species management, such as maximum sustainable yield or $F_{0.1}$.

One recurrent feature of aquatic ecosystems exploited by modern fisheries is the tendency for the biomass of large, long-lived, often piscivorous species to decline more rapidly than that of smaller, shorter-lived, often zooplanktivorous species (Kirkwood et al. 1994; Jennings et al. 1997; National Research Council 1999), a feature related to the usually low natural mortality of the former group (Myers and Doyle 1983). Therefore, where fleets target both large and small fishes (or use unselective gear), the contribution of fishes from the lower part of the food web to the aggregate catches will tend to increase over time. This was confirmed by the recent demonstration of a decline in the mean trophic level (TL) of organisms (fishes and invertebrates) landed globally by fisheries (Pauly et al. 1998).

Thus, the mean TL of organisms in landings from a given ecosystem could be used to integrate a vast array of biological features pertaining to the species therein, and its continuous decline, if associated with stagnating or declining catches, interpreted as indicating lack of sustainability at the ecosystem level (because overall biological production is highest at low TL; Pauly and Christensen 1995). This agrees

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with Caddy (1998) who suggested that "multispecies reference points could be derived from ecological/food web models."

However, if it is to become accepted as an index of the impact of fisheries on ecosystems, mean TL will have to be shown to be applicable in a variety of national settings, with a wide range of underlying statistical data, resource types, and fisheries. Also, issues of model sensitivity must be addressed, notably regarding the within-species changes of TL due to the change in size composition caused by fishing. We present such an evaluation here based on the mean TL of organisms in the landings of fisheries on the east coast (Maritimes, Quebec, and Newfoundland–Labrador), on the west coast (British Columbia), and in inland waters (lakes and rivers) of Canada. Two new models are developed for the quantitative assessment of the effects of size changes on the estimation of mean TL values.

Materials and methods

Catch/landings statistics

East coast

The landings data used for the east coast of Canada cover the period 1950–1997 and were supplied by the Government of Canada to the Food and Agriculture Organization (FAO) of the United Nations (www.fao.org) (similar FAO data sets were used in association with other sources for the west coast and inland waters of Canada). This data set, comprising 72 statistical categories that range from species (50) to genera (10) and higher groups (12), consists mainly of reports by or to Canadian authorities. These data do not include all the catches of distant-water fleets based in Europe, which fished until the 1970s in what subsequently became the Canadian Exclusive Economic Zone. Key features of this data set are provided in Table 1.

West coast

Statistics from a variety of sources were used to estimate the catches of the commercial fishery in British Columbia from 1873 to 1996. FAO statistics commenced in 1950. Annual reports to Ottawa from the Inspector of Fisheries for British Columbia commenced in 1873 and were published in "Canada Sessional Papers" by the Dominion Bureau of Statistics from 1919 to 1970. From 1952, landings data were also published in "British Columbia Catch Statistics." For some species, review articles were available that summarize commercial landings and provide factors for conversion from nonmetric units (Table 2).

Recreational catch statistics (for salmon) started in 1953; estimates for other species such as lingcod (*Ophiodon elongatus*) and rockfish are included in the annual recreational surveys only from 1981. Aboriginal salmon catches have been recorded by the Canadian Department of Fisheries and Oceans (DFO) since 1951. Minimum estimates of aboriginal catches for 1873–1950 were derived from Argue et al. (1990) and from estimates of precontact seafood consumption by First Nations (Hewes 1973).

The series of mean TLs constructed from these data exhibited strong fluctuations. We identified the simplest set of piecewise polynomials that would adequately describe the data using the algorithm described in Hintze (1998).

Inland waters

The freshwater landings data used here included FAO statistics (1950–1997) complemented by records for 1917–1968 collected by the Dominion Bureau of Statistics in collaboration with federal and provincial fisheries departments, records for 1969–1974 collected by Statistics Canada, records for 1976–1989 collected by the DFO

(available online: www.dfo-mpo.gc.ca/communic/statistics/stat_e.htm), and records for 1990–1997 collected by DFO Statistical Services, Ottawa.

For the inland waters data set, we excluded marine fishes caught in estuarine waters, notably Atlantic cod (*Gadus morhua*), Atlantic herring (*Clupea harengus*), and rainbow smelt (*Osmerus mordax*). Landings in the early twentieth century were reported as either raw or finished products and in imperial units, e.g., fresh, salted, or in oil, as barrels, cases, pounds, or hundredweights. Conversions to metric equivalents were performed using factors in the fisheries reports for 1947 and 1948 of the Dominion Bureau of Statistics. Species names from various sources had to be matched, as some species were not reported or were given different names in different years. The combined time series of inland water landings included only those species for which continuous data were available (Table 3).

TLs

The TL estimates used here all rely on diet composition data and on the equation

$$(1) \qquad TL_i = 1 + \sum_{j=1}^{n} DC_{ij}\, TL_j$$

where i is the predator, j the nth prey, and DC_{ij} is the diet composition, expressing the fractions of each j in the diet of i. Assignment of TL starts with plants and detritus, both with a definitional TL value of 1. Thus, a consumer eating 40% plants (TL = 1) and 60% herbivores (TL = 2) will have a TL of $1 + (0.4 \times 1 + 0.6 \times 2) = 2.6$.

The variance of the TL estimates from eq. 1, referred to here as the omnivory index (OI), is calculated from

$$(2) \qquad OI_i = \sum_{j=1}^{n} (TL_j - TL_{preys})^2 DC_{ij}$$

where TL_{preys} is the average TL of the n prey species of i and the other terms are as defined in eq. 1. We also use the standard error of TL, defined as the square root of the corresponding OI, for the catch pyramids described below.

The DC_{ij} and TL_j used here were obtained from two related sources: (1) mass-balance trophic models of ecosystems of the east and west coasts of Canada or adjacent areas, constructed with the ECOPATH software (Christensen and Pauly 1992; www.ecopath. org), and (2) published, species-specific diet composition data (for the DC_{ij}) and previous (ECOPATH-based) estimates of the corresponding TL_j, as incorporated in the "Food items table" of FishBase (Froese and Pauly 1998).

TL estimates obtained using source 1, pertaining to species or higher taxa, corresponded closely to independent estimates of TL assessed using stable isotope ratios of nitrogen from Prince William Sound, Alaska (Kline and Pauly 1998). Herein, use was made of the observation that for every link in a food chain, the concentration in animal tissues of the heavier isotope (^{15}N) increases by a nearly constant percentage ($\approx 3.4\%$) relative to that of ^{14}N. This suggests that TL estimates based on source 2 should also be reliable. The TL estimates of major species are summarized in Tables 1–3. Details of these and TL estimates for the other species considered in our analyses are documented in FishBase (Froese and Pauly 1998, with updates on www.fishbase.org).

Mean TLs of organisms in fisheries landings were calculated for each year using

$$(3) \qquad \overline{TL}_k = \sum_{i=1}^{m} Y_{ik}\, TL_i \Big/ \sum_{i=1}^{m} Y_{ik}$$

where Y_{ik} is the landings of species i in year k and TL_i is its TL.

Table 1. Key features of the data set used for analyzing Canadian east coast fisheries (1950–1997)[a] (also see Fig. 3A).

Group[b]	Groups/species included (TL)[c]
Molluscs	More than eight species of clams, mussels, oysters, quahogs, and scallops (2.1); northern shortfin squid (3.2); longfin squid (3.3)
Flatfishes	American plaice and witch flounder (3.1); flatfish nei (3.2); winter flounder, yellowtail flounder, and Greenland halibut (3.5); Atlantic halibut (4.5)
Other invertebrates	11 groups (about 30 species) from sea urchins and snow crabs (2.3)[d] to lobster (2.6)[e]
Other fishes	21 groups (about 100 species) from rainbow smelt (2.6) to swordfish (4.5)
Redfishes, basses, and shads	Sand lances (3.0); alewife (3.1); shad (3.2); wolffishes nei (3.4); lumpfish and angler (3.5); Atlantic redfish (3.6); striped bass (4.6)
Gadoids (excluding cod)	Atlantic tomcod (3.3); Greenland cod (3.5); red hake and haddock (3.6); saithe and roundnose grenadier (3.8); white hake and tusk (4.2); silver hake (4.3)
Small pelagics	Herring (3.1); pelagic fishes nei (3.2); mackerel (3.7)
Atlantic cod[f]	TL = 4.01 (from Bundy et al. 2000)

[a]Detailed spreadsheet available from first author; FAO catches are from FishBase (Froese and Pauly 1998; www.fao.org).

[b]Groups ranked by year at which 50% of cumulative landings occurred (with "most recent" group up) to emphasize species succession; weighted mean TL series based on individual species, not group means.

[c]Nei = FAO term for "not elsewhere identified"; details on TL estimates including sources of diet information and standard errors may be found in FishBase (Froese and Pauly 1998, with updates on www.fishbase.org) and in Bundy et al. (2000).

[d]TL estimate for *C. opilio* from diet composition data in Wieczorek and Hooper (1995) and mean prey TL in FishBase.

[e]TL estimate for *H. americanus* from diet composition data in Elner and Campbell (1987) and mean prey TL in FishBase.

[f]von Bertalanffy growth parameters and mortality for cod: $L_\infty = 130$ cm total length; $W_\infty = 24\,400$ g; $K = 0.12 \cdot \text{year}^{-1}$ (May et al. 1965); $M = 0.18 \cdot \text{year}^{-1}$ (Pinhorn 1975).

Table 2. Key features of the data set used for analyzing Canadian west coast fisheries (1873–1996)[a] (also see Fig. 3B).

Group[b]	Groups/species included (TL)[c]	Fishery	Data source(s)
Miscellaneous invertebrates	13 groups (about 30 species) from bivalves and sea urchins (2.1) to shrimps (2.6)	Commercial and some aquaculture (oysters)	Sessional papers; Elsey 1933
Hake	*Merluccius productus*	Commercial	DFO
Small pelagics	Pacific herring and pilchard (3.0); mackerel (3.3)	Commercial	1884–1937: sessional papers; pilchard (1938–1948): Culley 1971; herring (1938–1950): Hourston 1980
Marine mammals[d]	Harbour seal, miscellaneous whales, and sea lions (4.0); fur seals (4.2)	Commercial	Bigg 1969; Pike and MacAski 1969
Other fishes	17 groups (about 100 species) from smelts (3.0) to halibut (4.0) and tuna (4.2)	Mainly commercial	Sessional papers; Carrothers 1941; Hart and McHugh 1944; Ketchen 1986; Cass et al. 1990; Stocker 1994
Salmonids[e]	Coho, chinook, chum, pink, sockeye salmon, and steelhead trout (3.8)	Commercial	1873–1982: Shepard et al. 1985; Shepard and Argue 1989; 1983–1996: DFO
		Aboriginal	1873–1951: Hewes 1973; Argue et al. 1990; 1985–1994: DFO
		Recreational	1953–1994: DFO

[a]Extracted from detailed spreadsheet available from first and last authors.

[b]Groups ranked by year at which 50% of cumulative landings occurred (with most "recent" group up) to emphasize species succession; weighted mean TL series are based on individual series, not group means.

[c]Details on TL estimates including sources of diet information and standard errors may be found in FishBase (Froese and Pauly 1998, with updates on www.fishbase.org).

[d]Conversion from individual weights: harbour seal, 81 kg (Fisher 1952); northern fur seal skin, 160 kg (Jefferson et al. 1993); Steller sea lion, 535 kg (Schusterman 1981; Bigg 1988); humpback, 40 t; blue, 160 t; sei, 30 t; fin, 75; minke, 14 t; right, 80 t; gray, 35 t; sperm, 57 t; Baird's beaked whale, 12 t (Jefferson et al. 1993).

[e]Conversion from individual weights: coho and chum, 4.52 kg; chinook, 9.05 kg; pink, 1.81 kg; sockeye, 2.71 kg; steelhead trout, 4.52 kg (Argue et al. 1990).

Catch pyramids

The mean TLs estimated from eq. 3 are presented here as temporal trends and as "catch pyramids" that contrast the distribution of landings by TL at the start and end of the FAO time series of landings, i.e., 1950 and 1997. The approach used to construct the catch pyramids uses the standard errors of the TL_i to define triangular distributions (base of triangle = mean TL of each group ± 2 SE) to assign group-specific catches to different TL classes.

Changes of TLs

Caddy et al. (1998), commenting on the "fishing down the food web" approach initially presented in Pauly et al. (1998), pointed out that the TLs of individuals of a given fish or invertebrate species will vary between populations and different periods and especially between different ontogenic stages.

We accommodated nonontogenic variability of TL by concentrating on diet composition data from Canadian ecosystems. How-

Table 3. Key features of the data set used for analyzing Canadian inland water fisheries (1917–1997)[a] (also see Fig. 3C).

Group[b]	Species included (TL)[c]
Other fish	*Pimephales promelas* (2.1); *Hiodon alosoides* and *Lepomis gibbosus* (3.1); *Ameiurus nebulosus* and *Acipenser fulvescens* (3.3); *Ambloplites rupestris* (3.4); *Anguilla rostrata* (3.6); *Lota lota* (4.0)
Sauger	*Stizostedion canadense* (4.0)
Carp	*Cyprinus carpio* (2.2)
Perch	*Perca flavescens* (3.4)
Salmonids[d]	*Salvelinus fontinalis* (3.0); *S. alpinus* (4.4); *S. namaycush* (4.5)
Cisco	*Coregonus artedi* (3.5)
Sucker	*Catostomus commersoni* (2.6)
Pike	*Esox lucius* (4.5)
Walleye	*Stizostedion vitreum* (4.5)
Whitefish	*Coregonus clupeaformis* (2.9)

[a]Detailed spreadsheet available from first author.
[b]Grouped only for this table and Fig. 3C; weighted mean TL series based on landings and TL of individual species.
[c]Details on TL estimates and standard errors may be found on www.fishbase.org.
[d]Pacific salmon (especially coho and chinook) introduced into the Great Lakes and other freshwater bodies are not included, as biomasses (and hence landings) largely depend on continuous stocking.

Fig. 1. Relationship between TL estimates and body length (cm) in 180 species of fishes. The regression lines (forced through the origin, representing larvae with TL = 3 and length ≈1 cm) have slopes of $b_a = 0.24$ for first-order carnivores (broken line and open circles, representing herring and other small pelagic and demersal fishes) and $b_b = 0.63$ for higher-order carnivores (solid line and solid circles, representing cod-like and other large piscivorous demersal and pelagic fishes).
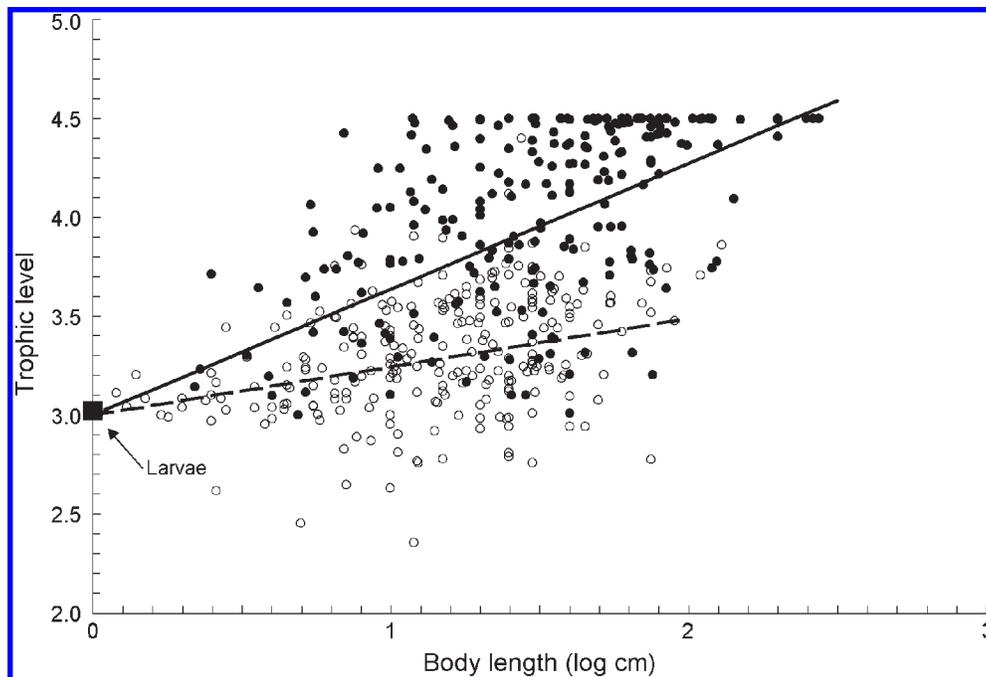
ever, we could not accommodate between-year variability of TL because suitable time series of diet composition could not be found. Moreover, we believe this form of variability to be small, e.g., a large piscivore cannot revert to feeding on herbivorous zooplankton when prey fishes are scarce. Indeed, feeding habits in fishes are largely a function of morphology and size (e.g., see De Groot 1981).

Ontogenic changes were accommodated by first documenting and quantifying general relationships between the TL and size of fishes. (Data were not available to document such relationships in invertebrates. Thus, we assume here that the TL of invertebrates does not change with fishing mortality. This assumption is briefly revisited in the Discussion.) This was done by first extracting from FishBase those species for which at least two TL values were available, of which one pertained to the adult stage. We found 180

species that met this criterion, represented by 578 TL estimates. In the absence of true herbivores among Canadian fishes, these species were then pooled into two sets: first-order carnivores, i.e., fishes whose adult TL ranges from 2.75 to 3.75, close to the TL = 3 typical of their larvae (which feed almost exclusively on herbivorous zooplankton), and higher-order carnivores, i.e., fishes whose adult TL reaches values higher than 3.75 (Froese and Pauly 1998; Cortés 1999).

Regression lines linking the TL estimates and the corresponding (log) length values of each group were then forced through the single point representing the larvae of both groups (TL = 3, length = 1 cm, i.e., log length = 0) (Fig. 1). This leads to equations of the form

(4) $TL = 3 + b \log_{10}(L)$

where the slope *b* expresses the change of TL with (log) body size, itself expressed in centimetres. This relationship generated relatively small differences of within-species mean TL when applied to observed length–frequency distributions of cod landings (Fig. 2). Nevertheless, we developed and tested two generic approaches — length and age based, respectively — for quantifying the effect on mean TL of changes in the size composition of exploited populations as a result of increasing fishing mortality.

Length-based relationship between fishing mortality and TL

Beverton and Holt (1956) showed that total mortality (*Z*) in fish populations whose individuals grow according to the von Bertalanffy growth function (VBGF) can be expressed by

$$(5) \qquad Z = [K(L_\infty - \overline{L})] / (\overline{L} - L_c)$$

where L_∞ is the asymptotic length, i.e., the mean size that the individuals in the population would reach if they were to live and grow indefinitely, *K* is the rate at which L_∞ is approached, and $\overline{L}$ is the mean length in the population computed from L_c upward. Here, L_c represents the length at entry into the fishery, assuming knife-edge selection. Using *Z* equals the sum of fishing (F) and natural (*M*) mortality, exploitation rate (E) defined as $E = F/Z$, *M/K* as the ratio of natural mortality to growth (with values usually between 1 and 3), and $E = 1 - (M/K)/(Z/K)$, we can rearrange eq. 5 to determine $\overline{L}$ as

$$(6) \qquad \overline{L} = [L_\infty + ([(M/K) / (1 - E)] L_c)] / ([(M/K) /$$
$$(1 - E)] + 1)$$

for $0 \leq E < 1$. Based on eq. 4, the change in TL (ΔTL) in a fish population where mean body sizes have been reduced by fishing can be estimated from

$$(7) \qquad \Delta\mathrm{TL} = b \log_{10} \left[\frac{L_\infty + \left(\left(\frac{M/K}{1 - E} L_c \right) / \left(\frac{M/K}{1 - E} + 1 \right) \right)}{L_\infty + (((M/K) \, L_c)/((M/K) + 1))} \right]$$

in which all parameters are as defined previously. The estimates of ΔTL thus obtained are approximate because the TL values corresponding to a mean length obtained from eq. 7 may differ from the mean TL value of an age-structured population, our next topic.

Age-based relationship between fishing mortality and TL

An explicit model for estimating the mean TL of an age-structured population in which TL changes linearly with (log) length is

$$(8) \qquad \mathrm{TL} = \frac{\left(\int_{t_r}^{t_c} N1_t A \mathrm{d}t + \int_{t_c}^{t_{max}} N2_t N3_t A \mathrm{d}t \right)}{\left(\int_{t_r}^{t_c} N1_t \mathrm{d}t + \int_{t_c}^{t_{max}} N2_t N3_t \mathrm{d}t \right)}$$

where $N1_t = e^{-M(t-t_r)}$, $N2_t = e^{-M(t_c-t_r)}$, $N3_t = e^{-F+M(t-t_c)}$, $A = 3 + b \times \log_{10}L_t$ (eq. 4), $L_t = L_\infty(1 - e^{-K(t-t_0)})$, i.e., the VBGF for growth in length with parameters L_∞ and *K* as defined above and t_0 setting the origin of the VBGF, t_r is the recruitment age, i.e., the age from which eq. 8 applies, t_c is the age at entry into the exploited stock, assuming knife-edge selection (i.e., corresponding to L_c), and t_{max} is the maximum age in the population.

Fishing mortality trends

We did not find data from which precise values of fishing mortality could be estimated for all the stocks included in the fisheries statistics described above. However, a time series of *F*, sufficient

Fig. 2. Effects of changing size distributions on estimation of mean TL in Nova Scotian cod in (A) 1971, (B) 1992, and (C) 1999 based on the TL–size relationship for higher-order carnivores in Fig. 1. Note that mean TL changed by ~2% from 1971 to 1999 compared with ~25% for mean length and maximum size (L_{max}).
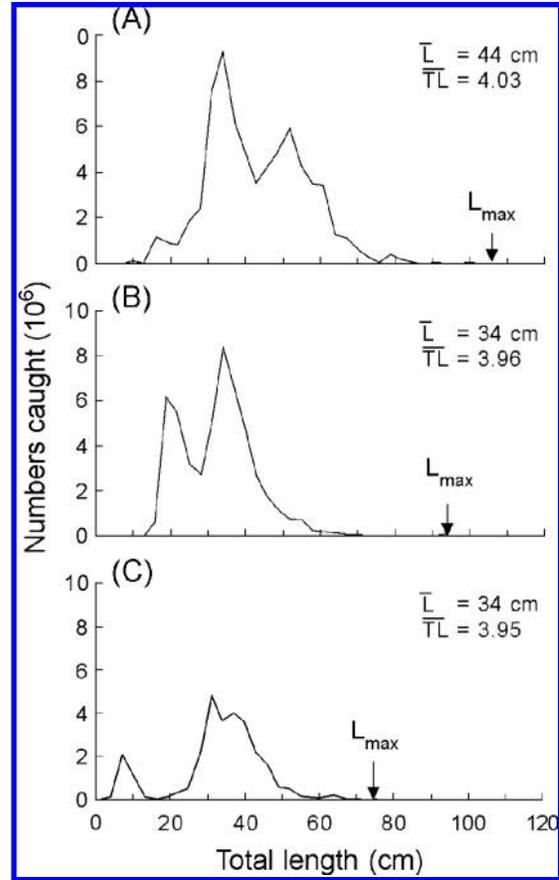

for estimating the potential effect of fishing on size compositions and hence on TL, is available for cod for the entire period covered here (Myers et al. 1995). Estimates of *F* for other east coast species, although for shorter periods, are also available in the database assembled by Myers et al. (1995), of which an updated version is included in FishBase (Froese and Pauly 1998). We obtained mean values of *F* by year for each species with suitable data by calculating average *F* weighted by the landing of each population of that species. These were subsequently grouped into a single estimate for "miscellaneous demersal fishes."

Results

The basic features of fisheries landings in the three areas considered here are illustrated in Fig. 3. For the east coast (Fig. 3A), overall catch trends were driven by cod landings until the mid- to late 1980s. On the west coast (Fig. 3B), overall catches are highly variable, due to the opening of successive "new" fisheries (marine mammals, Pacific herring (*Clupea pallasi*), Pacific hake (*Merluccius productus*)). In contrast, the landing statistics for inland waters (Fig. 3C) do not suggest any long-term trend.

We summarized the TL estimates from FAO statistics for these three areas in the form of catch pyramids to contrast the landings per TL class at the beginning (1950) and end

Fig. 3. Time series of aggregated fisheries landings from Canadian aquatic ecosystems (see text for sources): (A) east coast, 1950–1996; (B) west coast, 1873–1996; (C) inland waters, 1917–1997.
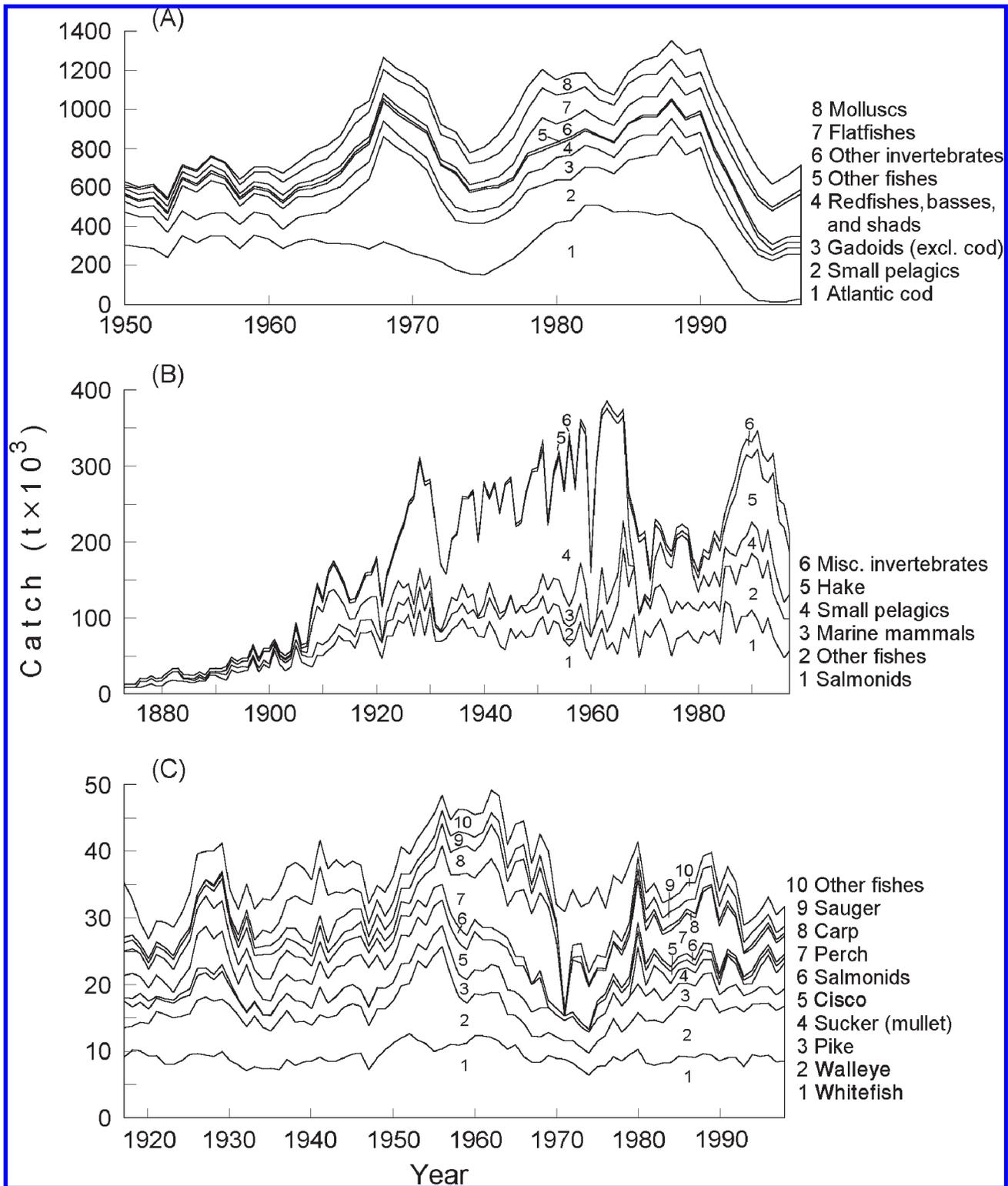
(1997) of the time series. The differences are very large for the east coast (Fig. 4A). The contribution of higher TL fish (especially cod) to the landings has decreased greatly, while that of invertebrates, of which the snow crab (*Chionoecetes opilio*) is now the most important, has greatly increased. For the west coast (Fig. 4B), the pyramid reflects the important contribution of Pacific herring to the 1950 landings. For inland waters (Fig. 4C), the pyramid represents a small decline in mean TL, from 3.62 in 1950 to 3.45 in 1997, without major shifts in the composition of the landings. However, the

Fig. 4. "Catch pyramids" representing fisheries landings (open histograms, finfishes; shaded histograms, invertebrates) as a function of their TL (A) on the east coast, (B) on the west coast, and (C) in inland waters. Based on FAO statistics for 1950 (left side of the pyramid) and 1997 (right side) and TL estimates documented in FishBase (which includes a routine for automatic construction of such pyramids for any area with FAO data; Froese and Pauly 1998).
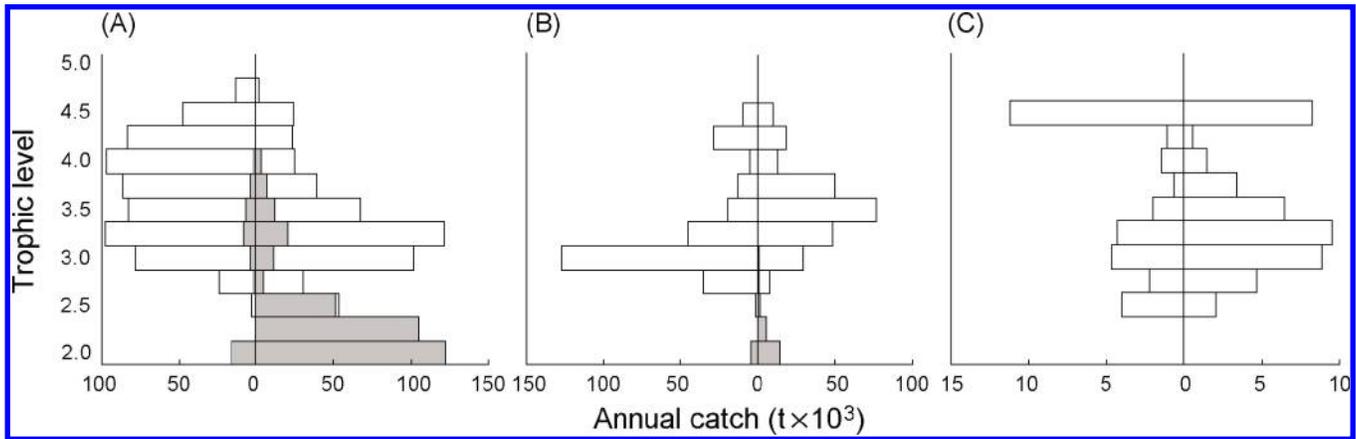
apparent decline is not borne out when longer time series data are used (Fig. 5C).

Trends in the mean TL of organisms in fishery landings for the three areas are illustrated in Fig. 5. There was a marked decline in the east coast fisheries from mean TL = 3.6–3.7 in the early 1950s to TL = 2.8–2.9 in the mid-1990s, or about $0.1 \cdot \text{decade}^{-1}$ (Fig. 5A). This decline persists if the analysis is made excluding cod, although the rate of mean TL decline is then halved, to about $0.05 \cdot \text{decade}^{-1}$.

The trends for the west coast (Fig. 5B) are more complex. The simplest set of piecewise polynomials that fits the data (overall $R = 0.50$) suggests two periods with different TL trends: a linear increase in mean TL from 1873 to 1894, with a slope of 0.215 TL$\cdot$decade^{-1}, followed by a period with fluctuating mean TL values and an overall negative TL trend of $-0.032 \cdot \text{decade}^{-1}$ (Fig. 5B, inset). Exclusion of Pacific herring leads to a more moderate rate of decline, while exclusion of Pacific hake leads to a steeper rate of decline.

For inland waters, only the FAO data show a downward trend in mean TL (Fig. 5C). The more detailed and longer series of Canadian statistics documented in Table 3 do not confirm the existence of this trend (Fig. 5C). This difference is due, to a large extent, to our criterion of excluding marine fishes taken in estuarine waters. For example, the inclusion of rainbow smelt, which have a low TL (2.5) and relatively high landings (about 10^4 t·year^{-1} since the mid-1960s), would have led to a decrease similar to that observed for the FAO data.

Application of our length-based (eq. 7) and age-based model (eq. 8) produced roughly similar results (Fig. 6). Both models predict relatively small decreases in mean TL, except at the very high exploitation rates. However, the models predict that TL will decrease rapidly with increasing E when length at first capture is very small relative to asymptotic length, meaning that the fish are exposed to fishing throughout most of their lives.

Figure 7 documents key aspects of application of our age-based model to the east coast data. Figure 7A shows the available time series of fishing mortality for cod and miscellaneous demersal fishes. Figure 7B illustrates the change in the mean TL of cod given the F values in Fig. 7A, while

Fig. 7C contrasts two series of mean TL for east coast catches, one uncorrected and the other corrected for the within-species effect of F-related body size changes on TL.

Discussion

Mean TL trends in inland waters

We start our discussion with freshwater ecosystems, as they tend to be small, at least relative to the range of most fishing craft. Human impact on these systems has therefore tended to occur earlier than accounted for by data such as assembled here. For instance, Smith (1995) noted that "Lake Ontario may have had the highest fishery yields of any of the other deepwater Great Lakes, but this occurred before the mid-1800s — before landings began to be recorded. The Atlantic salmon (*Salmo salar*) was the most-valuable species in the early fishery and was severely depleted before a quantitative account of the fishery could be made."

Thus, the stability suggested by our data for the inland waters of Canada does not preclude earlier anthropogenic changes that may have occurred in these ecosystems. Indeed, human interference, in the form of widespread introductions, has substantially altered the trophic structure of the Great lakes, as reflected, for example, in the relative abundance of coregonines (Fleischer 1992). Also, Pacific salmon, notably chinook (*Oncorhynchus tshawytscha*) and coho (*Oncorhynchus kisutch*), were introduced into the Great Lakes in several efforts ranging from hundreds to millions of individuals from the latter part of the nineteenth century up to the end of the twentieth century (Mills et al. 1993). These repeated introductions have resulted in self-reproducing populations that are generally too small to sustain anglers' catches. Hence, there has been the need for continuous restocking through hatchery programs, which, in the case of coho, are responsible for more than 90% of the total number of adult fish (Crawford 1997).

Our first conclusion, therefore, is that if time series of the mean TL of landed fish are to be useful for analyzing the impact of fisheries, the series must extend far enough into the past to cover major changes in the relative biomass of important ecosystem components. Also, such series must not

Fig. 5. Time series of mean TLs (weighted by landings) from Canadian aquatic ecosystems: (A) east coast, 1950–1997, with (solid circles) and without cod (open circles); (B) west coast, 1873–1996, with (solid circles) and without Pacific herring (open circles) or Pacific hake (open squares); insert shows fitted piecewise polynomial model and 95% confidence intervals; (C) inland waters, 1917–1997, with Canadian (solid circles) and FAO statistics (open circles).
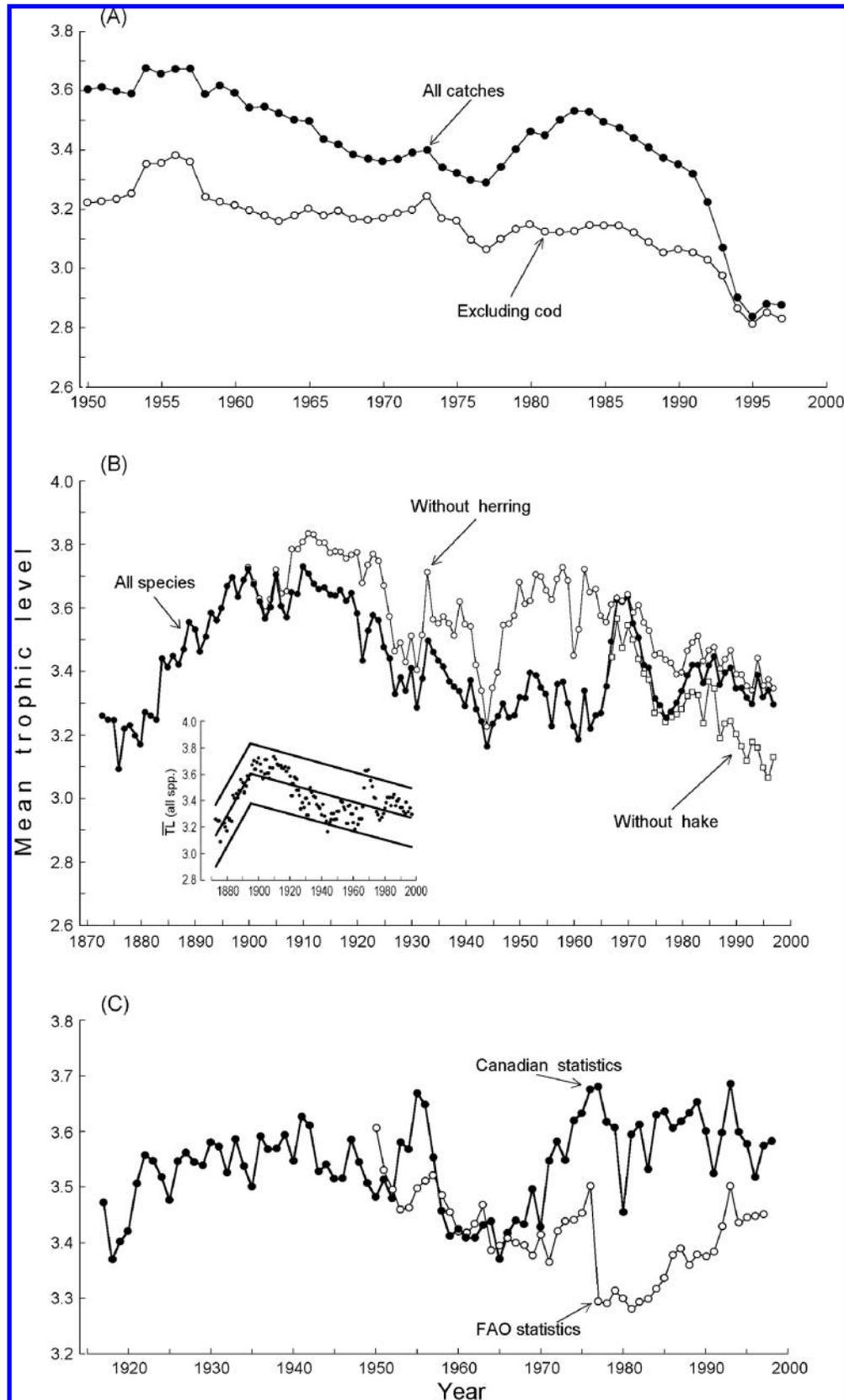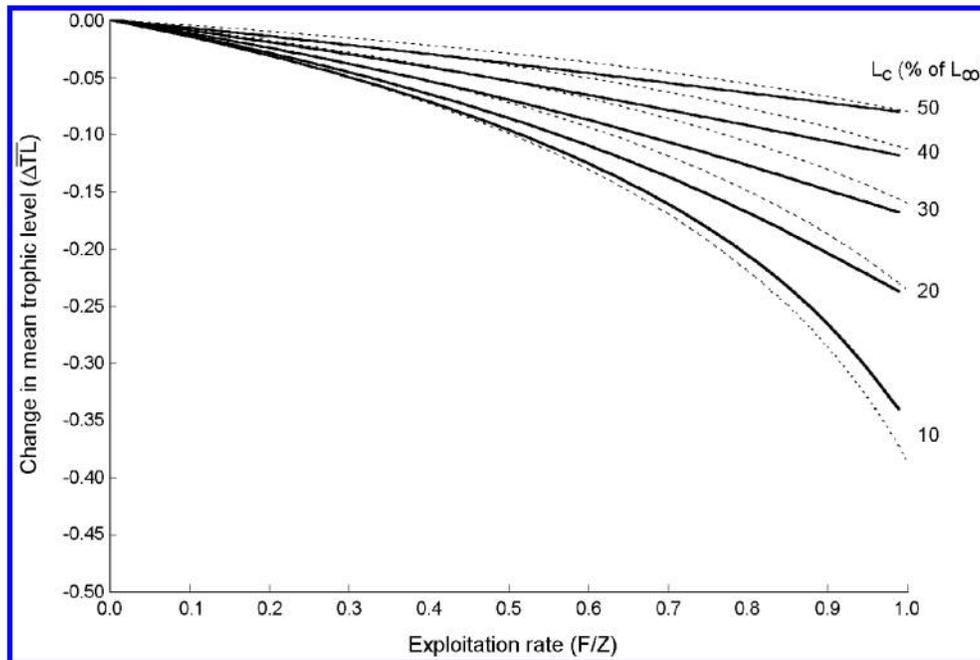
Fig. 6. Nomogram for estimating the effect of fishing (i.e., of $E = F/Z$) on the mean TL of a fish population with $M/K = 2$ for different values of the ratio L_c/L_∞ (see eq. 6 for definitions of E and M/K). Note that the length-based analysis (broken lines, from eq. 7) provides results roughly similar to those of the age-structured model (solid lines, from eq. 8).

be "contaminated" by anthropogenic impact other than withdrawals by fishing. In the case of Canadian inland waters, the confounding factor is stocking, which maintains relatively high biomass and catches of fishes with high TL (e.g., of Pacific salmon in the Great Lakes), counteracts any "fishing-down" effect, and thus precludes evaluation of sustainability based on mean TL.

Mean TL trends on the east coast

On the east coast, the operations until the 1970s of distant water fleets and the later deployment of a Canadian trawler fleet had a strongly negative impact on the mean TL of organisms in the landings. The decline in mean TL, while strongly influenced by fluctuations in the cod stock, was shown to occur also when this species is not included in the analysis.

Our new length- and age-based models produced roughly similar estimates of the effect of F on within-species mean TL. The differences between the results from the two models are accounted for by the fact that the length-based model predicts mean TL changes from a single mean length, while the age-based model estimates mean TL as integral of an age-structured population.

The application of the more accurate age-based model to cod and other demersal fishes showed that the within-species effect of size, and hence reduction in TL by fishing, is relatively small, at least when compared with the changes in mean TL due to the fluctuation of a single, abundant species (or its exclusion from the analysis, as shown for cod in the east coast and Pacific herring and Pacific hake in the west coast). This is especially true if the within-species effect involves taxa whose TL does not strongly increase with body size, as is the case for small pelagics (see Fig. 1) and probably for most invertebrates as well.

Overall, given their trend in mean TL, we conclude that the east coast fisheries are unsustainable at the ecosystem level.

Mean TL trends on the west coast

For the west coast, our results confirm Glavin (1996) who noted that overall landings tend to depend on the status of the latest "new" species. Presently, this new species is Pacific hake, and the development of a fishery for this high-TL predator is the reason why the mean TL of organisms in the fisheries is at its present height. Still, in spite of fluctuations caused by this and previous new fisheries (notably that for Pacific herring), the dominant trend in the twentieth century has been one of significant TL decline ($-0.032 \cdot decade^{-1}$). The preceding period of increasing TL ($0.215 \cdot decade^{-1}$), from 1873 to 1894, was largely due to the industrialization of the fisheries (formerly dominated by landings of low TL invertebrates), which enabled the catching of previously underexploited, large, high-TL predators (Pacific halibut (*Hippoglossus stenolepis*), marine mammals, etc.).

The catch pyramid for the west coast confirms the importance of long time series: the comparison of 1950 and 1997 (the period covered in FAO statistics) would suggest that the mean TL of organisms in the west coast fisheries has increased over time. The increase was due to the collapse of fisheries for small pelagics (predominantly Pacific herring), which have low TL, in the 1960s. Given our long time series of mean TL values and their overall trend, we conclude that the west coast fisheries are also unsustainable at the ecosystem level.

General features and uses of mean TL series

The time series of catches from the marine fisheries off the east and west coasts of Canada have covered sufficiently

Fig. 7. Relationships between F and mean TL of organisms in Canadian east coast fisheries landings: (A) landings-weighted mean fishing mortality of demersal fishes (thick line, open circles) and of cod (thin line, solid circles) estimated for each year k from $F'_k = F_{k-4} + 2F_{k-3} + 3F_{k-2} + 2F_{k-1} + F_k/9$ to simulate equilibrium; (B) changes in mean TL of cod predicted by eq. 8, given the F'_k values in Fig. 7A and the parameters in Table 1, footnote f; (C) original (from Fig. 5A) and corrected time series of mean TL, i.e., considering the effects of cod size reduction, a similar effect on other demersal fishes, and no effect for pelagic fishes and invertebrates.
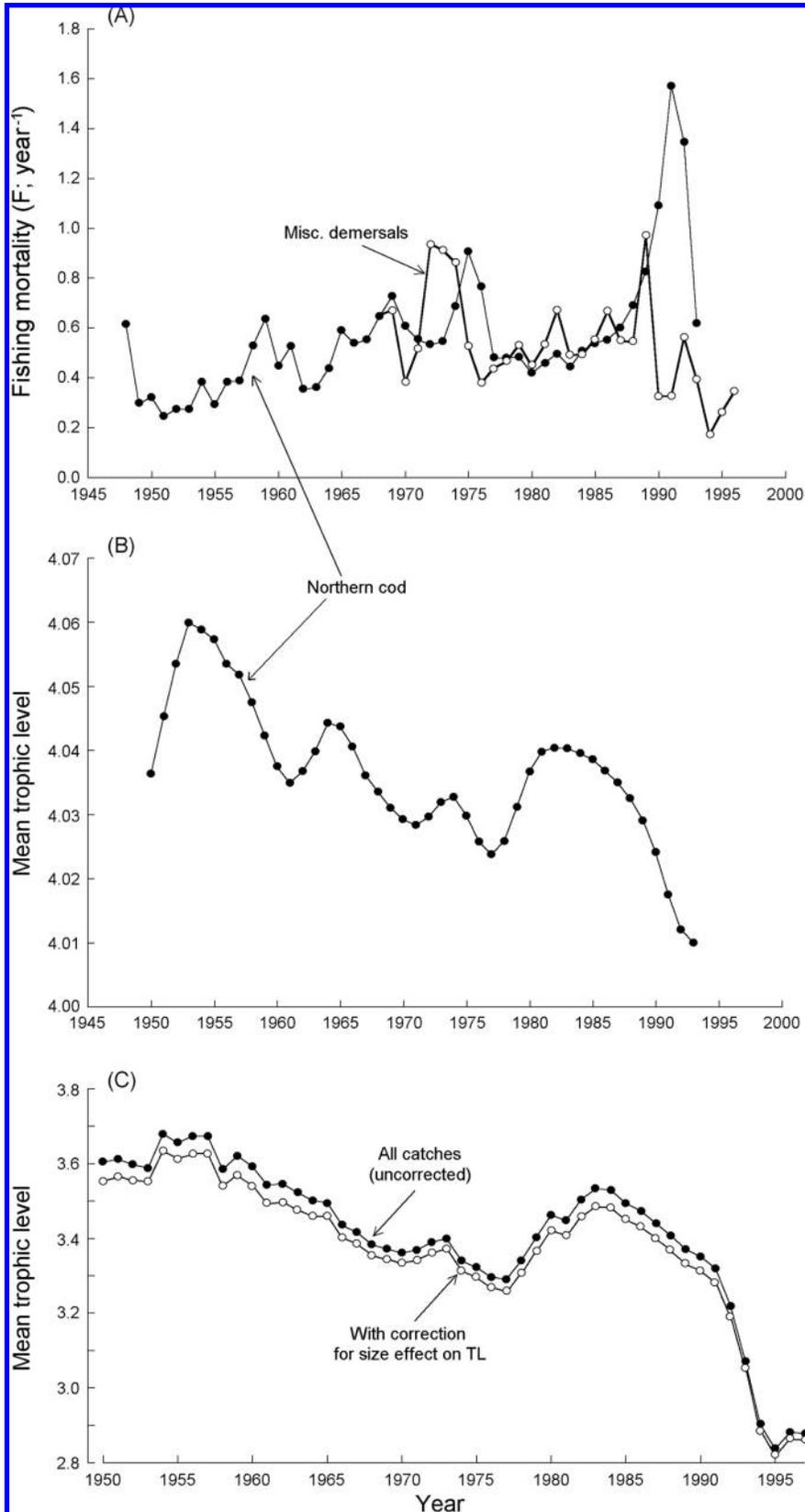
long periods for significant downward trends in the mean TL of the fisheries to appear, thus providing local confirmation of the global trend toward "fishing down marine food webs" documented in Pauly et al. (1998). As pointed out, the time series for inland waters was not adequate for this purpose.

However, it is probably too early to make definite recommendations on how mean TL changes of organisms in landings from a given area could be used to generate precise reference points for ecosystem-based management. Deriving and evaluating potential indices is presently a very active area of fishery and ecosystem research, with consensus on suitable candidates well beyond the horizon. Nevertheless, the present study and the previous analyses by Pauly et al. (1998) allow the identification of diagnostic features that may be considered when such recommendations are made.

(1) An increasing trend in mean TL with increasing or stable total catches may have a number of causes, of which a frequent one is the development of new fisheries for previously unexploited high-TL groups such as offshore and (or) deep-sea species.

(2) Stable mean TL associated with stable total catches suggests sustainability.

(3) a continuous downward trend in mean TL combined with stagnating catches implies absence of sustainability. A continuous downward trend also implies a change in the species mix that is caught, including a transition toward low-TL invertebrates as mean TL drops below 3, the lower limit for non-herbivorous fishes, documenting a fishery now relying strongly on invertebrates.

(4) A decline in mean TL combined with declining catches (including discards) in the absence of change in fished area or gear deployment may imply a food web collapse (possibly the reason for the accelerated mean TL decline in east coast noncod species in the early 1990s), with biological production diverted toward presently unexploited components of the ecosystem such as small benthic invertebrates and (or) jellyfish.

One way to use series of mean TL of organisms in fisheries catches that would combine these four diagnostics and allow drawing inferences on sustainability would be to plot the annual mean TL of "traditional" species (i.e., excluding catches of species not previously exploited) against the corresponding catches (including discards). Given the "pyramidal" nature of marine ecosystems, such plots should exhibit, given sustainability, a straight descending slope reflecting the relationship between biological production and mean TL, i.e., transfer efficiency (Pauly and Christensen 1995). On the other hand, lack of sustainability would lead to departures from linearity and in extreme situations (diagnostic 4) to the "backward-bending" curves of TL versus catch observed by Pauly et al. (1998).

Further, comparisons among mean TL series from similar ecosystems (e.g., around the North Atlantic or the North Pacific) may allow detection of similarities among the mean TL values at which plots of TL versus catches start to bend backward. This in turn may lead to the identification of a generic cutoff point for mean TL, at least for the ecosystem type in question. Obviously, such analyses would have to be conducted repeatedly, with different species groups excluded

in order to obtain results unaffected by minor fluctuations in the biomass and catches of individual species.

In any case, the time series used in such analyses should be as long and accurate as possible, lest they induce grossly erroneous interpretations. It was surprising that there was no consistent series of official Canadian catch data. Also, the landing series that may be constructed from official documents and statistics do not match the FAO series based on data supplied to the FAO by the Government of Canada, an FAO member state. Therefore, we cannot but wonder how the detailed assessments of various single-species fisheries routinely conducted in Canada can avoid being marred by the shifting baselines (Pauly 1995) that result from lack of consistent time series that reach well into the past.

Acknowledgments

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