

Comparing species and ecosystem-based estimates of fisheries yields

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Abstract

Three methods are described to estimate potential yields of commercial fish species: (i) single-species calculation of maximum sustainable yields, and two ecosystem-based methods derived from published results for (ii) energy flow and for (iii) community structure. The requirements imposed by food-web fluxes, and by patterns of relative abundance, provide constraints on individual species. These constraints are used to set limits to ecosystem-based yields (EBY); these limits, in turn, provide a comparison with the usual estimates of maximum sustainable yields (MSY). We use data on cod and haddock production from Georges Bank for the decade 1993-2002 to demonstrate these methods. We show that comparisons among the three approaches can be used to demonstrate that ecosystem based estimates of yields complement, rather than supersede, the single-species estimates. The former specify the significant changes required in the rest of the ecosystem to achieve a return to maximum sustainable levels for severely depleted commercial fish stocks. The overall conclusion is that MSY defines changes required in particular stocks, whereas EBY determines the changes required in the rest of the ecosystem to realize these yields. Species specific MSY only has meaning in the context of the prey, predators and competitors that surround it.

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1. Introduction

Management of marine fisheries has been, and is still largely based on the concept of maximum sustainable yields (MSY) of the major fish species of commercial value. There is now, however, considerable interest in ecosystem-based management (EBM) although this has yet to be made operational. The demise of management by MSY has been predicted frequently, for example by Larkin (1977), but survives in concept as well as in practice (Mace, 2001) because fishing effort to achieve MSY values for each species are readily calculated from population models and the MSY concept is enshrined in national and international legislation. It is likely that such numbers will be required for, at least, the medium term future.

We suggest that EBM is not an alternative to management by MSY but a complement. In MSY the focus is on the demography of a particular species. In EBM the focus is on the rest of the fish community and its enveloping ecosystem. The aim is not to produce different assessments for individual species but to assess the changes that must occur in the rest of the system to achieve MSY in a few selected species. These changes are especially significant for the restoration of severely depleted species such as cod in the North Atlantic. Such necessary restructuring will involve both the prey-predator relations between different trophic levels and also the competitive interactions between species within trophic groups. The former constraint is acknowledged in the doctrine of surplus production that underlies MSY procedures but the consequences of competition on MSY and even its multi-species adaptations (Worm et al, 2009) are generally ignored.

We illustrate these interactions by comparing three different estimates of yields of two commercially important species, cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*), on Georges Bank in the northwest Atlantic, during the decade 1993-2002. (1) We use the most recent MSY estimates from the U.S. National Oceanic and Atmospheric Administration (NOAA, 2008). (2) An end-to-end model of nutrient fluxes on Georges Bank (Fig. 1) (Steele et al., 2007; Collie et al, 2009) provides estimates of the constraints imposed by basic ecosystem productivity and food web structure on different feeding guilds of fish. (3) A study of changes in diversity and composition within the fish community over four decades (Gifford et al., 2009) defines limits on abundance of individual species within the feeding guilds. Taken together these results can be used to estimate changes that have occurred in this ecosystem, and that would need to be reversed to return to earlier, larger values. Since we do not know the exact causes of these changes, it is highly unlikely that they will be reversed. Yet some restructuring of the ecosystem appears necessary if we are to implement higher levels of yield in the two commercially harvested species, cod and haddock, comparable with historic values.

2. Individual Species Assessments

The classical method for estimating maximum sustainable yield, MSY, of any species was introduced by Beverton and Holt (1957) and made operational by Sissenwine and Shepherd (1987). It has the form,

$$(\text{Yield per recruit}) \times (\text{Number of recruits})$$

- (1) Yield per recruit is deduced from the rates of growth and mortality (including fishing) of the adults. Fishing effort is used as a variable to select the maximum yield
- (2) The probable number of recruits per year is estimated from available data, including young fish surveys.

The former estimate is mainly dependent on choice of fishing effort and the estimates are fairly reliable. But the latter is problematic, particularly for multi-year forecasts. Haddock, and cod data for Georges Bank, Fig. 2, show the considerable variability associated with recruitment estimates. This method is effective for the short term

assessments – months to one year – needed to determine annual values for Total Allowable Catch for a number of species, especially when pre-recruit surveys can provide actual data on expected recruits. Obviously there are problems in the longer term when annual recruitment fluctuates widely (Fig. 2). Attempts to correlate data on recruits per unit of Spawning Stock Biomass (SSB) with physical or biotic environmental information have rarely been successful in the longer term nor have they been useful in improving forecasts of yields (Myers, 1998).

As examples of these assessments, we take MSY values for cod and haddock on Georges Bank, Table 1, produced by NOAA Northeast Fisheries Science Center (NOAA, 2008). For recruits, the averages of the values from the upper range of SSB above the thresholds in Fig. 2 are used. It is often very difficult to assign limits to MSY values. So it appears to be customary to present assessments of MSY as single numbers without error bars, presumably to avoid the use of upper or lower limits as alternative options by special interest groups. NOAA (2008) provides confidence limits for haddock MSY, Table 1, but not for cod. As one indicator of cod variability we assume that yields derive predominantly from four consecutive year classes. Then the standard deviations of a four point running mean for an uncorrelated time series provides a very approximate measure of the s.d. of the cod MSY, Table 1.

3. Ecosystem Based Assessments

Two primary ecological processes control yields of individual species; prey-predator relations and competitive interactions. The former are used here to assess the overall productivity of *trophic groups*. The latter can determine the relative abundance of species within a *community*.

3.1 Trophic Based Yield

The second method of estimating annual yields, uses calculations of fluxes through the food web, Fig. 1, to determine production by three feeding guilds of fish – planktivores, benthivores and piscivores (Garrison and Link, 2000). Details of these calculations are given in Steele et al. (2007). To obtain values for maximum potential yields of dominant species, Table 2, we first convert guild production as $\text{gC.m}^{-2}.\text{yr}^{-1}$ to production of biomass for the Bank in kt.yr^{-1} (Collie et al., 2009). To convert this to individual species, it is necessary to estimate the fraction of biomass contributed to each guild by the dominant species in the guild. The data in Fig. 3 display the variability in this factor. Table 2 gives the mean values. To get maximum potential yields for haddock and cod we assume that these would be the dominant species in their respective benthivore and piscivore guilds. Production is then converted to potential yield to the fishery using the ratios determined for yield/production for the piscivore, cod, and the benthivore, haddock in the MSY calculations (NOAA, 2008). It is assumed that there is an appropriate level of fishing effort to maximize the yields. The values are given in Table 1 with the standard deviations derived from the data in Fig. 3 to provide a measure of variability.

3.2 Community Based Yield

Gifford et al. (2009) have shown how the Georges Bank fish community adapts to significant external stresses, exemplified by the responses to changes in the 1970's occasioned by increases in overall productivity and, somewhat later, by decreases in fishing effort (Fig. 4a). Throughout the last three decades, 1973-2002, there were marked fluctuations in abundance of individual species (Steele et al, 2007) but these were largely compensated for by relative regularity in overall measures such as total fish food intake and diversity indices (Gifford et al, 2009).

Gifford et al (2009) used food intakes to calculate Variance Ratios (Schluter, 1984),

$$VR = \text{Var}(\text{total intake}) / \sum \text{Var}(\text{species intake})$$

Evidence of compensation requires that $VR < 1$. For the years 1973-2002, VR for piscivores and benthivores were, respectively, 1.19 and 1.17. While for the total fish community $VR = 0.42$.

After 1975, the ranking of species by abundance showed overall regularity (Fig. 5b), despite considerable inter-annual variability (Fig. 5a). This regularity provides estimates of the expected abundances, and the standard deviations. We assume that production of the seven top ranked species is proportional to their abundance, Table 3, using the average of the production/biomass ratios for the three guilds (Steele et al, 2007). The observed percentage values for herring and mackerel production, averaged over 1993-2002 (Table 3) are within the range of the expected production of the top two species. In contrast, the values for cod and haddock for the same period rank seventh or greater (Table 3), emphasizing the problems in attempting to increase the yields of these two commercial species.

To obtain expected yields we, first, allocate production by the top seven species as a fraction of the total fish community production (Steele et al., 2007). The ratios of yield to production used in calculating MSY (NOAA, 2008) are used to obtain values for cod and haddock (Table 1), assuming that they are moved up to 3rd and 4th rank in Table 3, behind the dominant pelagic planktivores, herring and mackerel. This shift requires displacing more dominant species, including the piscivores silver hake, spiny dogfish, winter skate, and the benthivorous ocean pout.

4. Changes in community structure

To relate these numbers for the decade 1993-2002 to community structure over previous decades (Steele et al, 2007), we have allocated the top ranked two species for each year to the three feeding guilds, revealing certain patterns (Fig. 6). The dominance of the benthivore, haddock, ended about 1969 and was replaced by a piscivore:planktivore combination; initially cod then winter skate, finally spiny dogfish, for the former and

sand lance for the latter. This switch fits with the observed decline in the benthic food intake by fish (Fig.4 b).

Less expected is the abrupt transition in 1992-1993 from a piscivore: planktivore combination to a decade where the community was dominated by two planktivores – herring and mackerel. There is no evidence for large internal or external stresses that could have caused this transition. The piscivore diet contains about one third plankton (Garrison and Link, 2000). The fish component, primarily juvenile fish, are assumed to feed predominantly on plankton (Steele et al, 2007). Thus their food supply is mainly plankton based. The implication is that, because of the necessary differences in life histories and feeding strategies of different species, relatively small or smooth changes in overall categories of food can occasion rapid step changes in species composition that might be termed a “regime shift”.

4.1 Earlier data: 1921-1950

We do not have data on the guild structure for the period 1921-1950 when fishing effort was not excessive (Hennemuth and Rockwell, 1987) but the average catches of the two main commercial species, haddock and cod (Table 3) indicate that, on average, they occupied 2nd and 3rd rank, respectively, in abundance. The maximum for haddock was over 100 kt.yr⁻¹ (Hennemuth and Rockwell, 1987), indicating occasional occupation of the first rank. Also the relative ranks, with the benthivore dominant, confirm the assumption of a preponderance of benthos in the available food supply, implying that the conditions observed around 1963-1965, Fig. 4b, were typical of earlier environments.

5. Comparison of Yield Estimates

If we compare the mean values for the three estimates of maximum potential yield for cod and haddock derived here (Table 1), then there are large differences between the estimates. We have calculated limits for each estimate, using data in Figs. 2, 3 and 5(a). These can be considered minimal values based on a single source of variance for each yield. With these values there are no significant differences among the yields for each species. These comparisons emphasize that the function of our analysis is not to propose alternate values for yields but to display the ecological basis for a range of values. The choice of appropriate values for management purposes involves factors outside this analysis.

In this context, the notable feature to emerge from this analysis is not the reduction in yields of the main commercial species, cod and haddock, over the years 1963-2002, but the changes in ecosystem structure that accompanied these decreases. These changes can be assigned to three categories.

- (1) Decreased ranking of commercial species within feeding guilds. Cod have been overtaken by other piscivores; silver hake and the elasmobranchs spiny dogfish and winter skate. Haddock are outranked by another benthivore, ocean pout. Increased yields of cod and haddock would require changes in the hierarchy. This

implies displacement of higher ranking species within a feeding guild. The results of Steele et al (2007) and Gifford et al (2009) indicate that production by feeding guilds is linked to food supply, whereas abundance of individual species is not. Outstanding recruitment of the 2003 haddock year class has increased production of this stock, but the MSY is still significantly less than the long term average for 1921-1950 (Table 3). Thus it is not clear why cod and haddock stayed low in ranking, and apparently uncompetitive, within their guilds for two decades after fishing effort was reduced. This remains an ecological challenge.

- (2) Changed ranking of species in other guilds. The dominance of two pelagic species, herring and mackerel, in recent years, excludes a dominant demersal species from 2nd rank. Increased yield of demersal species requires elimination of a planktivore. In the food web depicted here, Fig. 1, changes in the allocation of plankton production between juvenile and adult fish can produce a switch between planktivores and piscivores. In many North Atlantic ecosystems (Choi et al, 2004; Heath, 2005), recent domination by pelagic species affects production of valuable commercial species such as cod, yet the dynamics of juvenile fish remain largely unknown (Houde, 1996; Heath, 2007; Steele et al, 2007).
- (3) Changes in benthic food intake. The switch from a preponderance of benthos to plankton in the food intake, decreases the potential yield of haddock and, to some extent, cod. To obtain increases in yields of commercially important demersal species such as haddock and cod imply changes in the lower part of the food web, Fig.1; in particular a switch between primary production going to benthos and plankton. This could be related to alteration of benthic habitat observed in several experimental studies (Hermsen et al, 2003; Collie et al, 2000; Hiddink et al, 2006). A reduction in suspension feeding benthos would result in production diverted to pelagic output (Collie et al, 2009) but the evidence to support this assumption is circumstantial.

In all three cases, the changes in ecosystem function or structure required to increase production of preferred species, involve altering the relations between individual species and communities. Some of the mechanisms inferred here result from changes in prey – predator relations, and these form the basis for most models of ecosystem responses. The causal processes proposed here, however, also imply a major role for competitive interactions in determining the abundance of species within the functional guilds. A return of cod and haddock yields to the levels in the period 1921-1950 would appear to require restructuring in all three categories – within feeding guilds, between guilds and in the benthic/pelagic allocation of primary production. At present there is inadequate information to determine how such changes could be implemented in terms of individual species responses. But it is necessary to recognize these constraints on species abundance and to consider strategies to overcome them.

6. Conclusions

The general decline in abundance of preferred commercial species such as cod and haddock is correctly attributed to overfishing. Reduction in fishing effort on targeted species is the first requirement for rational fisheries management. But, increasingly, we

recognize that overfishing a few species has consequences for the rest of the ecosystem, particularly after prolonged and excessive harvesting. If the production of preferred species is to be increased, we will need to accept consequential changes in ecosystem structure manifest as relations between individual species and communities.

The problem is that, rarely, can we identify the ecological processes that orchestrate the changes in structure. Often we cannot specify the direction of cause/effect. Thus the widespread switch from demersal piscivores to pelagic planktivores in the North Atlantic (Heath, 2005; Frank et al, 2005; Steele et al, 2007) can be explained as a trophic cascade (Frank et al, 2005); or as the result of large herring populations feeding on the eggs and larvae of cod (Speirs et al, 2010; Fauchald, 2010); or as a change in particular invertebrate components of the food web (Steele et al, 2007). For these reasons a return to abundance of a few preferred species is unlikely to involve a linear reversal of some historical change; nor even, as some models might suggest, a non-linear regime shift back to a previous structure (Scheffer, 2001)

The methods developed for this analysis - single species demography, energy flow through food webs and species/ biomass ranking – are generally available, so this approach should be applicable elsewhere. Methods to estimate food web fluxes are widely used (Plaganyi and Butterworth, 2004). When these are related to analysis of community hierarchies, the two major ecological processes – prey-predator relations and competitive interactions – can be combined to demonstrate the consequences of changing ecosystem structure on commercial fisheries. As illustration, we focused on the two formerly dominant commercial species on Georges Bank, but the analysis could be extended to include other commercial species such as yellowtail flounder.

In summary, we assert that it is not possible to achieve the MSY for individual species if we neglect the changes in the food web within which the species is embedded. Fisheries management should be concerned not only with changing the demography of a few commercially important species, but more with determining the changes that must occur in the rest of the system to achieve increased yields of preferred species. We have shown how the required changes can be inferred in one case. We cannot specify *a priori* how these changes will be achieved. Thus the focus of the ecosystem-based aspects of management should be less on obtaining more accurate forecasts for a few species, and more on strategies to alter food web and community structure in directions that will enhance food supply, and reduce competition for the preferred species.

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Table1. Estimates of cod and haddock fisheries yields from Georges Bank by three different methods based on data from 1993-2002 (mean and standard deviation). The standard deviations are calculated from the data in Figs 2,3,5(a).

	Cod	Haddock
Maximum Species Yield	31.2 ± 10.0	32.7 ± 9.1
Food Web Based Yield	20.9 ± 5.5	17.1 ± 5.2
Community Based Yield	28.7 ± 9.0	22.3 ± 6.7

Table 2. Values used to convert production rates to potential yield of biomass for Georges Bank. The area of the Bank is taken as 43,000 km², and the ratio of Carbon to Biomass as 0.114 (Steele et al, 2007)

Piscivores	Benthivores
Prodn by Guilds (gCm ² yr ⁻¹)	0.264 0.200 (Collie et al, 2009)

Dominant Sp/Guild (fraction)	0.41	0.43	(Collie et al, 2009)
	Cod	Haddock	
Prodn/Biomass (yr^{-1})	0.41	0.39	(Steele et al, 2007)
MSY/ B_{MSY} (yr^{-1})	0.21	0.206	(NOAA, 2008)
Yield/Prodn	0.51	0.53	
Yield for Bank (kt.yr $^{-1}$)	20.9	17.1	

Table 3. Comparing the ranking of diversity based estimates of fish production as percentage of the total, with observations of recent production and earlier catches (Hennemuth and Rockwell, 1987). The expected yields are based on the yield/production ratios for cod and haddock (Table 2)

Rank	1	2	3	4	5	6	7
Mean Prodн (%)	35.50	16.15	10.00	7.76	6.04	5.18	4.01
STD (%)	11.76	6.18	3.14	2.32	1.75	1.61	1.30
<i>Observed Prodн (%)</i> (1993-2002)	26.3 (Herr)	19.3 (Mack)	-	-	-	-	3.8 (Cod) 2.1 (Had)
Expected Yield (kt/yr)	101.9	46.4	28.7	22.3	17.3	14.9	11.5
<i>Observed catch</i> (1921-1950)		52.5 (Had)	22.4 (Cod)				

Text for Figures

Figure 1. A representation of the bottom-up fluxes in the Georges Bank food web, driven by input of NO₃, through a microbial food web with nutrient re-cycling, to planktonic and benthic components. These components are integrated as “Total Plankton” and “Total Benthos” to supply the diet of the fish groups. (adapted from Collie et al, 2009).

Fig. 2. Spawning stock/ recruit relations for (a) haddock, 1960-2002 and (b) cod, 1975-2002. Lines indicate average recruitment for different ranges of SSB (taken from NOAA, 2008). The upper ranges are used to estimate SD's for the MSY's (see text).

Fig. 3. Fraction of biomass contributed to each guild by the dominant species in that guild.

Fig 4. (a) External drivers of the Georges Bank ecosystem in terms of estimated fish production and landings

(b) Changes in the fraction of benthos in the diet of fish

Fig. 5 (a). Annual percentage abundance rankings of fish species for 1976-2002

(b) Average rankings for 1976-2002

Fig.6. Allocation of top ranked two species in the fish community to the three fish guilds

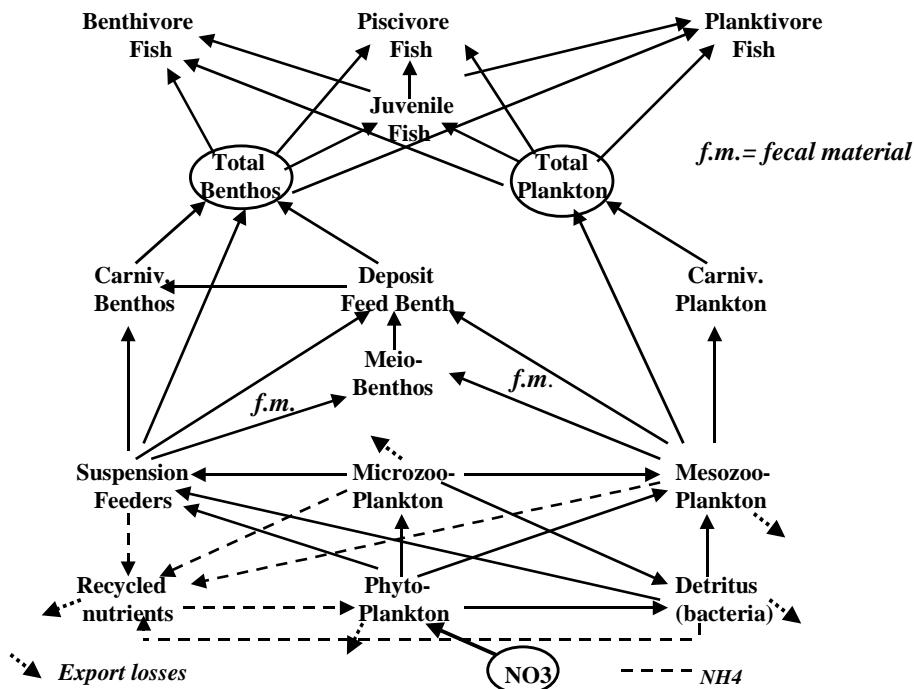


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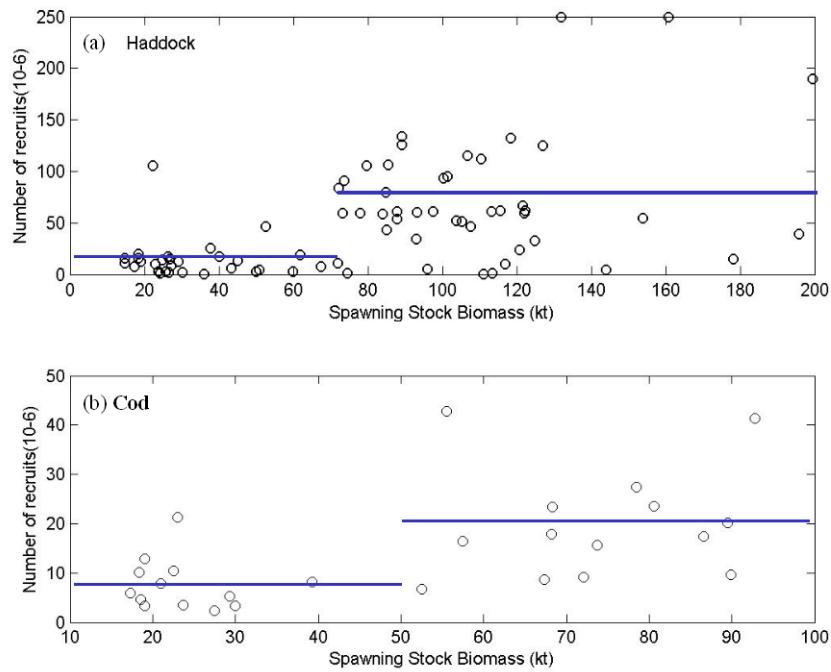


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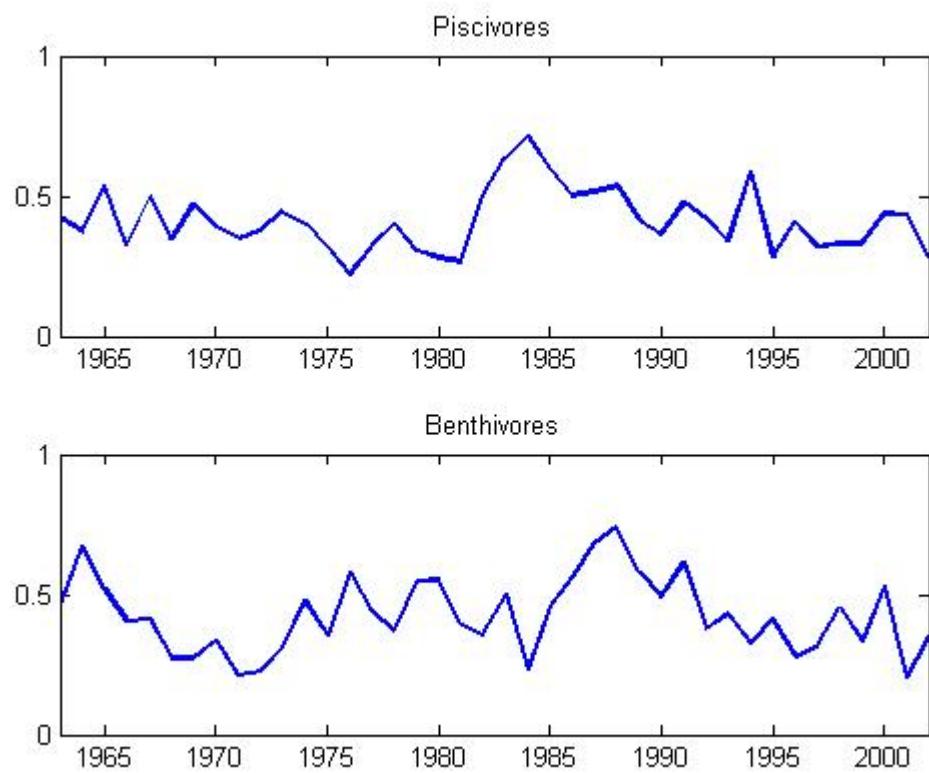


Fig. 3. Fraction of biomass contributed each year to the piscivore and benthivore guilds by the dominant species in that year.

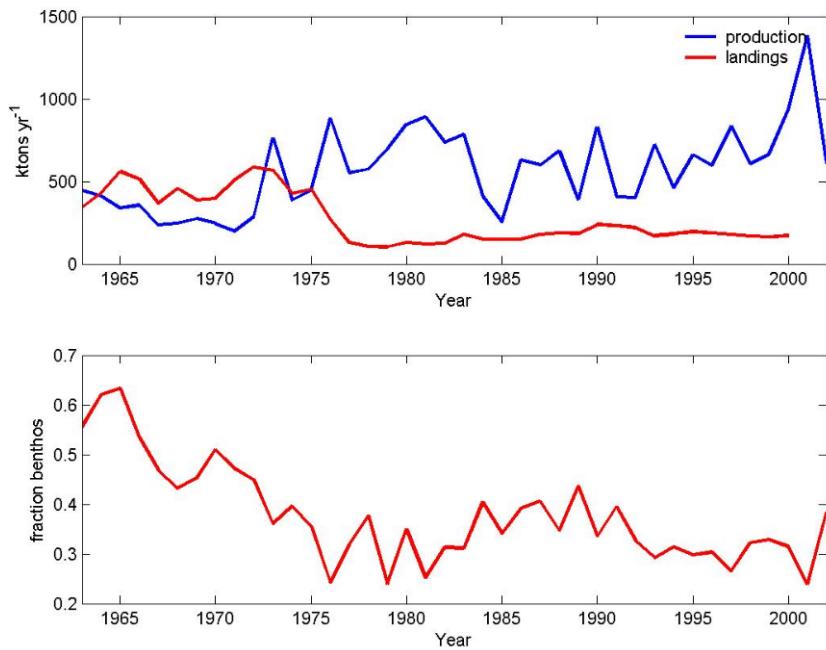


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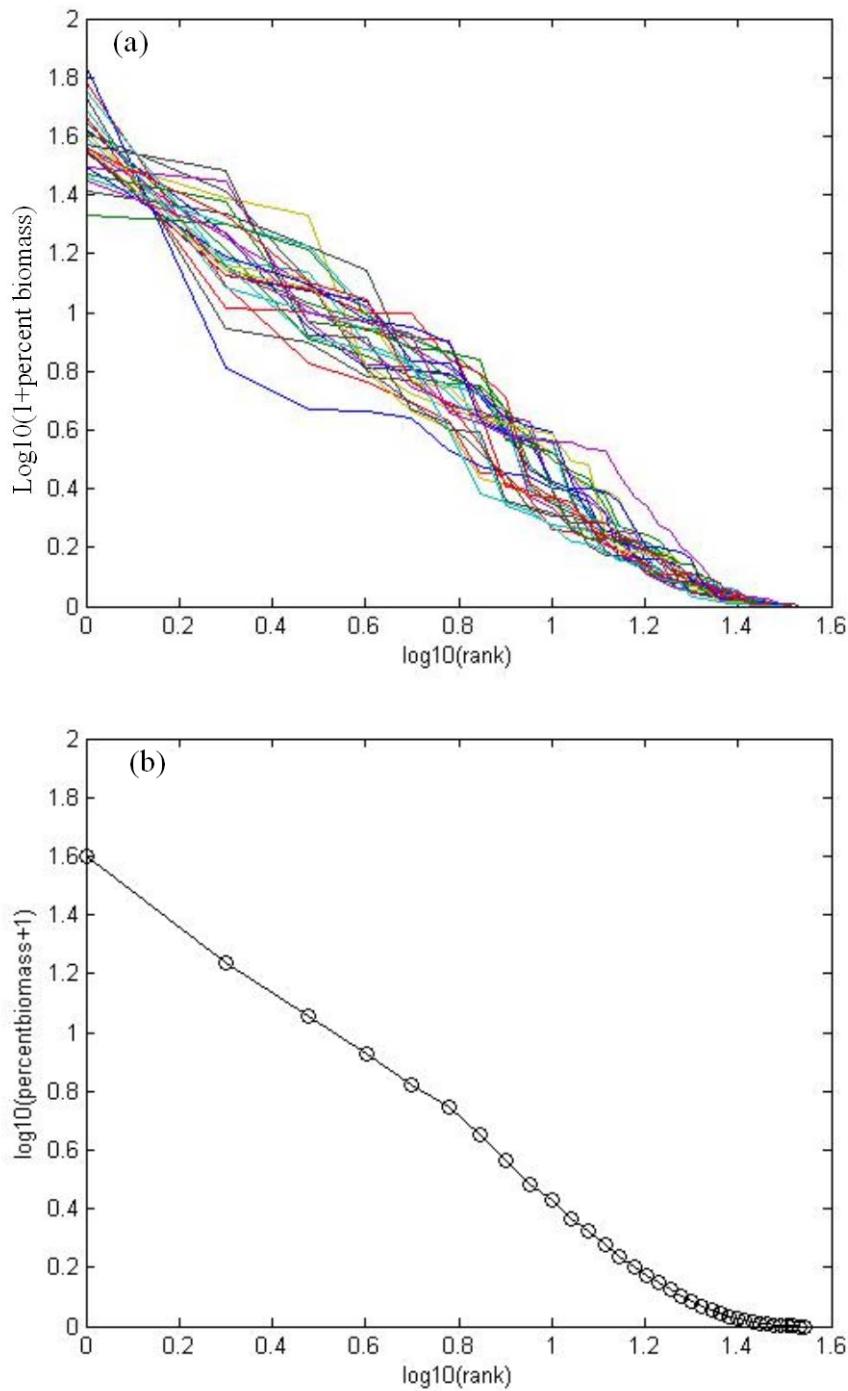


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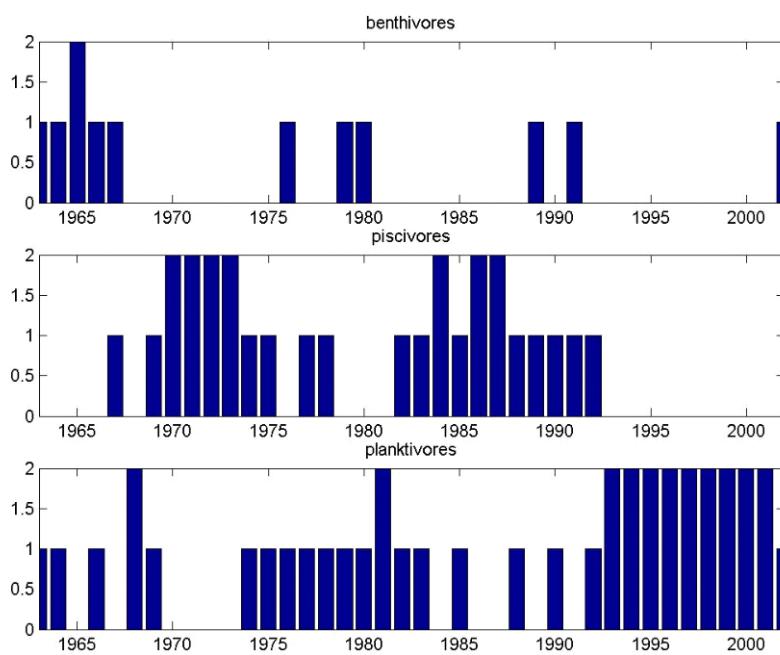


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