

Estimates of Prey Consumption and Trophic Impacts of Cetaceans in the USA Northeast Continental Shelf Ecosystem

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Abstract

Whales, dolphins and porpoises are significant consumers of prey resources in the USA Northeast Shelf marine ecosystem to a far greater extent than was realized two decades ago. Seasonal estimates of the consumption of finfish, squid and zooplankton by cetaceans were calculated for four regions of the Northeast Shelf system defined as Gulf of Maine, Georges Bank, Southern New England and Mid-Atlantic Bight. Estimates were based on seasonal cetacean abundance using standard mammalian metabolic models scaled as appropriate for assimilation, activity and migratory fasting. Estimates were made of mean body mass and proportion of the diet comprised of each of the three main prey types. Cetaceans of the Northeast Shelf were found to consume nearly 1.9 million tons annually, including about 1.3 million tons of fish, 337 000 tons of squid and 244 000 tons of zooplankton. Their predation on fish and squid exceeded tonnages harvested in the commercial fishing industry. Consumption estimates of fish dominated in most regions and seasons, primarily because of the widespread distribution and high relative abundance of large piscivorous fin whales, and secondarily due to the presence of humpback and minke whales and some of the smaller odontocetes. Zooplankton consumption, principally by right and sei whales and secondarily by other mysticetes, was significant in some seasons in the Gulf of Maine and Georges Bank regions. An assemblage which included a variety of teuthivorous odontocete species inhabiting the shelf break vicinity consumed substantial quantities of squid in all regions except the Gulf of Maine. Using a simple five-level trophic model and 10% estimated trophic transfer efficiency, the estimates implied that a significant fraction of the total net primary production, ranging from 11.7% in the Mid-Atlantic Bight to 20.4% in the Gulf of Maine, was required to the support cetacean apex predation.

Key words: cetaceans, ecosystems, food/feeding, Georges Bank, Gulf of Maine, Mid-Atlantic Bight, New England area, trophic relationships

¹ Deceased 13 August 1995

Introduction

The ecological roles of cetaceans in the trophic dynamics of marine ecosystems have been relatively poorly known until recently. For the continental shelf waters off the northeastern United States (the "Northeast Shelf"), it was commonly assumed that cetaceans were relatively unimportant consumers in the regional trophic system (e.g. Cohen *et al.*, 1982; Sissenwine *et al.*, 1984a). This assumption was likely based, at least in part, on a lack of information on the cetaceans. Prior to the Cetacean and Turtle Assessment Program (CETAP), conducted at the University of Rhode Island in 1979–82, there were very few reliable data on the species composition, abundance, distribution and seasonality of the cetacean community of the Northeast Shelf. The CETAP studies resulted in over 10 000 sightings of whales and dolphins (CETAP, 1982), enabling for the first time a quantitative assessment of their ecological impacts, i.e. levels of prey consumption in the Northeast Shelf ecosystem.

The Northeast Shelf, encompassing the continental shelf waters between North Carolina and Nova Scotia, is one of 49 defined Large Marine Ecosystems (LME) around the world (Sherman and Alexander, 1986, 1989; Sherman *et al.*, 1990, 1991, 1993, 1996). The marine environment of the Northeast Shelf is both physically and biological heterogeneous (Sherman *et al.*, 1988; 1996), ranging from the relatively uniform bottom relief in the southern portions to the complex bathymetry of Georges Bank and the Gulf of Maine to the north. The area encompasses a latitudinal range that includes both temperate and boreal water masses, and includes a number of complex features such as shoals, banks, basins and canyons. Nevertheless, patterns in the hydrography and biological communities in different parts of the Northeast Shelf enable subdivision into four more or less natural regions: the Gulf of Maine (GOM), Georges Bank (GBK), Southern New England (SNE) and the Mid-Atlantic Bight (MAB) (Fig. 1).

Whales, dolphins and porpoises are all carnivores, and they have few predators, so they function as apex predators in many marine ecosystems. Their diets include a wide variety of prey species, including pelagic, demersal and benthic fishes, euphausiids ("krill"), copepods and other crustacean zooplankton, shrimp, crabs, squid, octopods, birds and other marine mammals (Nemoto, 1970; Matthews, 1978; Gaskin, 1982; Evans, 1987).

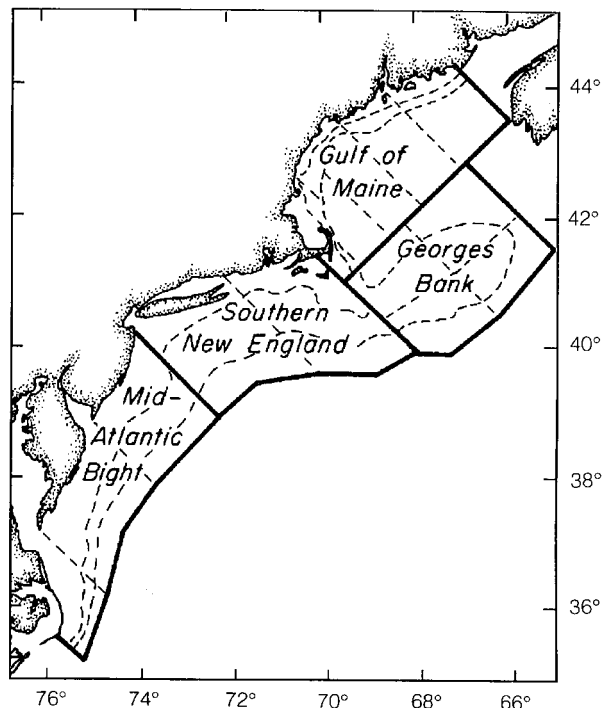


Fig. 1. The USA Northeast Shelf study area, showing the boundaries of the four regions defined for this study. The dashed lines show the individual CETAP aerial survey blocks, which numbered 35 in all. The area boundaries also indicate the bathymetry based on the 20 fathom (37 m) and 50 fathom (91 m) isobaths used in defining the individual survey blocks, and the outer edge of the study area approximately at the 2 000 m isobath.

Therefore they feed at different levels of marine food webs. Some species are specialists, feeding exclusively on a single prey type, while others are generalists with broader preferences. Nevertheless, one can classify the prey species of North Atlantic cetaceans into three broad categories – fish, squid (including other cephalopods) and zooplankton.

Many of the species consumed by cetaceans are likely to be either important target species of commercial fisheries, or linked to such species through the food web. Thus, predation by cetaceans is one factor which should be considered in multi-species fishery management models. In this paper an attempt is made to estimate seasonal and total prey consumption by cetaceans within the major regions of the Northeast Shelf. The objective here is not to test statistical hypotheses but to derive useful and realistic estimates of the impacts of cetaceans on

one marine ecosystem. It is also hoped that the results can serve as a useful comprehensive source of information for future understanding and management of the Northeast Shelf marine ecosystem.

Methods

The starting point was abundance estimates derived from the CETAP surveys, which were adjusted for several factors using all available data to produce what we feel are the most ecologically realistic estimates of abundance from the perspective of the entire community, not the most precise single-species estimates. At each step in the calculations where there was a need to choose between alternative values, our default choice was the more conservative option (i.e. that resulting in lower estimates) where one was not clearly preferable for biologically supportable reasons. We have intentionally not included estimates of statistical variability in our results. Since the initial abundance estimates are essentially the only input data with variances available, variances at any step in the results would simply be those initial values propagated through the model.

Study area

The CETAP study area was defined as the waters of the continental shelf from the shoreline to approximately the 2 000-meter isobath from Cape Hatteras, North Carolina to approximately the northern extent of USA jurisdiction (before the establishment of the Hague Line by the World Court) in the Gulf of Maine (Fig. 1). For this paper, the study area was divided into four regions by combining the CETAP aerial survey blocks to most closely approximate the regions defined by the National Marine Fisheries Service (NMFS) based on geography, bathymetry, hydrography and seasonal patterns of productivity and distribution, abundance and dominance within the plankton community (Sherman, 1980, 1986; Sherman *et al.*, 1982, 1988). The areas of the four regions, (with the percentage of the total study area in parentheses) were: GOM – 72 054 km² (25.9%), GBK – 69 004 km² (24.8%), SNE – 69 410 km² (24.9%) and MAB – 67 891 km² (24.4%).

Abundance estimates

Kenney *et al.* (1985) estimated seasonal abundances for each species in each survey block (the small areas shown by dashed lines in Fig. 1), based on data from the CETAP aerial surveys (CETAP, 1982). They defined seasons based on standard cal-

endar conventions. For this paper, those seasonal estimates were summed for each species across each of the four regions, resulting in an estimate of the total abundance of each species within each region and season.

Eighteen species of cetaceans were sighted during the CETAP aerial surveys (Table 1). Three categories – beaked whale, pilot whale and spotted dolphin – included two or more species within one genus, which were impossible to differentiate from aerial surveys and therefore combined. There were also a number of other categories of unidentified sightings, which in some cases represented significant numbers of animals in the estimates summed from Kenney *et al.* (1985). The estimated abundance of each unidentified category was partitioned among those species which could be included based on the relative proportions of their estimated abundances within that region and season, beginning with the narrowest categories (e.g. "fin or sei whale") and ending with the broadest (e.g. "unidentified large whale"). Some subjective judgments based on the complete CETAP sighting records were used in the partitioning. The abundance estimates were based on only a subset of the aerial surveys, but there were several other sources of sighting data. Thus there were a number of species where there were no abundance estimates for a region and season even though there were sightings, especially for those species which were uncommon or difficult to identify. The sighting maps in CETAP (1982) were visually examined to compare relative numbers of sightings of species with and without estimates. If there were only one or two sightings of a species with no abundance estimate for a region/season, that species was ignored. If there were more sightings, but still substantially fewer than for species with estimates for that region/season, then 5% of the appropriate unidentified categories was assigned to that species. Finally, if the number of sightings of a species with no estimate appeared to be more than about a quarter of species with estimates, it was assigned 10% of the unidentified individuals. For example, both common dolphins and sei whales were infrequent in summer in GBK and were not sighted on census tracks during aerial surveys. However the complete CETAP sighting data showed both species to be regularly present (CETAP, 1982), therefore 5% of the unidentified dolphins were counted as common dolphins, and 5% of the unidentified whales as sei whales. In another example, no sperm whales were sighted in GBK in the autumn during aerial surveys, but they were

relatively frequent in sightings from other sources, so 10% of the 43 unidentified large whales were counted as sperm whales.

For minke whales and harbor porpoises, which both tend to be solitary and inconspicuous, aerial surveys very likely seriously underestimate abundance (Kraus *et al.*, 1983; Barlow *et al.*, 1988; Palka, 1995). However, there are more recent estimates for both species for part of the CETAP study area from shipboard surveys for harbor porpoise conducted by the National Marine Fisheries Service (NMFS) (Blaylock *et al.*, 1995; Palka, 1995). The NMFS data were compared to ours for the same area and season to derive approximate values for the aerial survey bias in the CETAP data for these two species, which were then applied to the other areas and seasons. The NMFS weighted-average estimated abundances of harbor porpoises and minke whales in the northern GOM and lower Bay of Fundy for summer 1991 and 1992 were 47 200 and 2 650, respectively. The areas were not identical, however. Estimating visually, about 40% of the NMFS survey area was within our GOM region, and 40% of their total estimates would be 18 880 harbor porpoises and 1 060 minke whales. Those estimates were 9.3 and 10.6 times our summed GOM/summer estimates of 2 036 harbor porpoises and 100 minke whales, respectively, therefore a factor of 9.3 was used to adjust all of our harbor porpoise estimates for the aerial survey bias, and 10.6 for the minke whale estimates. These factors were considered conservative, since the NMFS surveys only covered about half of our GOM region.

Dive time corrections

It is recognized that for species which spend a large proportion of their time submerged, surveys from fast-moving aircraft will miss many individuals or groups while they are submerged. We used correction factors derived from data on the relative proportions of time spent at the surface and submerged (CETAP, 1982) for fin (4.846), humpback (3.645), and right whales (2.997). All other abundance estimates for large and medium-sized whales were also scaled for diving. Sei whales and minke whales belong to the same family as fins and humpbacks and are behaviorally similar, thus to be conservative the humpback correction factor was used. Also, the conservative factor for fin whale was used for sperm and beaked whales, that are known to dive for longer periods than fin whales (Evans, 1987; Jefferson *et al.*, 1993). Lacking any data for the

smaller and shorter-diving odontocetes, those abundances were not scaled for diving.

Standing stock

The total cetacean standing stock in each region and season was estimated by multiplying abundance by average body weight (from Kenney *et al.*, 1985; Table 1), which then was summed across all species. Biomass densities were calculated for each region and season by dividing standing stocks by the area of the region.

Basal metabolic rate

The basal metabolic rate (BMR, in kcal/day) of one individual was estimated for each species according to the standard mammalian metabolic model of Kleiber (1975):

$$BMR = 70 W^{0.75}$$

where W is the body weight in kg. For each species, the average body weights reported by Kenney *et al.* (1985; Table 1) were used.

Prey consumption rate

BMR was converted to consumption rate (kcal per day) by multiplying by factors to account for assimilation efficiency, active metabolism and fasting during migration. Assimilation efficiency was assumed to be 80% following Lockyer (1978; 1981a,b), resulting in a multiplication factor of 1.25. Active metabolism in cetaceans has been estimated at approximately 2 to 5 times BMR (Hinga, 1979; Lockyer, 1981b; Kenney *et al.*, 1986). A value of 2.5 times BMR was chosen at near the bottom of that range in order to scale for active metabolism. Animals which do not feed, or feed at significantly lower rates, during migration and/or on their wintering grounds must feed at a higher rate during the rest of the year to compensate (Mackintosh, 1966; Brodie, 1975; Matthews, 1978; Lockyer, 1981b; Evans, 1987). Since for most species, there is very little information on their distribution and behavior during the winter, a relatively low value was used here at 1.2 times. This factor was applied only to the baleen whales, and only during spring, summer, and autumn.

Daily consumption rate was converted to seasonal values of prey biomass consumed by multiplying by the average number of days in a season (91.3), by the proportion of the diet comprised of

TABLE 1. Cetacean species of the USA Northeast Shelf with estimated average body weights and dietary composition used in this study.

Species	Weight (kg)	Diet Composition (%)		
		Fish	Squid	Zooplankton
<i>Mysticetes:</i>				
Right whale, <i>Eubalaena glacialis</i>	40 000	–	–	100
Fin whale, <i>Balaenoptera physalus</i>	30 000	90	–	10
Sei whale, <i>Balaenoptera borealis</i>	13 000	–	–	100
Minke whale, <i>Balaenoptera acutorostrata</i>	4 500	95	–	5
Humpback whale, <i>Megaptera novaeangliae</i>	25 000	95	–	5
<i>Odontocetes:</i>				
Sperm whale, <i>Physeter macrocephalus</i>	20 000	20	80	–
Bottlenose whale, <i>Hyperoodon ampullatus</i>	4 700	5	95	–
Goose-beaked whale, <i>Ziphius cavirostris</i>	1 900	–	100	–
Beaked whale, <i>Mesoplodon</i> spp. ¹	1 200	–	100	–
Pilot whale, <i>Globicephala</i> spp. ²	850	10	90	–
Risso's dolphin, <i>Grampus griseus</i>	340	–	100	–
Bottlenose dolphin, <i>Tursiops truncatus</i>	150	100	–	–
White-sided dolphin, <i>Lagenorhynchus acutus</i>	120	90	10	–
Common dolphin, <i>Delphinus delphis</i>	65	85	15	–
Striped dolphin, <i>Stenella coeruleoalba</i>	55	40	60	–
Spotted dolphin, <i>Stenella</i> spp. ³	50	20	80	–
Spinner dolphin, <i>Stenella longirostris</i>	50	20	80	–
Harbor porpoise, <i>Phocoena phocoena</i>	45	95	5	–

¹ Includes four species – *M. mirus*, *M. densirostris*, *M. europaeus*, *M. bidens*

² Includes two species – *G. melas*, *G. macrorhynchus*

³ Includes two species – *S. attenuata*, *S. plagiodon*

fish, squid and zooplankton and by an energy density value for each prey type. The dietary proportions (Table 1) were from Kenney *et al.* (1985), with one exception. The diet of pilot whales was changed from 100% squid to 90% squid and 10% fish based on recent data showing significant interactions between pilot whales and the offshore non-USA and joint-venture midwater mackerel fishery which included samples of pilot whale stomachs containing mackerel (Waring *et al.*, 1990; Overholtz and Waring, 1991; Fairfield *et al.*, 1993). The energy content of fish and zooplankton was assumed to be 1 kcal per g wet weight (Clark and Prince, 1980; Sissenwine *et al.*, 1984a), while the energy content of squid was assumed to be 0.83 kcal per g (Croxall and Prince, 1982). Consumption estimates were then summed across all species for each region and season.

Primary production required

The total amount of primary production required to support the cetaceans of a region was es-

timated using a simplified model food chain with five trophic levels. The transfer efficiency from one trophic level to the next was assumed to be 10%, following Pauly and Christensen (1995). The general relationship was that the total amount of primary production required was calculated from the prey consumption rate using a factor of 10^n , where n is the number of trophic steps from the phytoplankton or the first trophic level to the given prey type. The trophic level (TL) values reported by Pauly and Christensen (1995) for non-tropical continental shelf systems were used: TL = 2.0 for herbivorous zooplankton, TL = 3.0 for schooling planktivorous fishes (e.g. herring or sand lance), and TL = 3.2 for squid. Primary production required was converted from energy to carbon by 13.3 kcal per g C (Platt, 1969). The resulting values were compared to published estimates of total primary production for the Northeast Shelf in order to estimate what proportion of the total phytoplankton production was eventually transferred up the food chain to whales and dolphins.

Results

Abundance and standing stock

Eighteen species of cetaceans were observed during the CETAP aerial line-transect surveys, and resulting estimates of abundance are given in Table 2. Those estimates tended to have large variances; with coefficients of variation ranging from 69% to 356% (median = 163%) (Kenney *et al.*, 1985). Minke whales were the most abundant of the baleen whales, with over 13 000 in the entire study area in the spring, followed in descending order by fin, sei, humpback and right whales. The most abundant odontocetes were harbor porpoises, with a peak population in spring of over 49 000. This was fol-

lowed by common dolphins and white-sided dolphins, both in excess of 40 000, and several other dolphin species with populations estimated at 11–16 000. The total cetacean population of the Northeast Shelf was over 210 000 animals. Sixteen species were most abundant during the spring and/or summer seasons; the two exceptions were common dolphins with peak abundance during the winter, and white-sided dolphins with peak abundance in the autumn.

Peak cetacean standing stock in the Northeast Shelf ecosystem was in the spring at over 320 000 tons, equivalent to a biomass density of 1 166 kg/km², followed by summer, autumn and winter

TABLE 2. Seasonal estimates of abundance for eighteen cetacean species for the USA Northeast Shelf, and in its four regions (see text for definitions).

Species	Season	Region				Northeast Shelf Total
		GOM	GBK	SNE	MAB	
Right whale	Winter	–	–	–	–	–
	Spring	233	128	32	–	393
	Summer	251	–	–	–	251
	Autumn	–	–	–	–	–
Fin whale	Winter	–	596	668	542	1 806
	Spring	1 793	1 381	794	1 066	5 034
	Summer	3 329	852	1 759	135	6 075
	Autumn	1 075	188	373	358	1 994
Sei whale	Winter	–	616	–	–	616
	Spring	174	1 982	–	–	2 156
	Summer	7	284	–	–	291
	Autumn	–	524	–	–	524
Minke whale	Winter	–	–	425	–	425
	Spring	3 129	6 800	3 361	193	13 483
	Summer	3 864	425	–	656	4 945
	Autumn	3 709	–	–	–	3 709
Humpback whale	Winter	–	–	–	–	–
	Spring	273	156	47	–	476
	Summer	663	40	–	–	703
	Autumn	47	273	–	–	320
Sperm whale	Winter	–	184	33	503	720
	Spring	–	164	290	1 187	1 641
	Summer	–	503	411	387	1 301
	Autumn	–	19	–	300	319
Bottlenose whale	Winter	–	–	–	–	–
	Spring	–	29	–	77	106
	Summer	–	–	–	–	–
	Autumn	–	–	–	–	–

TABLE 2. (Continued). Seasonal estimates of abundance for eighteen cetacean species for the USA Northeast Shelf, and in its four regions (see text for definitions).

Species	Season	Region				Northeast Shelf Total
		GOM	GBK	SNE	MAB	
Goose-beaked whale	Winter	–	–	–	–	–
	Spring	–	–	14	402	416
	Summer	–	–	218	43	261
	Autumn	–	–	–	–	–
Beaked whale	Winter	–	–	–	–	–
	Spring	–	533	111	121	765
	Summer	–	499	305	135	939
	Autumn	–	271	–	–	271
Pilot whale	Winter	–	974	955	304	2 233
	Spring	438	6 284	2 973	1 779	11 474
	Summer	–	4 890	893	3 056	8 839
	Autumn	225	543	2 516	6 527	9 811
Risso's Dolphin	Winter	–	–	28	777	805
	Spring	–	345	1 937	2 649	4 931
	Summer	–	1 872	6 794	3 168	11 834
	Autumn	–	3 089	12	2 725	5 826
Bottlenose Dolphin	Winter	–	1 511	827	774	3 112
	Spring	–	2 488	4 685	3 982	11 155
	Summer	–	3 670	3 497	4 902	12 069
	Autumn	–	573	333	4 809	5 715
White-sided Dolphin	Winter	7 353	4 957	37	–	12 347
	Spring	11 093	27 094	1 703	–	39 890
	Summer	27 029	10 987	–	–	38 016
	Autumn	25 474	16 545	4	–	42 023
Common Dolphin	Winter	1 052	10 775	22 714	10 562	45 103
	Spring	40	5 395	5 543	8 100	19 078
	Summer	198	633	1 411	1 959	4 201
	Autumn	–	16 182	12 473	2 010	30 665
Striped Dolphin	Winter	–	–	4 554	1 937	6 491
	Spring	–	1 482	2 571	7 972	12 025
	Summer	–	3 120	5 203	7 997	16 320
	Autumn	–	5 962	786	6 734	13 482
Spotted Dolphin	Winter	–	–	482	107	589
	Spring	–	–	901	1 074	1 975
	Summer	–	235	870	1 336	2 441
	Autumn	–	755	131	799	1 685
Spinner Dolphin	Winter	–	–	–	–	–
	Spring	–	–	–	302	302
	Summer	–	–	128	69	197
	Autumn	–	–	–	–	–
Harbor Porpoise	Winter	1 841	1 209	–	–	3 050
	Spring	29 481	17 391	2 548	–	49 420
	Summer	18 934	–	–	–	18 934
	Autumn	548	–	–	–	548

(Table 3). Two regions, GBK and MAB, had peak standing stocks during the spring, while the other two, GOM and SNE, had maxima during the summer. Both GOM and GBK showed very strong seasonal patterns, high during the warm part of the year and low during the colder seasons. The maximum regional cetacean standing stock was in GOM/spring at 148 072 tons or 2 055 kg/km². SNE and MAB exhibited maximum densities less than half the level of the two northern regions, and less variation between seasons.

In terms of the biomass of individual species within the Northeast Shelf study area (Table 4), fin whales were the dominant cetaceans in all seasons, representing 46–64% of the total standing stock (mean = 56.2%). Other species which comprised large proportions of the total cetacean standing stock in more than one season included minke whales, sperm whales, and sei whales. A total of six species comprised at least 5% of the total standing stock in at least one season, including only one small odontocete (Table 4).

TABLE 3. Standing stock (tons) and biomass densities (kg per km², in parentheses) of cetaceans in the USA Northeast Shelf ecosystem and in its four regions (see text for definitions).

Region	Season			
	Winter	Spring	Summer	Autumn
GOM	1 034 (14)	89 310 (1 239)	148 072 (2 055)	53 388 (741)
GBK	31 972 (463)	121 170 (1 756)	49 710 (720)	24 983 (362)
SNE	25 313 (365)	52 113 (751)	65 792 (948)	14 244 (205)
MAB	27 757 (409)	61 903 (912)	20 033 (295)	24 477 (361)
Northeast Shelf	86 076 (309)	324 496 (1 166)	283 787 (1 019)	117 092 (421)

TABLE 4. Dominant cetacean species of the USA Northeast Shelf and its component regions (see text for definitions); those comprising more than five percent of the cetacean standing stock.

Region	Season	Dominant Species (% of total standing stock)
GOM	Winter	White-sided dolphin (85.3), Harbor porpoise (8.0), Common dolphin (6.6)
	Spring	Fin whale (60.2), Minke whale (15.8), Right whale (10.4), Humpback whale (7.6)
	Summer	Fin whale (67.7), Minke whale (11.7), Humpback whale (11.2), Right whale (6.8)
	Autumn	Fin whale (60.4), Minke whale (31.3), White-sided dolphin (5.7)
GBK	Winter	Fin whale (55.9), Sei whale (25.0), Sperm whale (11.5)
	Spring	Fin whale (34.2), Minke whale (25.3), Sei whale (21.3)
	Summer	Fin whale (51.4), Sperm whale (20.2), Pilot whale (8.4), Sei whale (7.4)
	Autumn	Humpback whale (27.3), Sei whale (27.3), Fin whale (22.6), White-sided dolphin (7.9)
SNE	Winter	Fin whale (79.2), Minke whale (7.6), Common dolphin (5.8)
	Spring	Fin whale (45.7), Minke whale (29.0), Sperm whale (11.1)
	Summer	Fin whale (80.2), Sperm whale (12.5)
	Autumn	Fin whale (78.6), Pilot whale (15.0), Common dolphin (5.7)
MAB	Winter	Fin whale (58.6), Sperm whale (36.2)
	Spring	Fin whale (51.7), Sperm whale (38.4)
	Summer	Sperm whale (38.6), Fin whale (20.2), Minke whale (14.7), Pilot whale (13.0), Risso's dolphin (5.4)
	Autumn	Fin whale (43.9), Sperm whale (24.5), Pilot whale (22.7)
Northeast Shelf	Winter	Fin whale (63.0), Sperm whale (16.8), Sei whale (9.3)
	Spring	Fin whale (46.5), Minke whale (18.7), Sperm whale (10.1), Sei whale (8.6)
	Summer	Fin whale (64.3), Sperm whale (9.2), Minke whale (7.8), Humpback whale (6.2)
	Autumn	Fin whale (51.1), Minke whale (14.3), Pilot whale (7.1), Humpback whale (6.8), Sei whale (5.8), Sperm whale (5.4)

Fin whales were strongly dominant in nearly every individual region and season, in fact, in 13 of 16 instances (Table 4). The exceptions were GOM/winter, when white-sided dolphins were the dominant species, GBK/autumn when humpback and sei whales were co-dominant, and MAB/summer when sperm whales were dominant. Eleven of the eighteen species included in this study comprised at least 5% of the cetacean standing stock in at least one region/season.

Prey consumption

Over the course of a year, whales and dolphins consumed 1.87 million tons of prey within the Northeast Shelf system (Table 5). This total included approximately 1.3 million tons of finfish

(68.9% of the total), 337 000 tons of squid (18.0%), and 244 000 tons of zooplankton (13.0%). Consumption, like abundance, varied by region and season, and additionally by prey type. Fish were the dominant cetacean prey in nearly all regions and seasons, except for MAB in the summer and autumn, when squid was the prey consumed in the largest amount. Consumption of zooplankton by cetaceans was relatively low except in spring and summer in GOM and throughout the year in GBK. For the entire area, 40.7% of cetacean consumption was during the spring, followed by summer with 33.4%, autumn with 16.4%, and winter with 9.5%. Comparing regions, total consumption was substantially higher in the two northern areas. Cetacean consumption in GOM and GBK

TABLE 5. Estimated consumption of prey (tons) by cetaceans in four regions (see text for definitions) of the USA Northeast shelf.

Region	Season	Fish	Squid	Zooplankton	Total
GOM	Winter	5 808	767	0	6 575
	Spring	156 780	3 081	33 382	193 243
	Summer	265 988	2 771	39 534	308 293
	Autumn	118 249	3 001	8 428	129 678
	Total	546 825	9 620	81 344	637 789
GBK	Winter	35 077	10 627	17 694	63 398
	Spring	191 002	33 991	78 912	303 905
	Summer	65 013	40 981	13 318	119 312
	Autumn	40 485	14 475	16 969	81 929
	Total	331 577	100 074	126 893	558 544
SNE	Winter	42 658	7 760	3 275	53 693
	Spring	94 703	25 595	8 833	129 131
	Summer	93 998	34 300	9 611	137 909
	Autumn	24 406	9 909	2 038	36 353
	Total	255 765	77 564	23 757	357 086
MAB	Winter	30 774	20 280	2 468	53 522
	Spring	71 360	57 417	5 952	134 729
	Summer	24 761	32 950	1 170	58 881
	Autumn	27 718	39 580	1 956	69 254
	Total	154 613	150 227	11 546	316 386
Northeast Shelf	Winter	114 317	39 434	23 437	177 188
	Spring	513 845	120 084	127 079	761 008
	Summer	449 760	111 002	63 633	624 395
	Autumn	210 858	66 965	29 391	307 214
	Total	1 288 780	337 485	243 540	1 869 805

represented 34.1% and 29.9%, respectively, of the Northeast Shelf total, while only 19.1% of the total consumption occurred in SNE, and 16.9% in MAB.

Primary production required

Based on the estimates of prey consumed by cetaceans in our food chain model, the amounts of phytoplankton primary production channeled to cetaceans in each region were 59.23 g C per m² per yr in GOM, 51.86 in GBK, 39.02 in SNE, and 39.14 in MAB (the area-weighted mean was 47.46; SD = 8.68). Average annual phytoplankton production levels in the four regions reported by O'Reilly and Busch (1984) were: 290 g C per m² per yr in GOM, 379 in GBK, 301 in SNE, and 334 in MAB. The percentages of total annual primary production channeled to the cetaceans of the four Northeast Shelf regions were: 20.4% in GOM, 13.7% in GBK, 13.0% in SNE, and 11.7% in MAB (the mean was 14.8%; SD = 3.4).

Discussion

Abundance and standing stock

These results tended to be somewhat different than previous estimates based on the same survey data reported by CETAP (1982), Scott *et al.* (MS 1983), or Kenney *et al.* (1985). The differences can be accounted for by differences in the computation methods. For example, in the first two studies only the estimates for fin, humpback and right whales included a correction for diving, while Kenney *et al.* (1985) included no dive corrections. In none of the previous analyses were the unidentified sightings assigned to particular species. In all three of them the estimates for minke whales and harbor porpoises were seriously biased. We feel that including those factors has resulted in the best currently available estimates of abundance for the overall cetacean community. Unfortunately, there are no other comparable abundance estimates for the entire Northeast Shelf which might be useful for comparison or verification. The harbor porpoise surveys and other recent surveys by NMFS have covered only a relatively small subset of the CETAP study area and were limited to summer (Blaylock *et al.*, 1995), and although these data were useful for improving estimates of minke whales and harbor porpoises, the areas and seasons surveyed were too limited to provide critical comparisons for other species.

This study incorporated the estimated abundances from the unidentified sightings, into the

appropriate species based on proportions of identified sightings. It is likely that there were some errors in these assignments, but attempting to discriminate on any finer basis would have reduced the process to little more than "educated guessing" on each individual sighting. Not including the unidentified sightings at all would have introduced a much more significant bias.

Utilizing the minke whale and harbor porpoise data from the NMFS surveys to estimate an aerial survey bias factor has made our estimates of those two species much more realistic. The correction factors, 9.3 for harbor porpoise and 10.6 for minke whales, are similar to the value of 7.1 calculated from the estimate by Kraus *et al.* (1983), that aerial observers detected only 14% of porpoises seen by shore-based observers. The fact that the peak abundance estimate for harbor porpoise for the study area (49 420 in the spring) differs by less than 5% from the NMFS estimate of 47 200 for the population, indicates that the corrections resulted in realistic estimates. Including that change made both species, especially minke whales, much more significant components of the cetacean community than in the Scott *et al.* (MS 1983) analysis. It is possible that some errors would have been introduced here if there had been drastic distributional changes in either or both species between 1979–81 and 1991–92. For example, large differences between the 1991 and 1992 estimates of harbor porpoise in the NMFS study were believed to be due to distributional shifts in response to oceanographic conditions (Blaylock *et al.*, 1995).

By applying a dive correction to all large whale species, this study eliminated the serious bias in Scott *et al.* (MS 1983) introduced by correcting the estimates for only fin, humpback and right whales. Using the dive correction, however, may have biased the right whale estimates on to the high side. Kenney *et al.* (1995) suggested that using a correction based on diving data from individual right whales would produce overestimates, because right whales tend to occur in large aggregations, and because the aerial surveys typically circle right whale sightings for extended periods of time to obtain identification photographs of individuals. Therefore, when a single right whale is sighted, it increases the likelihood of detecting other right whales in the vicinity as they surface while the plane is circling. The estimate of right whales was 393 during the spring, but Knowlton *et al.* (1994) estimated the population at 295 as of the end of

1992. However, given the low numbers of right whales, the impact on the final consumption estimates would be relatively small, and it would only impact the zooplankton consumption estimates. Since humpback and fin whales are not individually identified from aerial photos and therefore not routinely circled, this bias is much less likely for those species. It is likely that correction factors estimated directly for long-diving species such as sperm whales and beaked whales might be markedly higher than the fin whale factor which was applied, however we lack data to justify using any other value. For most of the smaller toothed whales, there is probably little bias introduced by not using any dive correction factor. These species dive for shorter times than large whales and often occur in moderate to large herds, which are visually conspicuous at relatively long distances to aerial observers. The dive correction factors for these species, if at all necessary, would be substantially smaller than the smallest large whale factor.

Prey consumption

Whales, dolphins and porpoises of the Northeast Shelf annually consume about 1.28 million tons of fish, 337 000 tons of squid and 244 000 tons of zooplankton, for a total of 1.87 million tons. These estimates are substantially higher than those of Kenney *et al.* (1985) (276 000 tons fish, 244 000 tons squid, 45 000 tons zooplankton, and a total of 555 000 tons). That study did not include dive correction factors for any species or scale for active metabolism. The results of the present study are similar to, but more reliable than, the total consumption estimates by Scott *et al.* (MS 1983) (1.25 million tons fish, 318 000 tons squid, 174 000 tons zooplankton, and 1.74 million tons total), who used dive correction factors only for fin, humpback and right whales, used many higher body weights based on the limited data available at the time, used under-estimates of minke whale and harbor porpoise abundance, and assumed each species to be exclusively piscivorous, teuthivorous or planktivorous in the absence of better information.

Sissenwine (1986) estimated that cetaceans consumed 5.4 tons per km² of fish and squid on Georges Bank, using the Scott *et al.* (MS 1983) results as input data. Our results show total fish and squid consumption on Georges Bank as 432 000 tons, or 6.3 tons per km². The difference may be primarily due to the larger, corrected abundances of minke whales and harbor porpoises and the use

of a dive correction factor for sperm whales in our estimates. Overholtz *et al.* (1991) estimated that marine mammals consumed a total of 120 000 tons of fish annually from the Northeast Shelf, which is less than 10% of our estimated fish consumption. However, their estimate was based on a computer model including nine cetacean species and harbor seals feeding on four species of pelagic fishes (herring, mackerel, sand lance and silver hake). Their objective was not to realistically model cetacean predation, but to explore the impacts of different management schemes on pelagic fish populations.

How does cetacean predation on living resources of the Northeast Shelf compare to commercial fishery harvests? There is no relevant comparison for zooplankton which are not harvested by commercial fisheries. However, for fish and squid the cetacean predation was larger than commercial fishery harvests. Sherman *et al.* (1988) reported that total annual fish and squid landings from the Northeast Shelf ecosystem averaged 900 000 tons between 1969 and 1978 with a peak catch of 1.2 million tons in 1974, and recorded an average 470 000 tons per yr from 1979 on with an estimated maximum sustainable yield of 950 000 tons. Our estimate for total fish and squid consumption by cetaceans, 1.63 million tons, was larger than all of those landings totals by 1.4 times the 1974 peak landings, 1.7 times the estimated maximum sustainable yield, 1.8 times the 1969–78 average, and 3.5 times the post-1979 average. For comparison, Sissenwine (1986) estimated that cetacean consumption on Georges Bank was 88.5% of the fishery catch. For squid alone, NMFS (1994) reported total Atlantic coast squid landings of 32 000 tons in 1990, 39 000 tons in 1991, 45 000 tons in 1992, and 51 000 tons in 1993. Our estimated cetacean consumption of squid was 6.6 times the 1993 harvest.

There are other marine ecosystems where cetacean consumption (or consumption by all marine mammals) has been estimated to be extremely large or to approach or exceed fishery harvests. Laevastu and Larkins (1981) estimated marine mammal predation in the Bering Sea to remove 2.66 million tons of fish, 2.98 million tons of squid, and 2.01 million tons of zooplankton. Laws (1977) estimated very large predation rates by Southern Ocean marine mammals for both prior to 20th Century industrial whaling (190 million tons krill, 12 million tons squid, 4 million tons fish) and after depletion of whale stocks (43 million tons krill, 5 million tons

squid, 1 million ton fish). Both the Bering Sea and Southern are much larger in geographic extent than the Northeast Shelf, accounting for the substantially larger cetacean consumption totals. Bax (1991) summarized several studies comparing relative proportions of total fish consumption by marine mammals and commercial fisheries in six marine ecosystems including Georges Bank (using data from Sissenwine, 1986). The data presented show marine mammal consumption was estimated to be 167% of fishery harvests in the Barents Sea, 163% in the Benguela Current system, 107% in the eastern Bering Sea, 89% in Georges Bank, 2% in the North Sea and 0% in Balsfjorden. Our estimate that cetaceans consumed 346% of the average post-1979 fishery catches from the Northeast Shelf exceeds all of these, however, it is recognized that these recent fisheries are substantially depleted. Expressed as 171% of the estimated MSY, it seems to fit well with the data from the Barents Sea and Benguela Current systems. In another comparison, the predation by minke whales alone in the Northeastern Atlantic has been estimated by two different methods to exceed 1 million tons, and to equal or exceed commercial harvests of some fish stocks (Markussen *et al.*, 1992; Nordøy *et al.*, 1995).

Our consumption estimates were conservative, consistently using lower values in the computations when there was any question or choice (as in the selection of factors of 2.5 to scale from basal to active metabolism and 1.2 to correct mysticete feeding rates for migratory fasting). In comparison, a three-month migratory fast yielded a correction of 1.33 and a four-month fast yielded 1.5. Lockyer (1986) estimated that North Atlantic fin whales consumed 90% of their annual total within a five-month period, which resulted in a multiplicative factor of 2.16 during the peak feeding period.

The metabolic models used here scale for activity, but not for growth and reproduction. Reproduction, particularly lactation, is a major energy cost for cetaceans. Yasui and Gaskin (1986) estimated in the harbor porpoise that the additional cost of pregnancy and lactation represented 38–42% of total requirement for maintenance and activity, while Lockyer (1978, 1981a, b, 1986) has estimated the additional cost of reproduction in large baleen whales to be 20–25% of their usual metabolic requirements. Bernard and Hohn (1989) have also shown that the differential costs of pregnancy and lactation in spotted dolphins led to different feed-

ing strategies in pregnant *versus* lactating females; lactating females tended to have fuller stomachs which contained significantly higher proportions of flying fish (higher energy density) than squid. These data demonstrate that any increase in consumption estimates to account for reproduction would only need to consider reproductively active females, the factors would be substantially lower than the percentages given above, and so are not likely to have a serious bias in our estimates.

Primary production required

When estimates of prey consumption by cetaceans in the trophic model of this study are used it suggests that cetaceans require 14.8% of the total phytoplankton primary production. This is lower than the 24.9% average primary production required (PPR) estimated by Scott *et al.* (MS 1983) from slightly smaller estimates of total prey consumption. The regional patterns reported by Scott *et al.* (MS 1983) were also different (GOM – 15.4%, GBK – 25.5%, SNE – 31.0%, MAB – 27.8%). These differences can be accounted for by different trophic level (TL) values for squid in the food chain models. We used TL = 3.2 for squid, rather than the 4.0 value used by Scott *et al.* (MS 1983), and it had the effect of reducing the PPR for teuthivores (squid consumers) by 84%. Teuthivorous cetaceans occur primarily along the shelf break (CETAP, 1982; Hain *et al.*, 1985; Kenney and Winn, 1986), and there is no shelf break in the Gulf of Maine region, which explains why our estimate of PPR for GOM was the highest regional value, while it was the lowest value in the Scott *et al.* (MS 1983) estimates. On the other hand, a value similar to our 14.8% mean was reported by Huntley *et al.* (1991), and they estimated that an average of 12% (maximum 22.5%) of carbon fixed by phytoplankton was recycled to the atmosphere by the breathing activities of marine mammals and seabirds. In different geographic areas, Pauly and Christenson (1995) estimated the mean PPR for fishery harvests in non-tropical continental shelf systems at 35.3%. Our estimated mean PPR is less than half of their value, even though cetacean predation may be more than three times the fishery catches in the Northeast Shelf. At first glance, it seems that something must be in error. However, closer scrutiny of energetics suggests the difference could be due to differences in mean trophic level between cetacean prey and commercial harvests. Pauly and Christenson (1995) estimated a mean TL value of 3.5 for non-tropical shelf fisheries. Our mean TL, weighted for amount of

consumption of each prey type was 2.85. The PPR for equal harvests of TL = 3.5 stocks *versus* TL = 2.85 stocks is greater by a factor of 4.47 ($10^{2.5}/10^{1.85}$). In short, cetacean predation has a lesser impact on primary production than commercial fishery harvests because commercial fishers "feed" higher on the food chain than whales and dolphins.

Our trophic model is conservative because of the TL values we have used, though this affects only the PPR estimates, not the consumption estimates. The zooplankton eaten by fin, humpback, and minke whales, as well as some proportion of that eaten by sei and right whales, are comprised of euphausiids rather than copepods. Krill would have TL = 2.2 rather than 2.0 (Pauly and Christensen, 1995). In addition, some proportion of fishes consumed by cetaceans are probably at least partly piscivorous rather than entirely planktivorous. Pauly and Christensen's (1995) estimates of TL values for possible cetacean prey include mackerel (TL = 3.3–3.4), mullet (TL = 3.8), gadids (TL = 3.8), and jacks (TL = 3.8).

Conclusions

The results clearly show that whales, dolphins and porpoises are significant predators in the Northeast Shelf ecosystem. Their annual consumption of fishery resources may represent an amount from approximately one-third to more than three times greater than the annual harvests by fisheries from the same system taking into account the variations in catches over the last 2–3 decades. It is recognized these are estimates, however, such results are unlikely to be better than an approximation. These particularly relate to the obvious methodological difficulties of taking weights or metabolic rates of animals weighing many tons or developing precise estimates of abundance for cetaceans in areas as big as the Northeast Shelf. In addition, these animals are legally protected and cannot be sampled like fishes. Very few species have had long-term intensive studies, e.g. right whales (Knowlton *et al.*, 1994) and bottlenose dolphins (Scott *et al.*, 1990), which produced reliable information on parameters such as age structure, age at maturity, reproductive rates, and population growth rates.

A complicating factor in quantifying cetacean consumption is that many species may have changed in abundance since the 1979–81 CETAP surveys. The only species of the Northeast Shelf for which published trend data are available is the right whale.

Their population estimates show slow increasing rates at 2.5% (Knowlton *et al.*, 1994) and 3.8% (Kenney *et al.*, 1995), despite significant levels of anthropogenic mortality from ship strikes and fishing gear entanglements (Kraus, 1990; Kenney and Kraus, 1993) and suspected reproductive anomalies (Knowlton *et al.*, 1994). For most of the other cetacean species the known anthropogenic mortality is not thought to be high enough to deplete populations (Blaylock *et al.*, 1995), therefore it might be expected that many populations could be increasing. If 5% annual increase rates are assumed, populations would have more than doubled since 1979–81. However, there are very little data on limiting factors on cetacean populations to justify any annual rate of increase. Since they are apex predators, at some point their populations would be limited by food resources, through intra- and inter-specific competition (Hairston *et al.*, 1960; Hairston and Hairston, 1993).

Resource limitation of cetacean predators implies interspecific competition with other predators on the same resource(s). The other predators include the commercial fishing industry. This suggests that either cetaceans and fisheries presently compete, or will compete when cetacean populations grow large enough. Direct competition between cetaceans and fisheries is probably low, as cetaceans tend to prey on different species and/or age-classes and consume, on average, at a lower level on the food web. In the Northeast Shelf, there are no fisheries for copepods or euphausiids, and many of the squid species selected by cetaceans are similarly not harvested. At least some of the fish species eaten by cetaceans, however, may be important commercially, in particular herring and mackerel. So there may be competition between cetaceans and fisheries for these species, especially if cetaceans are selective in their predation. Sissenwine *et al.* (1984b) suggested that predation by cetaceans, especially fin whales, on Georges Bank herring stocks may have had a compensatory effect on the herring and significantly delayed herring recovery from depletion by overfishing. The model developed by Overholtz *et al.* (1991) showed that the type of feeding response by predators can significantly affect the population dynamics of prey fish populations. The level of competition between cetaceans and fisheries can also change with natural or anthropogenic shifts in fish stocks. Since the 1960s, there have been several shifts in dominance in Northeast Shelf pelagic fish stocks between herring (and mackerel) and sand lance (Sherman *et al.*, 1981,

1988; Sherman, 1986; Sissenwine, 1986; Fogarty *et al.*, 1991). Cetacean predation on small pelagic fishes has also shifted in parallel, with concomitant changes in cetacean distribution patterns (Payne *et al.*, 1986, 1990; Schilling *et al.*, 1992; Kenney *et al.*, 1996). Cetacean predation on sand lance would represent a lower level of direct competition with fisheries than feeding on herring, since there is no significant fishery for sand lance in the Northeast Shelf ecosystem.

The effects of cetaceans on fisheries, or of fisheries on cetaceans, are not straightforward or easily predictable (Katona and Whitehead, 1988). Given the multiplicity of predator-prey linkages in the Northeast Shelf food web, the effects, both direct and indirect, of cetacean apex predation on important commercial fishery stocks are extremely complex. Reliable prediction of these effects on fisheries, if possible at all, will be extremely difficult and will require sophisticated multi-species models (May *et al.*, 1979). The same is true for the other direction – effects of fisheries on cetacean populations. These can also be both indirect and significant. For example, an inshore shift in humpback whales in Newfoundland following the crash of offshore capelin stocks led to an increase in humpback entanglements and mortalities in inshore cod traps (Lien *et al.*, 1979; Perkins and Beamish, 1979; Whitehead and Carscadden, 1985; Lien, 1994). Kenney *et al.* (1996) suggested a similar shift in Gulf of Maine harbor porpoise following collapse of the Georges Bank herring stock may have increased entanglements in the sink gillnet fishery. Unraveling all of the inter-connecting linkages and fully understanding these sorts of effects will require a great deal of research effort.

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