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Estimates of Prey Consumption and Trophic Impacts of Cetaceans in the U.S. Northeast Continental Shelf Ecosystem

by

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ABSTRACT

Whales, dolphins, and porpoises are significant consumers of prey resources in the U.S. Northeast Shelf marine ecosystem — to a far greater extent than was realized only one or 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 - Gulf of Maine, Georges Bank, Southern New England, and Mid-Atlantic Bight. Estimates were based on seasonal cetacean abundances; standard mammalian metabolic models scaled as appropriate for assimilation, activity, and migratory fasting; and estimates of mean body mass and proportion of the diet comprised of each of the three main prey types. Cetaceans of the Northeast Shelf consume nearly 1.3 million metric tons annually, including 846,000 tons of fish, 280,000 tons of squid, and 166,000 tons of zooplankton. Their predation on fish and squid exceeds harvests by the commercial fishing industry within the same area. Consumption of fish dominates in most regions and seasons, primarily because of the widespread distribution and high relative abundance of large, piscivorous fin whales, and secondarily due to humpback and minke whales and some of the smaller odontocetes. Zooplankton consumption, principally by right and sei whales and secondarily by other mysticetes, is significant in some seasons in the Gulf of Maine and Georges Bank regions. An assemblage which includes a variety of teuthivorous odontocete species inhabiting the shelf break vicinity consumes 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, our estimates imply that a significant fraction of the total net primary production, ranging from 8.6% in the Mid-Atlantic Bight to 13.3% in the Gulf of Maine, is required to support cetacean apex predation.

INTRODUCTION

The ecological roles played by cetaceans in the trophic dynamics of marine ecosystems have until recently been relatively poorly known. 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.*, 1984*a*). 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 1979-1982, 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, on 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 (LMEs) around the world (Sherman and Alexander, 1986, 1989; Sherman *et al.*, 1990, 1991, 1993, in press). The marine environment of the Northeast Shelf is both physically and biological heterogeneous (Sherman *et al.*, 1988; in press). The area ranges 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; *i.e.* 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) — and they therefore feed at different levels of marine food chains. 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 (including krill).

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, so predation by cetaceans is one factor which should be considered in multi-species fishery management models. Scott *et al.* (MS 1983) was our preliminary attempt to estimate prey consumption by the cetaceans of the

Northeast Shelf. Since then, a number of improvements in the data on which the consumption estimates were based have been made available:

- Many of the body weights used in our 1983 analysis were probably significant overestimates, having been based on a few references with small sample sizes from a whaling industry that preferentially took the largest available individuals or from captive animals. Kenney *et al.* (1985) included an extensive review of the literature on body weights of the cetacean species found in the Northeast Shelf system, providing better estimates based on all of the available data.

- There was for a long time a degree of uncertainty concerning metabolic rates of marine mammals. The metabolic rates of terrestrial mammals had been widely studied, with basal metabolic rate predictable as a function of body weight according to widely accepted models developed by Kleiber (1975) and extended by Brody (1968). Early work by Laurence Irving and Per Scholander (Irving *et al.*, 1935, 1941; Scholander, 1940; Scholander *et al.*, 1942) suggested that marine mammals had higher basal metabolic rates than predicted by the Kleiber/Brody model. This view, which seemed to be supported by feeding rates of captive animals (Sergeant, 1969), was prevalent until recently (*e.g.* Kanwisher and Sundnes, 1966; Ridgway, 1972; Kanwisher and Ridgway, 1983). Our 1983 analysis used a metabolic model from Lockyer (1981*a*) for "near-basal" metabolism which resulted in estimates approximately 25-30% higher than the Kleiber/Brody prediction, and estimated total consumption using Sergeant's (1969) method of 4-5% of body weight per day, which yielded values nearly double the "near-basal" consumption estimates and which were almost certainly too large. Since then, an extensive body of research has accumulated supporting the conclusion that cetaceans do not differ significantly from "average" or "typical" mammals in their basal metabolic rates (Brodie, 1975*a,b*; Gaskin, 1978, 1982; Lavigne *et al.*, 1986*a,b*; Innes *et al.*, 1986, 1987; Huntley *et al.* 1987). This has enabled us to use the Kleiber/Brody standard mammalian metabolic models with confidence in their accuracy.

- Our 1983 analysis, because of a lack of sufficient data, assumed that each cetacean species fed only on one of the principal prey types, *i.e.* was exclusively piscivorous, teuthivorous, or planktivorous. The literature review by Kenney *et al.* (1985) included all available information on stomach contents and prey species and summarized estimates of the proportion of each species' diet comprised of each prey type.

- For some species, notably harbor porpoise and minke whale, subsequent research has provided more reliable estimates of their abundance.

- Our 1983 analysis used a food chain model that assumed a value of 10% for trophic transfer efficiency (Lindemann, 1942; Odum, 1968). We drew a number of criticisms for that assumption. Pauly and Christensen (1995) reanalyzed a large number of studies of different marine food chains, and directly estimated trophic efficiencies. Their results indicate that the 10% figure is a valid approximation for marine ecosystems. They also provided specific data on the trophic levels of various species of fish, squid, and crustaceans which we could use in constructing a more precise trophic model.

Kenney *et al.* (1985) also calculated estimation prey consumption rates for Northeast Shelf cetaceans. Those estimates accounted only for resting metabolism, with no scaling for activity, growth, or reproduction. There were also no corrections for any species for animals not seen because of diving behavior, nor for increased feeding to compensate for migratory fasting. Finally, the same biased CETAP survey data were used to estimate the abundance of harbor porpoises and minke whales.

This paper is an attempt to refine the models and analyses of Scott *et al.* (MS 1983) and Kenney *et al.* (1985) based on more reliable input data and realistic assumptions. The resulting data can then serve as a more accurate source of information useful for future analyses of the Northeast Shelf marine ecosystem. The central conclusion of our original model, that whales and dolphins are significant consumers of prey resources in the Northeast Shelf ecosystem, stands unchanged. Cetacean predation exceeds commercial fishery harvests of fish and squid, and requires a tenth or more of the total annual primary production. Predation by whales, dolphins, and porpoises is a factor which must be considered in Northeast Shelf multi-species fishery management models.

METHODS

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 U.S. jurisdiction in the Gulf of Maine (Fig. 1). The study area was partitioned into a number of aerial survey blocks which could be completed in one day's flying, which were further stratified by depth at the 20- and 50-fathom (37- and 91-m) isobaths. For this paper, we divided the study area into four regions by combining the most appropriate sets of the CETAP aerial survey blocks. These regions are very approximately those 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 and Jones, MS 1980; 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 km^2 (25.4%), GBK — 69,004 (24.8%), SNE — 69,410 (24.9%), and MAB — 67,891 (24.4%). The CETAP program, sampling design, and survey design are described in detail in Scott and Gilbert (1982), CETAP (1982), Kenney (1990), and Shoop and Kenney (1992).

Abundance Estimates:

A principal objective of the CETAP study was to estimate the abundance of each species occurring within the study area, based on aerial line-transect surveys (Burnham *et al.*, 1980; Scott and Gilbert, 1982). Each aerial survey of any block generated estimates of the density of each species within the block. Scott *et al.* (MS 1983) computed an area-weighted seasonal mean of all single-day block density estimates within a region and season. The original density data used in those calculations are no longer easily available. Kenney *et al.* (1985) recalculated a single seasonal abundance estimate for each species in each survey block (the small areas shown by dashed lines in Fig. 1), including all lines flown in all three years as replicate samples. For this paper, we summed the seasonal block estimates from Kenney *et al.* (1985) for each species within 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). (A few other species were sighted beyond the study area and/or from other survey efforts. As these did not have abundance estimates within any of the four Northeast Shelf regions, they have not been included here.) Many sightings, however, could not be positively identified to species. Three categories — beaked whale, pilot whale, and spotted dolphin — included two or more species within one genus which are impossible to differentiate from aerial surveys. (To avoid awkward descriptive terminology, references in this paper to "species" should be understood as including these three multi-species categories.) There were also a number of other categories of unidentified sightings, from as broad as "unidentified large whale" or "unidentified dolphin or porpoise" to narrower categories such as "fin or sei whale," "unidentified long-beaked dolphin," or "unidentified *Stenella*." In some cases those categories represented significant numbers of animals, *e.g.* the estimated abundance of unidentified *Stenella* within a region was almost always higher than the abundances for identified striped, spotted, and spinner dolphins. The estimated number of individuals in any unidentified category were distributed among the identified species based on the probabilities of occurrence of each species from the relative proportions of abundances in the identified categories within that region and season. These probabilities were sometimes adjusted slightly to account for species likely to occur in that region and season based on the total sighting plots (including more than the line-transect aerial survey data) in CETAP (1982), but which may not have been sighted by one of the aerial surveys.

For two species, it is very likely that the CETAP abundance estimates were extremely unrealistic. Both minke whales and harbor porpoise tend to be solitary and inconspicuous, so aerial surveys significantly undersample them and underestimate their abundance. For example, Kraus *et al.* (1983) reported that aerial observers detected only 14% of the harbor porpoises sighted by shore-based observers, and Barlow *et al.* (1988) showed that sightability of harbor porpoises is particularly sensitive to environmental conditions (sea state and cloud cover). However, for both species there have been more recent estimates for a portion of the study area from shipboard line-transect surveys for harbor porpoise conducted by the National Marine Fisheries Service (Blaylock *et al.*, in press; Palka, in press). A weighted-average estimate of abundance of harbor porpoise in the northern GOM and lower Bay of Fundy for summer 1991 and 1992 was 47,200 (Smith *et al.*, 1993; Palka, in press). That estimate is 23.2 times the summed GOM/summer estimate from our data. Similarly, the same 1991-92 harbor porpoise surveys resulted in an estimate of 2650 minke whales, 26.5 times the 100 estimated for GOM/summer from our data. Since the NMFS 1991-92 surveys included significant portions of the lower Bay of Fundy and Nova Scotian coastal waters that were not included in the CETAP surveys, a factor of 12 (approximately half) was selected to scale up our estimates in each region and season to more realistic values. In support of the validity of this approach, our estimated total spring abundance of harbor porpoise is 63,768, which is 94.5% of the 1992 NMFS estimate of 67,500 for the northern GOM (Smith *et al.*, 1993; Palka, in press).

Dive Time Corrections:

For species which spend a large proportion of their time submerged for extended periods, surveys from fast-moving aircraft necessarily miss many individuals or groups while they are submerged. It is possible to scale up abundance estimates to correct for diving if one has quantitative data on the relative proportions of time spent at the surface and submerged. Correction factors were developed during CETAP for fin, humpback, and right whales; these factors were 4.846, 3.645, and 2.997, respectively (CETAP, 1982). These factors were included for these three species in our preliminary analysis (Scott *et al.*, MS 1983). There are two potential problems. One is that using dive corrections for only three species can significantly bias the results by artificially weighting the effects of those species. The second is that there has been some concern that the correction factors are too large, possibly because they are based largely on data from single individuals, while the animals tend to be aggregated (*e.g.* Hain *et al.*, 1992; Kenney *et al.*, 1995). The proportion of time that at least one animal is visible at the surface should increase with size of aggregation.

Knowlton *et al.* (1994), using photoidentification of individual animals, independently estimated the abundance of right whales at the end of 1992 to be 295, with an average rate of increase of 2.5% per year since 1986. The uncorrected total spring abundance of right whales from our data (from surveys in 1979-1981) was 132 (78 GOM, 43 GBK, 11 SNE), which increases to 396 using the 2.997 dive correction. Back-calculating from the Knowlton *et al.* (1994) data, one might expect 200-230 right whales around 1979-1981. The dive correction factor for right whales was therefore reduced to 1.798, 60% of its original value, and the fin and humpback factors reduced identically to 60% to remain consistent (2.908 and 2.187, respectively). All other large whale abundances were then also scaled for diving to minimize bias. The fin whale factor was applied to sei whales, sperm whales, and all of the beaked whales, while minke whale abundances were corrected using the right whale factor (the smallest of the three). Lacking any data for the smaller 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; see 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):

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

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

Prey Consumption Rate:

BMR was converted to consumption rate (kcal/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; 1981*a*,*b*), resulting in a factor of 1.25x.

- Active metabolism in cetaceans has been estimated at approximately 2 to 5 times BMR (Hinga, 1979; Lockyer, 1981*b*; Kenney *et al.*, 1986). We chose to use a value of 2.5x, near the bottom of that range, 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; Brody, 1975*a*; Matthews, 1978; Lockyer, 1981*b*; Evans, 1987). If the winter fast is six months, they must double their energy intake during the other six months. A four-month fast requires increasing feeding by a factor of 1.5x, a three-month fast, 1.33x. We have used a factor of 1.5x previously (Scott *et al.*, MS 1983; Kenney *et al.*, 1986). Since for most species, however, we still have very little information on their distribution or behavior during the winter, we have chosen to use a relatively low value here, 1.2x. This factor was applied only to the baleen whales, and only during spring, summer, and fall.

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 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 foreign and joint-venture midwater mackerel fishery, including samples of pilot whale stomachs containing mackerel (Waring *et al.*, 1990; Overholtz and Waring, 1991; Fairfield *et al.*, 1993). Pilot whales taken in the Faroe Islands drive fishery also have significant quantities of fish in their stomachs (Desportes and Mouritsen, 1993). The energy content of fish and zooplankton was assumed to be 1 kcal/gm wet weight (Clark and Prince, 1980; Sissenwine *et al.*, 1984), while the energy content of squid was assumed to be 0.83 kcal/gm (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 estimated using a simplified model food chain with five trophic levels (Fig. 2). The transfer efficiency from one trophic level to the next was assumed to be 10%, following Pauly and Christensen (1995), *i.e.* 1 kcal consumed by a piscivorous cetacean requires 10 kcal of zooplankton consumed by fish, and 100 kcal of phytoplankton production consumed by zooplankton. The general relationship is that the total amount of primary production required is calculated from prey consumption rate using a factor of 10^n, where n is the number of trophic steps from the phytoplankton to the given prey type, or trophic level - 1. We used the trophic level (TL) values reported by Pauly and Christensen (1995) for non-tropical continental shelf systems: 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. The food chain as shown in Figure 2 implies TL=4.0 for squid, as was used in Scott *et al.* (MS 1983), however we have opted to use the lower value to be conservative. Primary production required was converted from energy to carbon by 13.3 kcal/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 is 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, with resulting estimates of abundance (Table 2). Minke whales were the most abundant of the baleen whales, with over 7,500 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 almost 64,000. This was followed by common dolphins and white-sided dolphins, both in excess of 40,000, and several dolphin species with populations estimated at 11-12,000. The total cetacean population of the Northeast Shelf is over 220,000 animals.

Peak cetacean standing stock in the Northeast Shelf ecosystem was in the spring — over 200,000 metric tons, equivalent to a biomass density of 755 kg/km^2 — followed by summer, fall, and winter (Table 3). Two regions, GBK and MAB, also had peak standing stocks during the spring, while the other two, GOM and SNE, had maxima during the summer. Standing stocks and biomass densities varied between regions, and differed strongly between seasons (Fig. 3). Both GOM and GBK showed a very strong seasonal signal, high during the warm part of the year and low during the colder seasons. The maximum regional cetacean standing stock/biomass density was in GOM/spring — 90,027 tons or 1249 kg/km^2. SNE and MAB exhibited maximum densities about 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, fin whales were the dominant cetacean species in all seasons, representing 43 - 61% of the total standing stock (mean = 52.1%). 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, and a total of eight species comprised at least 5% of the total standing stock in at least one season:

- Winter: fin whale—57.8%, sperm whale—15.4%, sei whale—11.4%, common dolphin—5.2%.
- Spring: fin whale—43.7%, minke whale—16.4%, sei whale—10.8%, sperm whale—9.5%.
- Summer: fin whale—61.3%, sperm whale—8.8%, minke whale—7.0%, humpback whale—5.9%.
- Fall: fin whale—45.7%, minke whale—11.9%, pilot whale—10.6%, sei whale—6.9%, white-sided dolphin—6.4%, humpback whale—6.1%.

Fin whales similarly were strongly dominant in nearly every individual region and season, in fact, in 13 of 16 instances. The exceptions were GOM/winter, when white-sided dolphins were the dominant species, GBK/fall with sei whales dominant, and MAB/summer with sperm whales dominant. Twelve of the eighteen species which were included in this study comprised at least 5% of the cetacean standing stock in at least one region/season:

- GOM/Winter: white-sided dolphin—83.4%, harbor porpoise—10.1%, common dolphin—6.5%.
- GOM/Spring: fin whale—58.6%, minke whale—14.3%, right whale—10.2%, humpback whale—7.4%.
- GOM/Summer: fin whale—66.5%, humpback whale—11.1%, minke whale—10.8%, right whale—6.7%.
- GOM/Fall: fin whale—59.3%, minke whale—28.5%, white-sided dolphin—9.4%.
- GBK/Winter: fin whale—49.3%, sei whale—29.4%, sperm whale—10.1%.
- GBK/Spring: fin whale—30.7%, sei whale—25.4%, minke whale—21.1%, pilot whale—6.6%.
- GBK/Summer: fin whale—46.1%, sperm whale—18.2%, pilot whale—12.5%, sei whale—8.8%.

- GBK/Fall: sei whale—29.6%, humpback whale—22.4%, fin whale—18.5%, white-sided dolphin—10.8%, common dolphin—5.7%, Risso's dolphin—5.7%.
- SNE/Winter: fin whale—74.3%, common dolphin—9.1%, minke whale—6.6%, pilot whale—5.0%.
- SNE/Spring: fin whale—43.9%, minke whale—25.9%, sperm whale—10.7%, pilot whale—7.8%.
- SNE/Summer: fin whale—77.0%, sperm whale—12.0%, Risso's dolphin—5.6%.
- SNE/Fall: fin whale—68.7%, pilot whale—21.9%, common dolphin—8.3%.
- MAB/Winter: fin whale—66.6%, sperm whale—35.1%.
- MAB/Spring: fin whale—49.5%, sperm whale—36.8%.
- MAB/Summer: sperm whale—33.4%, pilot whale—18.7%, fin whale—17.5%, minke whale—11.8%, Risso's dolphin—7.7%, bottlenose dolphin—5.3%.
- MAB/Fall: fin whale—36.3%, pilot whale—31.2%, sperm whale—20.2%, Risso's dolphin—5.2%.

Prey Consumption:

Over the course of a year, whales and dolphins consume 1.29 million metric tons of prey within the Northeast Shelf system (Table 4). This total includes approximately 846,000 tons of finfish (65.5% of the total), 280,000 tons (21.7%) of squid, and 166,000 tons (12.8%) of zooplankton. Consumption, like abundance, varies by region and season, and additionally by prey type. Fish are the dominant cetacean prey in nearly all regions and seasons, except for MAB in the summer and fall, when squid is the prey consumed in the largest amount. Consumption of zooplankton by cetaceans is relatively low except in spring and summer in GOM and throughout the year in GBK. For the entire area, 40.0% of cetacean consumption was during the spring, followed by summer with 32.5%, fall with 17.6%, and winter with 9.9%. Comparing total consumption between regions, rates are substantially higher in the two northern areas. Cetacean consumption in GOM and GBK each represented nearly identical proportions of the Northeast Shelf total (31.9% and 31.5%, respectively), while only 19.0% of the total consumption occurred in SNE, and 17.7% in MAB.

Primary Production Required:

Going from the amount of prey consumed by cetaceans to the total phytoplankton production required to support that consumption through the food chain model, the amounts of primary production channeled to cetaceans in each region were 38.70 gm C/m^2/yr in GOM, 37.92 in GBK, 27.42 in SNE, and 28.67 in MAB (weighted mean = 33.25). Average annual phytoplankton production levels in the four regions reported by O'Reilly and Busch (1984) were: GOM — 290 gm C/m^2/yr, GBK — 379, SNE — 301, and MAB — 334 (averages were computed as means of the sub-region data weighted by areas of the sub-regions). The percentages of total annual primary production channeled to the cetaceans of the four Northeast Shelf regions were: GOM — 13.3%, GBK — 10.0%, SNE — 9.1%, and MAB — 8.6% (weighted mean = 10.3%).

DISCUSSION

Abundance and Standing Stock:

Over 220,000 whales, dolphins, and porpoises inhabit the Northeast Shelf. The most abundant species are small odontocetes, while the most dominant in terms of standing stocks are the baleen whales, especially the fin whale. All but two species were most abundant during the spring and/or summer seasons. The exceptions were common dolphins with peak abundance during the winter, and white-sided dolphins with peak abundance in the fall.

Our results tended to be somewhat different than the abundance estimates reported in CETAP (1982) or the abundance and standing stock estimates reported in Scott *et al.* (MS 1983) or Kenney *et al.* (1985). For example, our standing stock estimates averaged 24% higher than those in Scott *et al.* (MS 1983) and 125% higher than those in Kenney *et al.* (1985). The differences can be accounted for by differences in the computation methods: the averaging method, whether or not dive correction factors were included for particular species, the magnitudes of the dive correction factors, the inclusion of the unidentified categories, the use of NMFS data for minke whales and harbor porpoises, and the values used for body weights. There are no other comparable abundance estimates for the Northeast Shelf which might be useful for comparison. The NMFS harbor porpoise surveys covered only a relatively small subset of the CETAP study area (NMFS, 1994*b*; Blaylock *et al.*, in press). Though we found their data useful for improving estimates of two species, for the other species the area surveyed was too small to provide critical comparisons.

We feel that the estimates of cetacean abundance we have presented here, though perhaps not strictly rigorous in statistical terms, are the best currently available for the entire cetacean community in its entirety, given the existing data and considering all of the variables and factors which we have included:

- We have included estimated abundances from the unidentified sightings into the appropriate species based on probabilities of occurrence. It is likely that there are 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 abundances from the NMFS surveys has made our estimates for those two species much more realistic. Instituting that change made both species, but 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 were introduced here if there have been drastic distribution changes in either or both species between 1979-1981 and 1991-1992. For example, the large differences between the 1991 and 1992 NMFS harbor porpoise estimates were probably due to distributional shifts in response to oceanographic conditions (Palka, in press).

- By applying a dive correction to all large whale species, we have eliminating the serious bias introduced by correcting the estimates for only fin, humpback, and right whales. We have addressed the concern that these factors were too high by utilizing an independent estimate of abundance of right whales to reduce the factors by 40%. 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 substantial bias introduced by not using any dive correction factor. These species dive for shorter times than large whales and occur in moderate to large herds which are visually conspicuous at relatively long distances to aerial observers. We would expect that dive correction factors for these species, if necessary, would be substantially smaller than the smallest large whale factor. The only species where there might be a bias from no correction factor would be harbor porpoise. Much of this was corrected by using the NMFS survey data, since many fewer are missed from a slow-moving vessel than a fast-moving airplane. The NMFS estimates were not corrected for diving (Palka, in press). Given that Kraus *et al.* (1983) estimated that vessel surveys see only half of the porpoises seen from shore, the maximum value of a dive correction factor would be 2. However, the NMFS estimates were corrected for surfaced animals that are simply missed by observers by using two independent observer teams (Palka, in press), so the actual value should be significantly less than 2. Not including a dive correction for porpoises is therefore not a serious bias.

Prey Consumption:

Whales, dolphins and porpoises of the Northeast Shelf annually consume about 846 thousand tons (ktons) of fish, 280 ktons of squid, and 166 ktons of zooplankton, for a total of nearly 1.3 million tons (mtons). These estimates are substantially higher that those of Kenney *et al.* (1985):

- 276 ktons fish, 244 ktons squid, 45 ktons zooplankton — 555 ktons total,

who did not include dive correction factors for any species or scale for active metabolism. Our results are in between those of Scott *et al.* (MS 1983) for near-basal and total consumption:

- near-basal: 836 ktons fish, 184 ktons squid, 74 ktons zooplankton — 1,093 ktons total
- total: 1,250 ktons fish, 318 ktons squid, 174 ktons zooplankton — 1,742 ktons total.

That analysis included higher dive correction factors, but only for fin, humpback and right whales, higher body weights, and biased minke whale and harbor porpoise abundance estimates; assumed each species to be exclusively piscivorous, teuthivorous, or planktivorous; and used an unreliable method to estimate total consumption which resulted in over-estimates.

Sissenwine (1986) estimated that cetaceans consumed 5.4 tons/km^2 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 341.3 ktons, or 4.9 tons/km^2. Since the Georges Bank area defined by NMFS is somewhat smaller than ours, the differences here may be due mostly to the differences in the defined regions. Overholtz *et al.* (1991) estimated that marine mammals consumed a total of 120 ktons of fish annually from the Northeast Shelf, which is only 14% 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?* Concerning the zooplankton, whales feed on copepods and krill, which are not harvested by commercial fisheries, so there is no relevant comparison. Cetacean predation, however, is larger than commercial fishery harvests of fish and squid. Sherman *et al.* (1988) reported that total annual fish and squid landings from the Northeast Shelf ecosystem averaged 900 ktons between 1969 and 1978 with a peak catch of 1.2 mtons in 1974, averaged 470 ktons/yr from 1979 on, and had an estimated maximum sustainable yield of 950 ktons. Our estimate for total fish and squid consumption by cetaceans, 1,126 ktons, represents 94% of the 1974 peak landings, 119% of the estimated MSY, 125% of the 1969-1978 average, and 240% of the post-1979 average. Cetaceans are taking more than twice the current fishery harvests. For comparison, Sissenwine (1986) estimated that cetacean consumption on Georges Bank was 88.5% of the fishery catch. For squid alone, NMFS (1994*a*) reported total Atlantic coast squid landings of 32 ktons in 1990, 39 ktons in 1991, 45 ktons in 1992, and 51 ktons in 1993. Our estimated cetacean consumption of squid is 5.5 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 mtons of fish, 2.98 mtons of squid, and 2.01 mtons of zooplankton. The total consumption, 7.65 mtons is nearly six times our total for the Northeast Shelf, however, the area involved is much larger. Laws (1977) estimated predation rates for Southern Ocean marine mammals for both prior to 20th Century industrial whaling, and after depletion of whale stocks:

- pre-whaling: 190 mtons krill, 12 mtons squid, 4 mtons fish — 206 mtons total
- post-whaling: 43 mtons krill, 5 mtons squid, 1 mton fish — 49 mtons total.

Those totals represent 160 times and 38 times, respectively, our estimated total consumption for the Northeast Shelf, but, again, the area involved is very much larger. Finally, Bax (1991) summarized several studies comparing relative proportions of total fish consumption by marine mammals, commercial fisheries, and the fish themselves in six marine ecosystems, including Georges Bank (using data from Sissenwine, 1986). Marine mammal consumption is 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 cetaceans are eating 240% of the average post-1979 fishery catch from the Northeast Shelf exceeds all of these, however expressed as 119% of the estimated MSY, it seems to fit very well with the data from these other systems.

Our consumption estimates are likely to be somewhat conservative. Our metabolic models scale for activity, but not for growth and reproduction. Reproduction, particularly lactation, is a major energetic 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. Lockyer (1978, 1981*a*,*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) showed that the differential costs of pregnancy and lactation in spotted dolphins led to different feeding 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. Since any increase in consumption estimates to account for reproduction would only need to consider reproductively active females, the factors would be substantially lower that the percentages given above, and so this is not likely a serious bias in our estimates.

Primary Production Required:

Using our estimates of prey consumption by cetaceans in our trophic model, cetaceans require 10.3% of the total phytoplankton primary production. This is lower than the 14.8% average primary production required (PPR) estimated by Scott *et al.* (MS 1983) based on near-basal consumption rate, and much less than their average of 24.9% based on total consumption. The regional patterns in Scott *et al.* (MS 1983) were also different:

- near-basal: GOM — 9.5%, GBK — 15.4%, SNE — 17.6%, MAB — 16.5%
- total: GOM — 15.4%, GBK — 25.5%, SNE — 31.0%, MAB — 27.8%

The differences can be accounted for by different trophic level 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). This has the effect of reducing the PPR for teuthivores 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. This explains why our estimate of PPR for GOM was the highest regional value, while it was the lowest value in the Scott *et al.* estimates. A similar value to our 10.3% mean was reported by Huntley *et al.* (1991), who estimated that an average of 12% (maximum 22.5%) of carbon fixed by phytoplankton was recycled to the atmosphere by the breathing of marine mammals and seabirds.

Pauly and Christenson (1995) estimated the mean PPR for fishery harvests in non-tropical continental shelf systems at 35.3%. Our mean PPR of 10.3% is less than one-third of their value, even though cetacean predation may be more than double fishery catches in the Northeast Shelf.

At first glance, it seems that something must be in error. However, the difference is due to differences in mean trophic level between cetacean prey and commercial harvests. Pauly and Christenson (1995) estimated a mean TL of 3.5 for non-tropical shelves. Our mean TL, weighted for amount of consumption of each prey type, is 2.92. The PPR for equal harvests of TL=3.5 stocks versus TL=2.92 stocks is greater by a factor of 3.80 ($10^{2.5}/10^{1.92}$). In short, cetacean predation has a lesser impact on primary production than commercial fishery harvests because commercial fishers "feed" higher on the food chain.

Our trophic model is likely conservative because of the TL values we have used, though this has no effect on consumption estimates, only on PPR estimates. The zooplankton eaten by fin, humpback, and minke whales, as well as some proportion of that eaten by sei and right whales, is 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 Christenson'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).

Fry (1988) attempted to estimate the trophic levels of a variety of Northeast Shelf species by stable isotope methods, and found that the level of enrichment of ^{15}N produced the most consistent and reliable results. The TL values for a variety of cetacean prey estimated from his Figure 4 include krill (2.5), sand lance (3.2), herring (3.5), generalist fish (3.2-4.0), piscivorous fish (3.4-4.5), and squid (3.4). We recalculated our PPR estimates using the following TL values based on Fry (1988):

- zooplankton prey of sei whales (assuming 60% copepods and 40% krill) — 2.2
- zooplankton prey of right whales (100% copepods) — 2.0
- zooplankton prey of fin, minke, and humpback whales (100% krill) — 2.5
- fish prey of baleen whales (sand lance) — 3.2
- fish prey of toothed whales — 3.5
- squid — 3.4

The resulting PPR estimates (gm C/m^2/day) and percentages of total primary production were: GOM — 72.91 (25.1%), GBK — 73.33 (19.3%), SNE — 49.51 (16.4%), and MAB — 52.33 (15.7%), with weighted means of 62.16 gm C/m^2/day and 19.2%. This represents an 86% increase over the PPR estimated using our original model. If the higher TL values are more realistically representative of Northeast Shelf cetacean prey, and Pauly and Christensen's (1995) estimate of 35.3% is also reasonable for the Northeast Shelf, then well over half of the total primary production of the ecosystem is required to support cetaceans and fisheries together.

Conclusions

Our results show clearly that whales, dolphins, and porpoises are significant predators of fishery resources in the Northeast Shelf ecosystem. Their annual consumption may represent an amount from approximately the same as to more than twice the annual harvests by fisheries from the same system, given the amount of variability in catches over the preceding quarter of a century. We are confident in the quality of our data, nevertheless such results can never be better than an approximation of reality. We cannot expect to obtain the level of detail in data for cetaceans that we have for fishes. Besides the obvious methodological difficulties of measuring weights or metabolic rates of animals weighing many tons, developing precise estimates of abundance for cetaceans in areas as big as the Northeast Shelf is both difficult and costly. In addition, these animals are legally protected, so they cannot be sampled like fishes. Only for those very few species where there have been long-term intensive studies, such as right whales (Knowlton *et al.*, 1994) or bottlenose dolphins (Scott *et al.*, 1990), has research produced reliable information on parameters like age structure, age at maturity, reproductive rates, or population growth rates.

A complicating factor in quantifying cetacean consumption is that many species may have changed in abundance since the 1979-1981 CETAP surveys. The only species of the Northeast Shelf for which we have trend data is the right whale. Their population seems to be increasing slowly, at rates estimated at 2.5% (Knowlton *et al.*, 1994) or 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 there is little or no known anthropogenic mortality, and so we might expect their populations to also be increasing. At 5% annual increase rates, populations would have more than doubled since 1979-1981. However, we have very little data on limiting factors on cetacean populations. Since they are apex predators, we would expect their populations to be limited by food resources, through intra- and inter-specific competition (Hairston *et al.*, 1960; Hairston and Hairston, 1993). For apex predator species which are not resource-limited, we would expect populations to grow until reaching their carrying capacity, when they will be resource-limited (Colinvaux, 1993).

Resource limitation of cetacean predators implies interspecific competition with other predators on the same resource. The other predators include the commercial fishing industry. This viewpoint would suggest that either cetaceans and fisheries presently compete, or eventually will compete when cetacean populations reach their carrying capacities. Direct competition between cetaceans and fisheries is probably low. Cetaceans tend to prey on different species and/or age classes than fisheries, and harvest on average lower on the food chain. 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 particularly 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.* (1984*b*) suggested that predation by cetaceans, especially fin whales, on Georges Bank herring stocks may have had a depensatory effect on the herring and significantly delayed herring recovery from depletion by overfishing. The model developed by Overholtz *et al.* (1991) showed that 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 1960's, there have been several shift 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.*, in press). 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 and 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 is 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.* (in press) 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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REFERENCES

Barlow, J., C.W. Oliver, T.D. Jackson, and B.L. Taylor. 1988. Harbor porpoise, *Phocoena phocoena*, abundance estimation for California, Oregon, and Washington: II. Aerial surveys. *Fish. Bull.* 86: 433-444.

Bax, N.J. 1991. A comparison of the fish biomass flow to fish, fisheries, and mammals in six marine ecosystems. *ICES Mar. Sci. Symp.* 193: 217-224.

Bernard, H.J. and A.A. Hohn. 1989. Differences in feeding habits between pregnant and lactating spotted dolphins (*Stenella attenuata*). *J. Mamm.* 70: 211-215.

Blaylock, R.A., J.H.W. Hain, L.J. Hansen, D.L. Palka, and G.T. Waring. 1995, in press. *U.S. Atlantic and Gulf of Mexico Marine Mammal Stock Assessments.* NOAA Technical Memoorandum NMFS-SEFC-363. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service Southeast Fisheries Science Center, Miami, FL.

Brodie, P.F. 1975*a*. Cetacean energetics: an overview of intraspecific size variation. *Ecology* 56: 152-161.

Brodie, P.F. 1975*b*. Form, function, and energetics of Cetacea. Pp. 44-58 *in:* R.J. Harrison, ed. *Functional Analysis of Marine Mammals*, Vol. 3. Academic Press, New York, NY.

Brody, S. 1968. *Bioenergetics and Growth*. Hafner Publishing Co., London. 1023 pp.

Burnham, K.P., D.R. Anderson, and J.L. Laake. 1980. Estimation of density from line transect sampling of biological populations. *Wildl. Monogr.* 72: 1-202.

Cetacean and Turtle Assessment Program (CETAP). 1982. *A Characterization of Marine Mammals and Turtles in the Mid- and North-Atlantic Areas of the U.S. Outer Continental Shelf, Final Report*. Contract No. AA551-CT8-48. U.S. Department of the Interior, Bureau of Land Management, Washington, DC. 586 pp.

Clark, A. and P.A. Prince. 1980. Chemical composition and caloric value of food fed to mollymauk chicks *Diomedea melanophris* and *D. chrysostoma* at Bird Island, South Georgia. *Ibis* 122: 488-494.

Cohen, E.B., M.D. Grosslein, M.P. Sissenwine, F. Steimle, and W.R. Wright. 1982. Energy budget of Georges Bank. *Can. Spec. Pub. Fish. Aq. Sci.* 59: 95-107.

Colinvaux, P. 1993. *Ecology 2*. John Wiley & Sons, New York. 688 pp.

Croxall. J.P. and P.A. Prince. 1982. Caloric content of squid (Mollusca: Cephalopoda). *Brit. Antarc. Surv. Bull.* 55: 27-32.

Desportes, G. and R. Mouritsen. 1993. Preliminary results on the diet of long-finned pilot whales off the Faroe Islands. *Rep. Int. Whal. Comm., Spec. Iss.* 14: 305-324.

Evans, P.G.H. 1987. *The Natural History of Whales and Dolphins*. Facts on File, New York. 343 pp.

Fairfield, C.P., G.T. Waring, and M.H. Sano. 1993. Pilot whales incidentally taken during the distant water fleet Atlantic mackerel fishery in the mid-Atlantic Bight, 1984-1988. *Rep. Int. Whal. Comm., Spec. Iss.* 14: 107-117.

Fry, B. 1988. Food web structure on Georges Bank from stable C, N, and S isotopic compositions. *Limnol. Oceanogr.* 33: 1182-1190.

Fogarty, M.J., E.B. Cohen, W.L. Michaels, and W.W. Morse. 1991. Predation and the regulation of sand lance populations: an exploratory analysis. *ICES Mar. Sci. Symp.* 193: 120-124.

Gaskin, D.E. 1978. Form and function in the digestive tract and associated organs in Cetacea, with a consideration of metabolic rates and specific energy budgets. *Oceanogr. Mar. Biol. Ann. Rev.* 16: 313-345.

Gaskin, D.E. 1982. *The Ecology of Whales and Dolphins*. Heinemann Educational Books Ltd., London. 459 pp.

Hain, J.H.W., M.A.M. Hyman, R.D. Kenney, and H.E. Winn. 1985. The role of cetaceans in the shelf edge region of the northeastern United States. *Mar. Fish. Rev.* 47(1): 13-17.

Hain, J.H.W., M.J. Ratnaswamy, R.D. Kenney, and H.E. Winn. 1992. The fin whale (*Balaenoptera physalus*) in the waters of the northeastern U.S. continental shelf. *Rept. Int. Whal. Comm.* 42: 653-669.

Hairston, N.G. and N.G. Hairston. 1993. Cause-effect relationships in energy flow, trophic structure, and interspecific interactions. *Am. Nat.* 142: 379-411.

Hairston, N.G., F.E. Smith, and L.B. Slobodkin. 1960. Community struture, population control, and competition. *Am. Nat.* 94: 421-425.

Hinga, K.R. 1979. The food requirements of whales in the Southern Hemisphere. *Deep-Sea Res.* 26: 569-577.

Huntley, A.C., D.P. Costa, G.A.J. Worthy, and M.A. Castellini, eds. 1987. *Approaches to Marine Mammal Energetics*. Special Publication No. 1. Society for Marine Mammalogy, Lawrence, KS. 253 pp.

Huntley, M.E., M.D.G. Lopez, and D.M. Karl. 1991. Top predators in the Southern Ocean: a major leak in the biological carbon pump. *Science* 253: 64-66.

Innes, S., D.M. Lavigne, W.M. Earle, and K.M. Kovacs. 1986. Estimating feeding rates of marine mammals from heart mass to body mass ratios. *Mar. Mamm. Sci.* 2(3): 227-229.

Innes, S., D.M. Lavigne, W.M. Earle, and K.M. Kovacs. 1987. Feeding rates of seals and whales. *J. Anim. Ecol.* 56: 115- 130.

Irving, L., P.F. Scholander, and S.W. Grinnell. 1941. The respiration of the porpoise, *Tursiops truncatus*. *J. Cell. Comp. Physiol.* 17: 145-168.

Irving, L., O.M. Solandt, D.Y. Solandt, and K.C. Fisher. 1935. The respiratory metabolism of the seal and its adjustment to diving. *J. Cell. Comp. Physiol.* 7: 137-151.

Kanwisher, J.W. and S.H. Ridgway. 1983. The physiological ecology of whales and porpoises. *Sci. Am.* 248: 110-120.

Kanwisher, J. and G. Sundnes. 1966. Thermal regulation in cetaceans. Pp. 397-409 *in:* K.S. Norris, ed. *Whales, Dolphins, and Porpoises.* University of California Press, Berkeley, CA.

Katona, S. and H. Whitehead. 1988. Are Cetacea ecologically important? *Oceanogr. Mar. Biol. Ann. Rev.* 26: 553-568.

Kenney, R.D. 1990. Bottlenose dolphins off the northeastern United States. Pp. 369-396 *in:* S. Leatherwood and R.R. Reeves (eds). *The Bottlenose Dolphin*. Academic Press, San Diego, CA.

Kenney, R.D., M.A.M. Hyman, R.E. Owen, G.P. Scott, and H.E. Winn. 1986. Estimation of prey densities required by western North Atlantic right whales. *Mar. Mamm. Sci.* 2(1): 1-13.

Kenney, R.D., M.A.M. Hyman, and H.E. Winn. 1985. *Calculation of Standing Stocks and Energetic Requirements of the Cetaceans of the Northeast United States Outer Continental Shelf.* NOAA Tech. Memo. NMFS-F/NEC-41. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Woods Hole, MA. 99 pp.

Kenney, R.D. and S.D. Kraus. 1993. Right whale mortality: a correction and an update. *Mar. Mamm. Sci.* 9: 445-446.

Kenney, R.D., P.M. Payne, D.W. Heinemann, and H.E. Winn. 1995, in press. Shifts in Northeast Shelf cetacean distributions relative to trends in Gulf of Maine/Georges Bank finfish abundance. *In:* K. Sherman, N.A. Jaworski, and T.J. Smayda, eds. *Marine Ecosystem Management: The Northeast Shelf.* Blackwell Scientific Publications, Cambridge, MA.

Kenney, R.D. and H.E. Winn. 1986. Cetacean high-use habitats of the northeast United States continental shelf. *Fish. Bull.* 84(2): 345-357.

Kenney, R.D., H.E. Winn, and M.C. Macaulay. 1995. Cetaceans in the Great South Channel, 1979-1989: Right whale (*Eubalaena glacialis*). *Cont. Shelf. Res.* 15(4/5): 385-414.

Kleiber, M. 1975. *The Fire of Life, An Introduction to Animal Energetics.* R.E. Kreiger Publishing Co., Huntington, NY. 453 pp.

Knowlton, A.R., S.D. Kraus, and R.D. Kenney. 1994. Reproduction in North Atlantic right whales. *Can. J. Zool.* 72(7): 1297-1305.

Kraus, S.D. 1990. Rates and potential causes of mortality in North Atlantic right whales. *Mar. Mamm. Sci.* 6: 278-291.

Kraus, S.D., J.R. Gilbert, and J.H. Prescott. 1983. A comparison of aerial, shipboard, and land-based survey methodology for the harbor porpoise, *Phocoena phocoena*. *Fish. Bull.* 81: 910-913.

Laevastu, T. and H.A. Larkins. *Marine Fisheries Ecosystem, Its Quantitative Evaluation in Management.* Fishing News Books, Farnham, Surrey, U.K. 167 pp.

Lavigne, D.M., S. Innes, G.A.J. Worthy, and K.M. Kovacs. 1986*a*. Metabolic rate-body size relations in marine mammals. *J. Theor. Biol.* 122: 123-124.

Lavigne, D.M., S. Innes, G.A.J. Worthy, K.M. Kovacs, O.J. Schmitz, and J.P. Hickie. 1986*b*. Metabolic rates of seals and whales. *Can. J. Zool.* 64: 279-284.

Laws, R.M. 1977. Seals and whales of the Southern Ocean. *Phil. Trans. R. Soc. London, B, Biol. Sci.* 279: 81-96.

Lien, J. 1994. Entrapments of large cetaceans in passive inshore fishing gear in Newfoundland and Labrador (1979-1990). *Rep. Int. Whal. Comm., Spec. Iss.* 15: 149-157.

Lien, J., S. Johnson, and B. Merdsoy. 1979. Whale distribution in Newfoundland during 1979. *Osprey* 11(2): 21-32.

Lindeman, R.L. 1942. The trophic-dynamic aspect of ecology. *Ecology* 23(4): 399-418.

Lockyer, C. 1978. A theoretical approach to the balance between growth and food consumption in the fin and sei whales, with special reference to the female reproductive cycle. *Rep. Int. Whal. Comm.* 28: 243-249.

Lockyer, C. 1981*a*. Estimation of the energy costs of growth, maintenance, and reproduction in the female minke whale (*Balaenoptera acutorostrata*), from the Southern Hemisphere. *Rep. Int. Whal. Comm.* 31: 337-343.

Lockyer, C. 1981*b*. Growth and energy budgets of large baleen whales from the Southern Hemisphere. Pp. 379-487 *in:* FAO Advisory Committee on Marine Resources Research, Working Party on Marine Mammals. *Mammals in the Sea, Vol. III, General Papers and Large Cetaceans*. Food & Agriculture Organization of the United Nations, Rome.

Lockyer, C. 1986. Body fat condition in North Atlantic fin whales, *Balaenoptera physalus*, and its relationship with reproduction and food resource. *Can. J. Fish. Aq. Sci.* 43(1): 142-147.

Mackintosh, N.A. 1966. The distribution of southern blue and fin whales. Pp. 125-144 *in:* K.S. Norris, ed. *Whales, Dolphins, and Porpoises.* University of California Press, Berkeley, CA.

Matthews, L.H. 1978. *The Natural History of the Whale*. Columbia University Press, New York. 219 pp.

May, R.M., J.R. Beddington, C.W. Clark, S.J. Holt, and R.J. Laws. 1979. Management of multispecies fisheries. *Science* 205: 267-277.

National Marine Fisheries Service (NMFS). 1994*a*. *Fisheries of the United States, 1993.* Current Fishery Statistics No. 9300. U.S Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Silver Spring, MD. 121 pp.

National Marine Fisheries Service (NMFS). 1994*b*. *Status of Fishery Resources Off the Northeast United States for 1993.* NOAA Technical Memorandum NMFS-F/NEC-101. U.S Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Northeast Fisheries Science Center, Woods Hole, MA. 140 pp.

Nemoto, T. 1970. Feeding patterns of baleen whales in the oceans. Pp. 241-252 *in:* J.H. Steele, ed. *Marine Food Chains*. Univ. of California Press, Berkeley, CA.

Odum, E.P. 1968. Energy flow in ecosystems: a historical review. *Am. Zool.* 8: 11-18.

O'Reilly, J.E. and D.A. Busch. 1984. Phytoplankton primary production on the northwestern Atlantic shelf. *Rapp. P.-v. Reún. Cons. Int. Explor. Mer* 183: 255-268.

Overholtz, W.J., S.A. Murawski, and K.L. Foster. 1991. Impact of predatory fish, marine mammals, and seabirds on the pelagic fish ecosystem of the northeastern USA. *ICES Mar. Sci. Symp.* 193: 198-208.

Overholtz, W.J. and G.T Waring. 1991. Diet composition of pilot whales *Globicephala* sp. and common dolphins *Delphinus delphis* in the Mid-Atlantic Bight during spring 1989. *Fish. Bull.* 89: 723-728.

Palka, D.L. In press. Abundance estimate of the Gulf of Maine harbor porpoise. *Rep. Int. Whal. Comm., Spec. Iss.* 16.

Pauly, D. and V. Christensen. 1995. Primary production required to sustain global fisheries. *Nature* 374: 255-257.

Payne, P.M., J.R. Nicolas, L. O'Brien, and K.D. Powers. 1986. The distribution of the humpback whale *Megaptera novaeangliae* on Georges Bank and in the Gulf of Maine in relation to densities of the sand eel *Ammodytes americanus*. *Fish. Bull.* 88: 687-696.

Payne, P.M., D.N. Wiley, S.B, Young, S. Pittman, P.J. Clapham, and J.W. Jossi. 1990. Recent fluctuations in the abundance of baleen whales in the southern Gulf of Maine in relation to changes in selected prey. *Fish. Bull.* 88: 687-696.

Perkins, J.S. and P.C. Beamish. 1979. Net entanglements of baleen whales in the inshore fishery of Newfoundland. *J. Fish. Res. Board Can.* 36: 512-528.

Platt, T. 1969. The concept of energy efficiency in primary production. *Limnol. Oceanogr.* 14: 653-659.

Ridgway, S.H. 1972. Homeostasis in the aquatic environment. Pp. 590-747 *in:* S.H. Ridgway, ed. *Mammals of the Sea, Biology and Medicine.* C.C. Thomas, Springfield, IL.

Schilling, M.R., I. Seipt, M.T. Weinrich, S.E. Frohock, A.E. Kuhlberg, and P.J. Clapham. 1992. Behavior of individually-identified sei whales *Balaenoptera borealis* during an episodic influx into the Gulf of Maine in 1986. *Fish. Bull.* 90: 749-755.

Scholander, P.F. 1940. Experimental investigations on the respiratory function in diving mammals and birds. *Hvalrad. Skr.* 22: 1-131.

Scholander, P.F., L. Irving, and S.W. Grinnell. 1942. On the temperature and metabolism of the seal during diving. *J. Cell. Comp. Physiol.* 19: 67-78.

Scott, G.P. and J.R. Gilbert. 1982. Problems and progress with the U.S. BLM-sponsored CETAP surveys. *Rep. Int. Whal. Comm.* 32: 587-599.

Scott, G.P., R.D. Kenney, T.J. Thompson, and H.E. Winn. 1983. Functional roles and ecological impacts of the cetacean community in the waters of the northeastern U.S. continental shelf. Document C.M.1983/N:12. International Council for the Exploration of the Sea, Copenhagen. 32 pp.

Scott, M.D., R.S. Wells, and A.B. Irvine. 1990. A long-term study of bottlenose dolphins on the West Coast of Florida. Pp. 235-244 *in:* S. Leatherwood and R.R. Reeves (eds). *The Bottlenose Dolphin.* Academic Press, San Diego, CA.

Sergeant, D.E. 1969. Feeding rates of Cetacea. *FiskDir. Skr. Ser. Havunders.* 15: 246-258.

Sherman, K. 1980. MARMAP, a fisheries ecosystem study in the northwest Atlantic: fluctuations in ichthyoplankton-zooplankton components and their potential for impact on the system. Pp. 9-37 *in:* F.P. Diemer, F.J. Vernberg, and D.Z. Mierkes, eds. *Advanced Concepts in Ocean Measurements for Marine Biology.* University of South Carolina Press, Charleston, SC.

Sherman, K. 1986. Measurement strategies for monitoring and forecasting variability in large marine ecosystems. Pp. 203-236 *in:* K. Sherman and L.M. Alexander, eds. *Variability and Management of Large Marine Ecosystems.* AAAS Selected Symposia No. 99. Westview Press, Boulder, CO.

Sherman, K. and L.M. Alexander, eds. 1986. *Variability and Management of Large Marine Ecosystems.* AAAS Selected Symposia No. 99. Westview Press, Boulder, CO. 319 pp.

Sherman, K. and L.M. Alexander, eds. 1989. *Biomass Yields and Geography of Large Marine Ecosystems.* AAAS Selected Symposia No. 111. Westview Press, Boulder, CO. 493 pp.

Sherman, K., L.M. Alexander, and B.D. Gold, eds. 1990. *Large Marine Ecosystems: Patterns, Processes, and Yields.* Publ. No. 90-30S. American Association for the Advancement of Science, Washington, DC. 242 pp.

Sherman, K., L.M. Alexander, and B.D. Gold, eds. 1991. *Food Chains, Yields, Models, and Management of Large Marine Ecosystems.* Westview Press, Boulder, CO. 320 pp.

Sherman, K., L.M. Alexander, and B.D. Gold, eds. 1993. *Stress, Mitigation, and Sustainability of Large Marine Ecosystems.* AAAS Press, Washington, DC. 376 pp.

Sherman, K., J.R. Green, J.R. Goulet, and L. Ejysmont. 1982. Coherence in zooplankton of a large northwest Atlantic ecosystem. *Fish. Bull.* 81: 855-862.

Sherman, K., M. Grosslein, D. Mountain, D. Busch, J. O'Reilly, and R. Theroux. 1988. The continental shelf ecosystem off the northeast coast of the United States. Pp. 279-337 *in:* H. Postema and J.J. Zijlstra, eds. *Ecosystems of the World 27: Continental Shelves.* Elsevier Press, Amsterdam.

Sherman, K., N.A. Jaworski, and T.J. Smayda, eds. 1995, in press. *Marine Ecosystem Management: The Northeast Shelf.* Blackwell Scientific Publications, Cambridge, MA.

Sherman, K. and C.M. Jones. 1980. The zooplankton component of a northwest Atlantic ecosystem. Document C.M.1980/L:67. International Council for the Exploration of the Sea, Copenhagen.

Sherman, K., C. Jones, L. Sullivan, W. Smith, P. Berrien, and L. Ejsymont. 1981. Congruent shifts in sand eel abundance in western and eastern North Atlantic ecosystems. *Nature* 291: 486-489.

Sissenwine, M.P. 1986. Perturbation of a predator-controlled continental shelf ecosystem. Pp. 55-85 *in:* K. Sherman and L.M. Alexander, eds. *Variability and Management of Large Marine Ecosystems. AAAS Selected Symposia No.* 99. Westview Press, Boulder, CO.

Sissenwine, M.P., E.B. Cohen, and M.D. Grosslein. 1984*a*. Structure of the Georges Bank ecosystem. *Rapp. P.-v. Reún. Cons. Int. Explor. Mer* 183: 243-254.

Sissenwine, M.P., W.J. Overholtz, and S.H. Clark. 1984*b*. In search of density dependence. Pp. 119-137 *in:* B. R. Melteff, ed. *Proceedings of the Workshop on Biological Interactions Among Marine Mammals and Commercial Fisheries in the Southeastern Bering Sea.* Alaska Sea Grant Report 84-1. Alaska Sea Grant College Program, University of Alaska, Fairbanks, AK.

Shoop, C.R. and R.D. Kenney. 1992. Distributions and abundances of loggerhead and leatherback sea turtles in northeastern United States waters. *Herpetol. Monogr.* 6: 43-67.

Smith, T., D. Palka, and K. Bisack. 1993. *Biological Significance of Bycatch of Harbor Porpoise in the Gulf of Maine Demersal Gillnet Fishery*. NEFSC Ref. Doc. 93-23. U.S. Department of Commerce, National Oceanic and Atmospheric Admininistration, National Marine Fisheries Service, Northeast Fisheries Science Center, Woods Hole, MA.

Waring, G.T., P. Gerrior, P.M. Payne, B.L. Barry, and J.R. Nicolas. 1990. Incidental take of marine mammals in foreign fishery activities off the northeast United States, 1977-1988. *Fish. Bull.* 88: 347-360.

Whitehead, H. and J. Carscadden. 1985. Predicting inshore whale abundance — whales and capelin off the Newfoundland coast. *Can. J. Fish. Aquat. Sci.* 42: 976-981.

Yasui, W.Y. and D.E. Gaskin. 1986. Energy budget of a small cetacean. *Ophelia* 25: 183-197.

Table 1. Cetaceans of the U.S. Northeast Shelf, with estimated average body weights and dietary composition used in this paper

		Percent of Diet Comprised of:		
Species	Weight (kg)	Fish	Squid	Zooplankton
<u>Mysticetes:</u>				
Right whale, *Eubalaena glacialis*	40,000	0	0	100
Fin whale, *Balaenoptera physalus*	30,000	90	0	10
Sei whale, *Balaenoptera borealis*	13,000	0	0	100
Minke whale, *Balaenoptera acutorostrata*	4,500	95	0	5
Humpback whale, *Megaptera novaeangliae*	25,000	95	0	5
<u>Odontocetes:</u>				
Sperm whale, *Physeter macrocephalus*	20,000	20	80	0
Bottlenose whale, *Hyperoodon ampullatus*	4,700	5	95	0
Goose-beaked whale, *Ziphis cavirostris*	1,900	0	100	0
Beaked whale, *Mesoplodon* spp.[1]	1,200	0	100	0

Table 1. (continued)

Pilot whale, *Globicephala* spp.[2]	850	10	90	0
Risso's dolphin, *Grampus griseus*	340	0	100	0
Bottlenose dolphin, *Tursiops truncatus*	150	100	0	0
Atlantic white-sided dolphin, *Lagenorhynchus acutus*	120	90	10	0
Common dolphin, *Delphinus delphis*	65	85	15	0
Striped dolphin, *Stenella coeruleoalba*	55	40	60	0
Spotted dolphin, *Stenella* spp.[3]	50	20	80	0
Spinner dolphin, *Stenella longirostris*	50	20	80	0
Harbor porpoise, *Phocoena phocoena*	45	95	5	0

(1) Includes 4 species — *M. mirus, M. densirostris, M. europaeus, M. bidens*

(2) Includes 2 species — *G. melas, G. macrorhynchus*

(3) Includes 2 species — *S. attenuata, S. plagiodon*

Table 2. Seasonal estimates of abundance for eighteen cetacean species for the U.S. Northeast Shelf, and in four regions of the Shelf — Gulf of Maine (GOM), Georges Bank (GBK), Southern New England (SNE), and Mid-Atlantic Bight (MAB).

		Region				Northeast Shelf
Species	Season	GOM	GBK	SNE	MAB	*Total*
Right whale	Winter	0	0	0	0	0
Right whale	Spring	140	77	19	0	236
Right whale	Summer	151	0	0	0	151
Right whale	Fall	0	0	0	0	0
Fin whale	Winter	0	357	401	325	1083

Table 2. (continued)

Fin whale	Spring	1075	828	476	639	3018
Fin whale	Summer	1997	511	1055	81	3644
Fin whale	Fall	645	113	223	215	1196
Sei whale	Winter	0	491	0	0	491
Sei whale	Spring	139	1581	0	0	1720
Sei whale	Summer	5	226	0	0	231
Sei whale	Fall	0	418	0	0	418
Minke whale	Winter	0	0	237	0	237
Minke whale	Spring	1747	3796	1876	107	7526
Minke whale	Summer	2157	237	366	0	2760
Minke whale	Fall	2070	0	0	0	2070
Humpback whale	Winter	0	0	0	0	0
Humpback whale	Spring	164	94	28	0	286
Humpback whale	Summer	398	24	0	0	422
Humpback whale	Fall	28	164	0	0	192
Sperm whale	Winter	0	110	20	302	432
Sperm whale	Spring	0	98	174	712	984
Sperm whale	Summer	0	302	247	232	781
Sperm whale	Fall	0	11	0	180	191
Bottlenose whale	Winter	0	0	0	0	0
Bottlenose whale	Spring	0	17	0	46	63
Bottlenose whale	Summer	0	0	0	0	0
Bottlenose whale	Fall	0	0	0	0	0
Goose-beaked whale	Winter	0	0	0	0	0
Goose-beaked whale	Spring	0	0	8	241	249
Goose-beaked whale	Summer	0	0	130	26	156
Goose-beaked whale	Fall	0	0	0	0	0
Beaked whale	Winter	0	0	0	0	0
Beaked whale	Spring	0	319	66	72	457
Beaked whale	Summer	0	299	183	81	563
Beaked whale	Fall	0	162	0	0	162
Pilot whale	Winter	0	974	955	304	2233
Pilot whale	Spring	438	6284	2973	1779	11474
Pilot whale	Summer	0	4890	893	3056	8839
Pilot whale	Fall	225	543	2516	6527	9811

Table 2. (continued)

Risso's Dolphin	Winter	0	0	28	777	805
Risso's Dolphin	Spring	0	345	1937	2649	4931
Risso's Dolphin	Summer	0	1872	6794	3168	11834
Risso's Dolphin	Fall	0	3089	12	2725	5826
Bottlenose Dolphin	Winter	0	1511	827	774	3112
Bottlenose Dolphin	Spring	0	2488	4685	3982	11155
Bottlenose Dolphin	Summer	0	3670	3497	4902	12069
Bottlenose Dolphin	Fall	0	573	333	4809	5715
White-sided Dolphin	Winter	7353	4957	37	0	12347
White-sided Dolphin	Spring	11093	27094	1703	0	39890
White-sided Dolphin	Summer	27029	10987	0	0	38016
White-sided Dolphin	Fall	25474	16545	4	0	42023
Common Dolphin	Winter	1052	10775	22714	10562	45103
Common Dolphin	Spring	40	5395	5543	8100	19078
Common Dolphin	Summer	198	633	1411	1959	4201
Common Dolphin	Fall	0	16182	12473	2010	30665
Striped Dolphin	Winter	0	0	4554	1937	6491
Striped Dolphin	Spring	0	1482	2571	7972	12025
Striped Dolphin	Summer	0	3120	5203	7997	16320
Striped Dolphin	Fall	0	5962	786	6734	13482
Spotted Dolphin	Winter	0	0	482	107	589
Spotted Dolphin	Spring	0	0	901	1074	1975
Spotted Dolphin	Summer	0	235	870	1336	2441
Spotted Dolphin	Fall	0	755	131	799	1685
Spinner Dolphin	Winter	0	0	0	0	0
Spinner Dolphin	Spring	0	0	0	302	302
Spinner Dolphin	Summer	0	0	128	69	197
Spinner Dolphin	Fall	0	0	0	0	0
Harbor Porpoise	Winter	2376	1560	0	0	3936
Harbor Porpoise	Spring	38040	22440	3288	0	63768
Harbor Porpoise	Summer	24432	0	0	0	24432
Harbor Porpoise	Fall	708	0	0	0	708

Table 3. Standing stocks (metric tons) and biomass densities (kg/km^2, in parentheses) of cetaceans in the U.S. Northeast Shelf ecosystem.

Region	Season			
	Winter	Spring	Summer	Fall
Gulf of Maine	1,058	55,036	90,027	32,645
	(15)	(764)	(1249)	(453)
Georges Bank	21,713	80,853	33,220	18,339
	(315)	(1172)	(481)	(266)
S. New England	16,197	32,544	41,078	9,744
	(233)	(469)	(601)	(140)
Mid-Atlantic Bight	17,227	38,696	13,911	17,787
	(254)	(570)	(205)	(262)
Northeast Shelf	56,195	207,129	178,236	78,514
	(202)	(755)	(640)	(282)

Table 4. Estimated consumption of prey (metric tons) by cetaceans in four regions of the U.S. Northeast Shelf.

Region	Season	Prey Type			
		Fish	Squid	Zooplankton	Total
GOM	Winter	5,985	778	0	6,763
GOM	Spring	102,070	3,260	20,963	126,292
GOM	Summer	168,956	2,886	23,663	195,505
GOM	Fall	75,791	3,005	4,954	83,750
GOM	Total	352,802	9,928	49,580	412,310
GBK	Winter	24,902	8,238	13,566	46,797
GBK	Spring	124,632	30,754	58,605	213,991
GBK	Summer	43,817	33,492	9,600	86,909
GBK	Fall	31,809	13,681	13,206	58,697
GBK	Total	225,160	86,165	94,978	406,302

Table 4. (continued)

SNE	Winter	29,670	7,340	1,956	38,965
SNE	Spring	59,091	21,592	5,191	85,874
SNE	Summer	58,277	27,782	5,764	91,823
SNE	Fall	17,029	9,909	1,218	28,157
SNE	Total	164,067	66,623	14,130	244,820
MAB	Winter	20,531	13,772	1,480	35,783
MAB	Spring	46,078	40,279	3,562	89,918
MAB	Summer	17,436	27,549	684	45,668
MAB	Fall	19,879	35,694	1,175	56,749
MAB	Total	103,924	117,294	6,900	228,118
TOTAL	Winter	81,087	30,128	17,002	128,217
TOTAL	Spring	331,871	95,885	88,320	516,076
TOTAL	Summer	288,486	91,708	39,712	419,905
TOTAL	Fall	144,509	62,290	20,553	227,352
TOTAL	Total	845,953	280,010	165,587	1,291,551

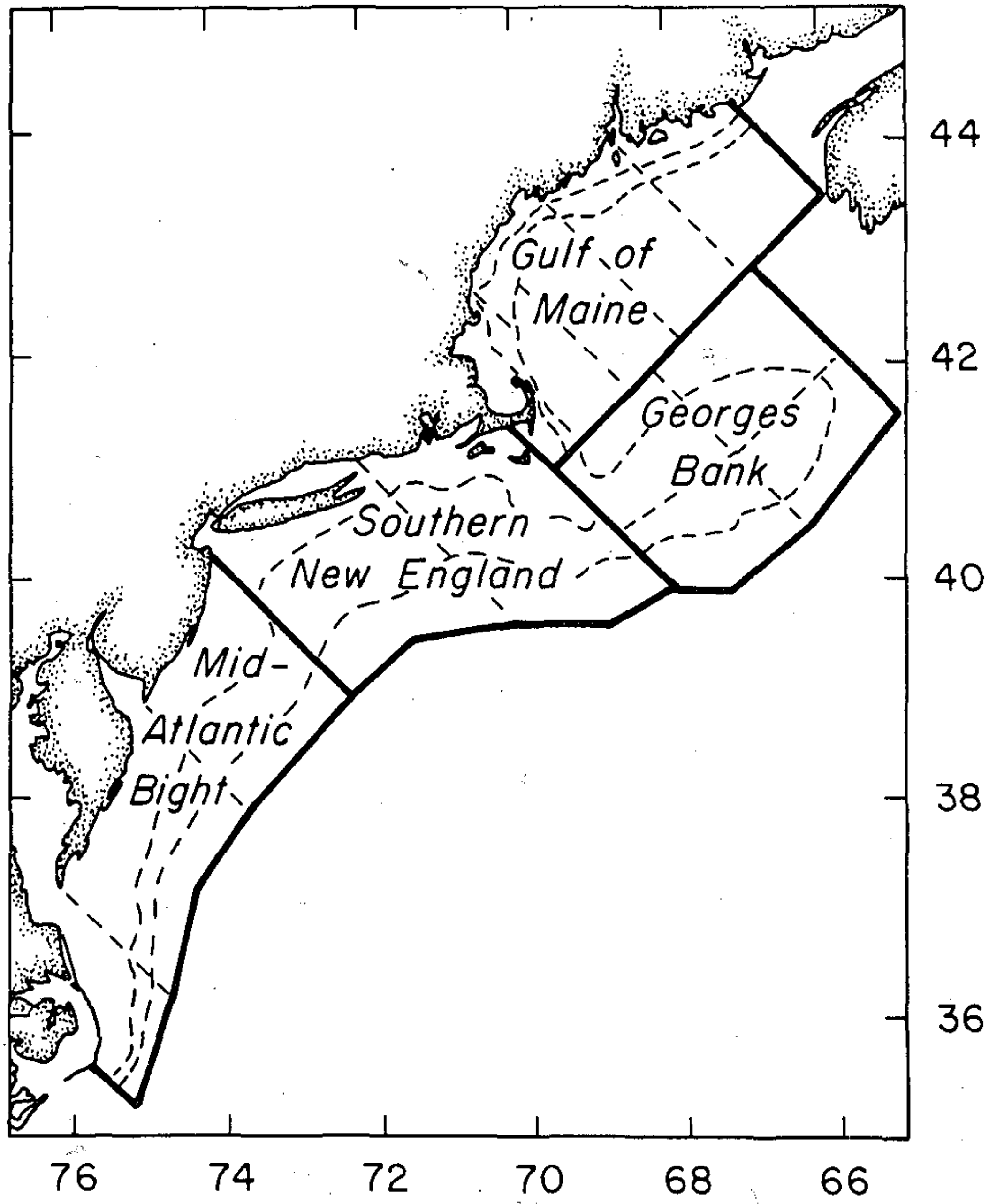

Figure 1. The U.S. Northeast Shelf study area, showing the boundaries of the four regions defined for this study. The dashed lines show the individual CETAP aerial survey blocks, which were separated along the 20-fathom (37-m) and 50-fathom (91-m) isobaths. The outer edge of the study area is approximately at the 2000-m isobath.

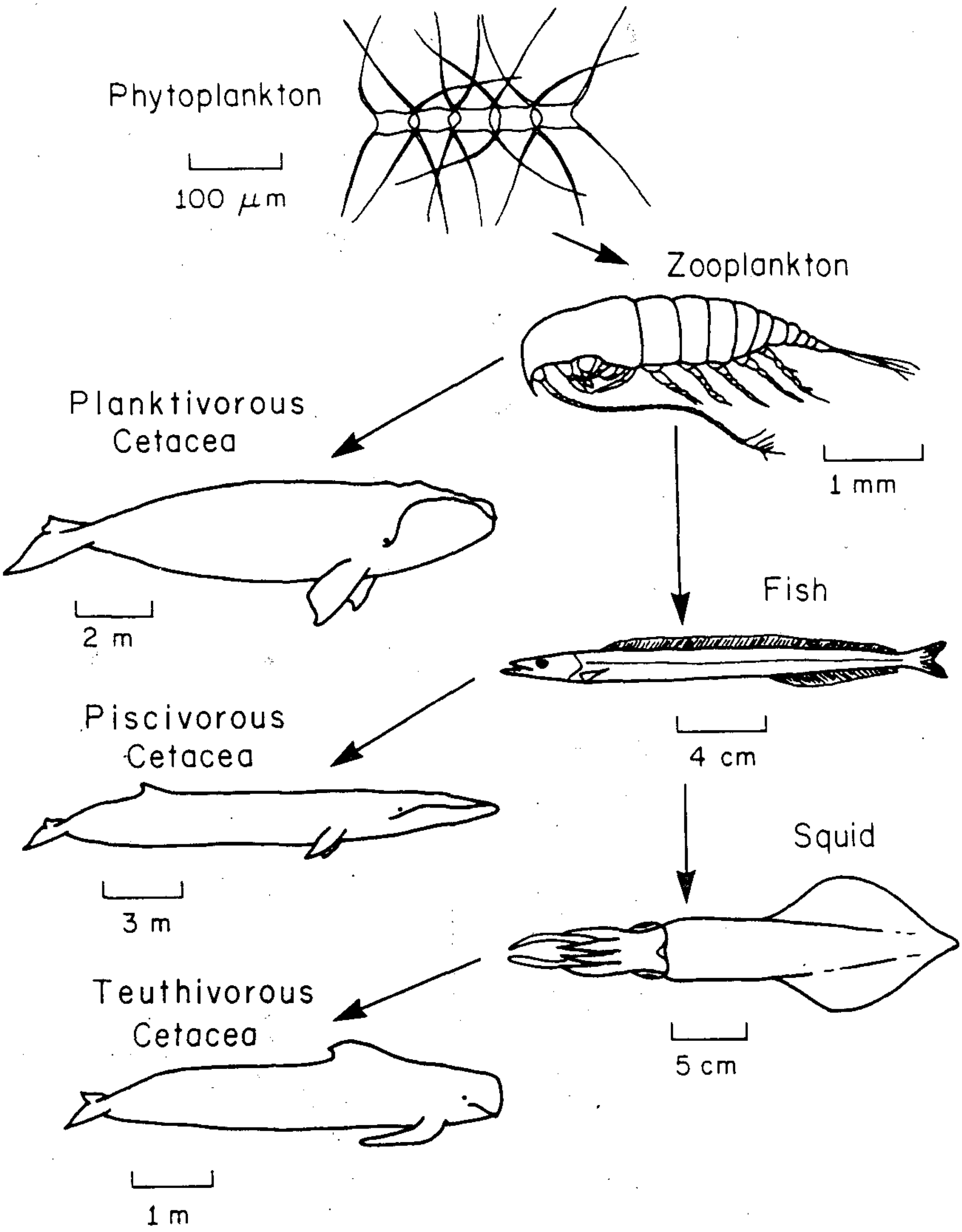

Figure 2. Model food chain utilized in this study, showing a typical species within each compartment of the food chain (top to bottom): *Chaetoceros* sp. (diatom), *Calanus finmarchicus* (copepod), *Eubalaena glacialis* (right whale), *Ammodytes* sp. (sand lance), *Balaenoptera physalus* (fin whale), *Loligo pealei* (long-finned squid), and *Globicephala melas* (longfinned pilot whale). In the numerical details of our model, the squid feed more on zooplankton than on fishes, at trophic level 3.2 rather than 4.0 as implied by the diagram.