Recent Fluctuations in the Abundance of Baleen Whales in the Southern Gulf of Maine in Relation to Changes in Selected Prey

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Abstract.– Significant changes in the biomass of sandlance *Ammodytes* spp. and in the abundance of the copepod *Calanus finmarchicus* in the southern Gulf of Maine co-occurred with a shift in the occurrence and abundance of four species of baleen whales in the region. During the years 1982–88 the abundance of sandlance was negatively correlated to the abundance of *C. finmarchicus* ($r_s = -0.883$, $P<0.05$). Peak years of abundance for *C. finmarchicus* during 1982–88 in the study area were the lowest years of abundance for sandlance. The abundance of *C. finmarchicus* and sandlance was at a regional maximum during 1986 and 1988, respectively.

The abundance of humpback and fin whales were marginally correlated to each other ($r_s = 0.3338$, $P< 0.08$). The abundance of humpbacks was negatively correlated with right whales ($r_s = -0.7753$, $P<0.001$) and sei whales ($r_s = -0.5507$, $P<0.01$). The patterns of occurrence for right and sei whales were significantly related to each other ($r_s = 0.6842$, $P< 0.001$). Right and sei whales were common in the region only during 1986, when copepod abundance reached a regional maximum and sandlance abundance a regional minimum. These patterns of whale occurrence reflect known prey preferences, and are therefore expected between the pisciverous humpback and fin whales and the highly planktiverous right and sei whales.

We hypothesize that the spatial distribution and abundance of baleen whales in the Gulf of Maine can be characterized as a series of ecological responses to human-induced changes in the abundance of planktiverous finfish.

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During the mid-1970s, a dramatic increase in the abundance of sandlance *Ammodytes* spp.* precipitated a significant change in the abundance and composition of the ichthyofauna in the shelf waters of the northeastern United States (Smith et al. 1978, 1980; Morse 1982). The population explosion of sandlance coincided with a 50% reduction in total finfish biomass in the same region between 1968 and 1975 (Clark and Brown 1977). This decrease was primarily due to the commercial depletion of stocks of herring *Clupea harengus* and mackerel *Scomber scombrus* (Anthony and Waring 1980, Grosslein et al. 1980). A concurrent increase in sandlance abundance following the depletion of North Sea herring and mackerel stocks led Sherman et al. (1981) to suggest that sandlance had taken over ecological niches previously occupied by these species in many areas of the Northwest Atlantic.

Since the mid-1970s sandlance have become increasingly important in the Gulf of Maine as prey for commercial fish (Bowman et al. 1984), seabirds (Powers and Backus 1987), pinnipeds (Payne and Selzer 1989), and baleen whales (Overholtz and Nicolas 1979, Hain et al. 1982, Payne et al. 1986). Sandlance were the only confirmed prey of the humpback whale *Megaptera novaeangliae* between 1975 and 1979 (Hain et al. 1982, Mayo 1982) and the only prey significantly correlated with the distribution of humpbacks in the Gulf of Maine between 1978 and 1982 (Payne et al. 1986). Also, fin whales *Balaenoptera physalus*, sympatric with humpbacks in this region, have frequently been observed exploiting sandlance (Overholtz and Nicolas 1979).

Two other species of large baleen whales, the northern right whale *Eubalaena glacialis* and the sei whale *Balaenoptera borealis*, also occur in

* Two species of this genus, *A. americanus* and *A. dubius*, occur in the shelf waters of the northeastern United States (Richards et al. 1963, Reay 1970, Richards and Kendall 1973, Meyer et al. 1979, Richards 1982).

the Gulf of Maine (CeTAP 1982, Watkins and Schevill 1982, Kraus 1985, Schevill et al. 1986, Weinrich et al. 1986, Hamilton and Mayo 1990). Both of these species have been characterized principally as "skim feeders" (Nemoto 1959, Kawamura 1974, Nemoto and Kawamura 1977) which subsist primarily on dense swarms of calanoid copepods, notably *Calanus finmarchicus* in the North Atlantic (Mitchell 1975a, 1975b; Jonsgard and Darling 1977; Mitchell and Chapman 1977; Winn et al. 1986; Wishner et al. 1988; Mayo and Marx 1990), in preference to schooling fish (Watkins and Schevill 1979).

This similarity in prey preference led Mitchell (1975a) to hypothesize that competition between these two whale species might have adversely affected the recovery of the right whale in the western North Atlantic. However, sandlance are also known to play an important trophic role as a major predator of copepods, especially *C. finmarchicus* (Monteleone and Peterson 1986, Meyer et al. 1979). Given their abundance and prey selectivity towards copepods, Kenney et al. (1986) proposed that sandlance represented a more significant competitor to right whales for copepodite prey than sei whales (as suggested by Mitchell 1975a).

The existence of some degree of intra- and interspecific competition between right/sei whales and sandlance (ecologically similar species) for a common prey is generally accepted, but is difficult to demonstrate. An overlap in preferred prey is at best a qualitative phenomenon, and offers only "soft corroboration" (from Strong et al. 1984) as evidence for competition between these species. Another approach (used by Smith 1968, 1970; Eck and Wells 1987), which we have adopted for the purpose of this study, is to look for a demonstrable shift in the ecological balance between competing species, or the complete replacement of one competing species by another. In this paper we examine the ecological relationships between sandlance and two of its major predators, the humpback and fin whale; between sandlance and its major prey, the copepod *Calanus finmarchicus*; and between sandlance and two potential competitors for *C. finmarchicus* in this region, the right and sei whale.

Methods

Study area

In this paper we have focused on Stellwagen Bank (Fig. 1), a glacial deposit of sand and gravel in the southwest Gulf of Maine that is associated with high levels of biological productivity and a rapidly developing commercial whalewatching industry. The margins of the bank are defined by the 40-m isobath with depths as low as 18 m. Since the early 1980s whalewatching vessels have provided intensive survey coverage of cetaceans in the area from June through September of each year.

Collection and treatment of data

Fisheries data Data on the abundance of sandlance used here were collected on Stellwagen Bank and immediately adjacent waters by National Marine Fisheries Service, Northeast Fisheries Center (NMFS/NEFC) biologists and technicians during standardized NMFS/NEFC spring bottom-trawl surveys. The NMFS/NEFC survey area has been spatially stratified into approximate ecological units based principally on depth (see Grosslein 1969). Stellwagen Bank is a principal bathymetric feature in the Gulf of Maine–NMFS/NEFC stratum #26. The number of sandlance caught per tow in stratum #26 (for each spring survey) was transformed into logarithmic values, and the mean number of sandlance (transformed data) was considered representative of Stellwagen Bank and used in all further analyses, a procedure which follows that described in Payne et al. (1986).

The *Calanus finmarchicus* data were also collected by NMFS/NEFC personnel. A transect across the Gulf of Maine has been sampled with the Hardy Continuous Plankton Recorder (CPR) since 1961 (Jossi and Smith 1990). Since the early 1980s a desired sampling frequency of one transect per month has been generally achieved. Data used in this study came from the 10-nautical-mile section of the transect centered on Stellwagen Bank. Water passing through the CPR is filtered with bolting silk having mean aperture dimensions of 225 × 234 μ. All large zooplankton ($\geq$2 mm) in the sample are identified and enumerated. Counts of smaller ($\leq$2 mm) zooplankton are made from an aliquot ($\sim$1/45) of the sample. Counts were converted to number of organisms per 100 m^3, and then transformed to log base 10 for subsequent calculations. Further details of this procedure are given in Colebrook (1975) and in Jossi and Smith (1990). All reference to copepod data and abundance used in this study exclusively concern *C. finmarchicus*.

The abundance of sandlance (expressed as the mean of the log-transformed number of sandlance per tow/year) and of the copepod *C. finmarchicus* (log-transformed number of individuals/100 m^3/year) were compared by first ranking the data by year, 1982–88 (N = 7), then calculating Spearman's coefficient of rank correlation (r_s) (Zar 1984). The data are therefore compared on an ordinal, rather than on an absolute, scale; this is because of the magnitude of the difference in the scale of the data that were brought together for this study.

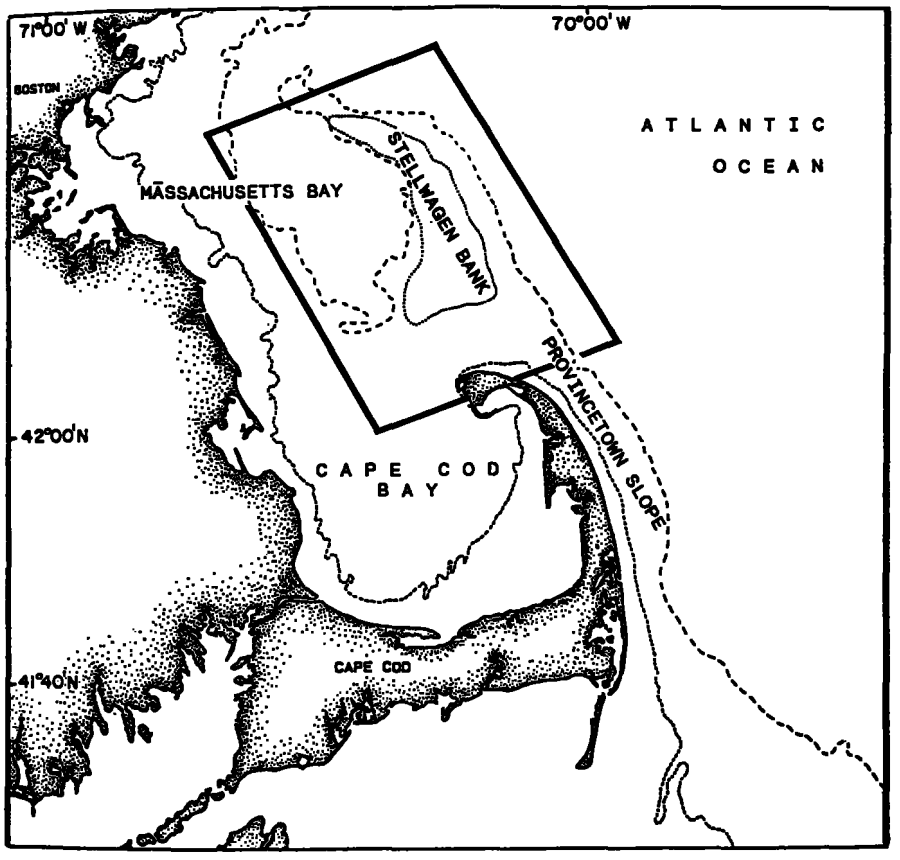

Figure 1
Baleen whale study area in southern Gulf of Maine (outlined) and geographical regions referred to throughout the text.

Whale sighting data Data for this study on the occurrence and distribution of humpback, fin, right, and sei whales were collected by naturalists working aboard commercial whalewatching vessels during the study period 1982–88. Data recorded from these vessels for all cetacean sightings include species, group size, time, location (using LORAN-C), behavior, and the photographically confirmed identity of individual animals. Vessels ran 4-hour cruises to the Stellwagen Bank and Massachusetts Bay areas from two ports: Provincetown and Plymouth, Massachusetts. The cruise track of the whalewatching vessels was decided by the captain based upon the greatest number of whale sightings recorded on the previous trip or day; consequently, sampling was neither random nor systematic. Nonetheless, the intensity of the coverage resulted in extremely comprehensive surveys of the region during most of the study period. The information collected aboard these vessels in this region represents one of the most detailed databases available anywhere on a multispecies group of whales.

Data used in this study were taken from the first cruise of each day from each of the two ports and considered a reliable index of relative abundance of whales in the area. The total number of whales observed during each morning whalewatching trip from each port was summed by species and month, June–September (the period when coverage from whalewatching vessels was effectively continuous). These totals were then divided by the number of trips each month (each trip was considered a unit of effort), resulting in an index of whale abundance, expressed as number of whales/effort/month for each species between 1982 and 1988. While there are undoubtedly biases associated with the collection of these data, the intensity of coverage is such that this index can be used to accurately monitor relative changes in the local abundance and distribution of whales.

Using these sighting data, the temporal co-occurrence between the four whale species within the study area was tested by ranking the mean number of whales/effort/month (by species), then calculating Spearman's coefficient of rank correlation (r_s) (Zar 1984) between species for all paired data, 1982–88 ($N = 28$ for each possible pairing).

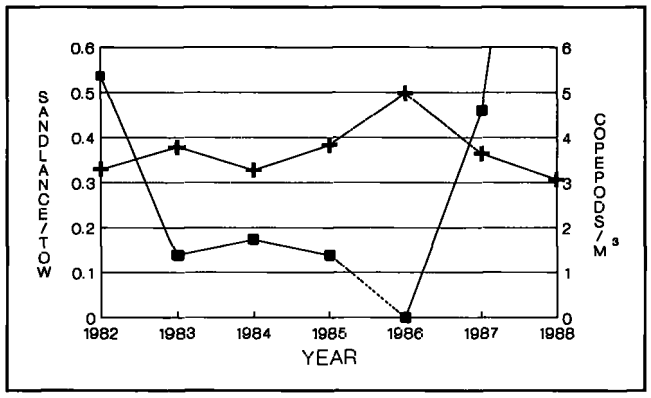

Figure 2
Stratified mean number of sandlance (■) per tow (log transformation) on left, and the number of copepods *Calanus finmarchicus* (+) per m^3 (log transformation) on right. Note: the scale for sandlance is different from that of copepods.

Results

Changes in abundance of sandlance and copepods

The mean number of sandlance per tow (log transformation) collected during spring bottom-trawl surveys ranged between years (Fig. 2) from a minimum 0.000 (in 1986) to a maximum 4.066 per tow (in 1988). Two trends were apparent. The data show a decline in catches from 1982 to the zero value of 1986. Catches increased in 1987, peaking in 1988 to 4.066 sandlance per tow (log value). The number of sandlance caught in 1988 was a regional abundance maximum for spring surveys, 1968–88 (from information presented in Nelson and Ross 1989).

The log-transformed values of *C. finmarchicus*/m^3 of water collected in the CPR ranged from 3.270 (in 1984) to 4.988 (in 1986), and generally increased on Stellwagen Bank between 1982 and 1986 (Fig. 2). The increase was most apparent between 1984 and 1986. The number of *C. finmarchicus* collected in 1986 was one order of magnitude greater than that collected during any other year of the study. Following 1986 the number of *C. finmarchicus* declined rapidly to 3.640 (log value) in 1987, then to 3.070 (log value) in 1988 (Fig. 2).

The abundance of sandlance on Stellwagen Bank was inversely related to the abundance of *C. finmarchicus* ($r_s = -0.883$, $P<0.05$, $N=7$). The three years when the spring tow values for sandlance were the lowest (1983, 1985, and 1986) were the three peak years for *C. finmarchicus* (Fig. 2). Conversely, the number of *C. finmarchicus* recorded on Stellwagen Bank during 1988 was one of the lowest throughout the study period. This is the year when the sandlance reached its maximum peak of abundance.

Changes in whale abundance

Humpback and fin whales showed a similar trend in abundance ($r_s = 0.3338$, $P<0.074$, Table 2), although the variation in the observed number of humpbacks between years was much more pronounced than for fin whales. The number of humpbacks/year increased from 3.59 whales/effort in 1982 to 9.00 whales/effort in 1985 (Table 1, Fig. 3). During 1986 humpback abundance declined to the minimum value recorded during the study period of 0.23 whales/effort. A small increase in 1987 was followed by a much larger increase in 1988 to 6.98 whales/effort (Fig. 3).

Less dramatic fluctuations between years were evident in the number of fin whales from 1982 to 1988. The abundance of fin whales declined from the maximum value of 3.71 whales/effort in 1984 to the low values of 1.9 and 1.4 whales/effort recorded in 1986 and 1987, respectively (Fig. 3). Although the numbers of fin whales/effort were lower in 1986–87 than in previous years, they did not change by more than an order of magnitude, as did other whale species. The number of fin whales increased to 3.61 whales/effort in 1988.

The strongest positive correlation occurred between right and sei whales ($r_s = 0.6842$, $P<0.0001$, Table 2). The right whale is a rare but regularly occurring species whose temporal occurrence in the study area has been generally restricted to the months of late-winter through early-spring (Winn et al. 1986, Brown and Winn 1989, Hamilton and Mayo 1990). This pattern was generally repeated in all years of the study period except 1986. Excluding 1986, there were only 12 right whale sightings from 1982 to 1988, and during most years there were no sightings (Table 1). However, in 1986, 174 right whale sightings (0.95 whales/effort) were recorded, and right whales were observed virtually every day throughout the summer (Hamilton and Mayo 1990).

Sightings of sei whales on Stellwagen Bank, and in Cape Cod Bay, are very rare in any season (CeTAP 1982, Mayo et al. 1988). We did not observe sei whales in the study area between 1982 and 1985 (Table 1). However, their numbers increased significantly in 1986 (when they were commonly observed) to 0.26 whales/effort (Table 1, Fig. 3). The occurrence of sei whales in 1986 was followed by an equally dramatic decline during 1987 (2 sightings, 0.01 sei whales/effort) and 1988 (no sightings). Between 1982 and 1988, the sei whale and right whale were abundant only during 1986 (Fig. 3), when the abundance of *C. finmarchicus* also reached a recorded regional maximum (Wishner et al. 1988).

Table 1

Total number of whales counted, number of surveys (effort), and number of whales (by species) per survey in southern Gulf of Maine (in parentheses) for each month and year of the study, 1982–88.

Year	Month	No. of surveys	No. of whales (per survey)			
			Humpback	Fin	Right	Sei
1982	June	27	90(3.33)	45(1.67)	0.00	0.00
	July	31	228(7.35)	33(1.06)	0.00	0.00
	Aug.	31	54(1.74)	227(7.32)	0.00	0.00
	Sept.	27	45(1.67)	63(2.33)	4(0.15)	0.00
	Total	116	417(3.59)	368(3.17)	4(0.03)	0.00
1983	June	46	229(4.98)	60(1.30)	0.00	0.00
	July	43	266(6.19)	192(4.47)	0.00	0.00
	Aug.	36	169(4.69)	172(4.78)	0.00	0.00
	Sept.	28	96(3.43)	37(1.32)	0.00	0.00
	Total	153	760(4.97)	461(3.01)	0.00	0.00
1984	June	43	317(7.37)	26(0.60)	0.00	0.00
	July	45	382(8.49)	224(4.98)	0.00	0.00
	Aug.	47	261(5.55)	232(4.94)	0.00	0.00
	Sept.	33	133(4.03)	141(4.27)	0.00	0.00
	Total	168	1093(6.51)	623(3.71)	0.00	0.00
1985	June	40	411(10.30)	143(3.58)	0.00	0.00
	July	53	400(7.55)	122(2.30)	0.00	0.00
	Aug.	46	654(14.21)	154(3.35)	0.00	0.00
	Sept.	31	63(2.03)	24(0.78)	0.00	0.00
	Total	170	1528(8.99)	443(2.61)	0.00	0.00
1986	June	44	16(0.36)	62(1.41)	2(0.05)	0.00
	July	54	20(0.37)	136(2.52)	6(0.11)	2(0.04)
	Aug.	51	4(0.08)	93(1.82)	44(0.86)	19(0.37)
	Sept.	34	2(0.05)	102(3.00)	122(3.58)	26(0.76)
	Total	183	42(0.23)	344(1.88)	174(0.95)	47(0.26)
1987	June	55	30(0.55)	56(1.02)	2(0.04)	0.00
	July	61	36(0.59)	48(0.79)	1(0.02)	2(0.03)
	Aug.	55	76(1.38)	150(2.73)	0.00	0.00
	Sept.	47	12(0.25)	52(1.10)	5(0.11)	0.00
	Total	218	154(0.71)	306(1.40)	8(0.04)	2(0.01)
1988	June	55	199(3.62)	253(4.60)	0.00	0.00
	July	62	535(8.63)	263(4.24)	0.00	0.00
	Aug.	62	455(7.34)	160(2.58)	0.00	0.00
	Sept.	52	424(8.15)	159(3.06)	0.00	0.00
	Total	231	1613(6.98)	835(3.61)	0.00	0.00

Table 2

Spearman Rank Correlation Coefficients (r_s) (upper number) and statistical level of significant difference (P) (lower number) between the abundance (whales/effort) of four baleen whale species on Stellwagen Bank, 1982–88. N = 28 for all paired tests.

	Humpback	Fin	Right	Sei
Humpback	1.0000	0.3338	−0.7753	−0.5507
	0.0000	0.0740	0.0001	0.0019
Fin		1.0000	−0.3250	−0.1461
		0.0000	0.0643	0.4248
Right			1.0000	0.6842
			0.0000	0.0001
Sei				1.0000
				0.0000

Several significant negative relationships also occurred between whale species (Table 2), most noticeably between humpbacks and right whales (r_s = −0.7753, P<0.0001), humpbacks and sei whales (r_s = −0.5507, P<0.0019), and fin whales and right whales (r_s = −0.3250, P<0.0643). This supports an intuitive interpretation of the data shown in Figure 3, notably the obvious phenomenon of low humpback and fin whale abundance in 1986, the only year right and sei whales were observed in significant numbers.

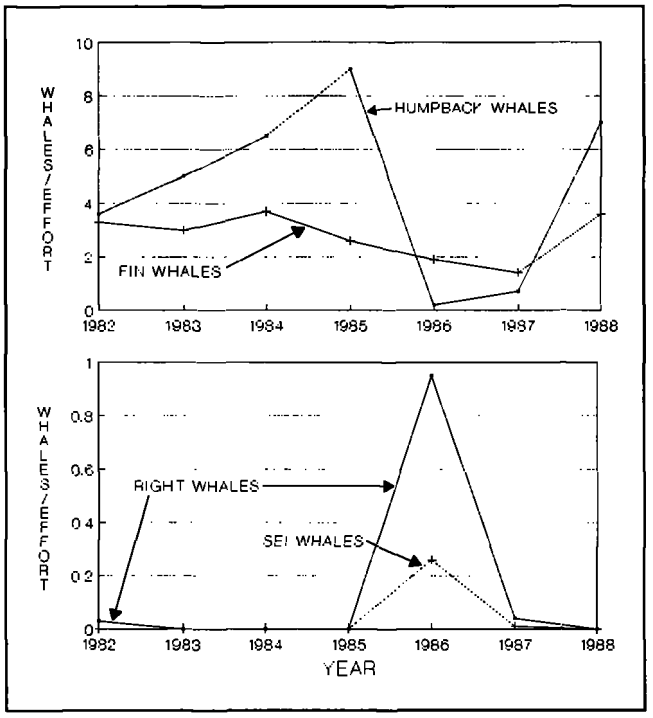

Figure 3
Average number of baleen whales per unit effort for each year of the study by species. Note: the scale for humpback and fin whales (upper) is different from that of right and sei whales (lower).

Discussion

The data presented here strongly suggest that major changes which occurred in the abundance and distribution of humpback, fin, right, and sei whales in the Stellwagen Bank area, 1982–88, were not independent of each other. During 1986 a dramatic decline in the abundance of humpback and fin whales also co-occurred with the unusual occurrence of right and sei whales during the summer of the same year. During 1987 and 1988 the abundance of baleen whales returned to a pattern similar to that observed in years prior to 1986 (right and sei whales absent, humpback and fin whales abundant). Concurrent with changes in whale abundance, an increase in copepod abundance on Stellwagen Bank in 1986 correlated with a significant decline in local sandlance abundance.

These correlations likely reflect both the similarities and dissimilarities in prey preferences of individual whale species, and the predator-prey relationship between sandlance and copepods. Given the documented preference of both right and sei whales for copepods (Nemoto 1959, Mitchell 1975a, Nemoto and Kawamura 1977, Watkins and Schevill 1979), a strong positive correlation between the two species should be expected. A similar correspondence exists between humpback and fin whales, both of which show an apparent preference for schooling fish in this region (Watkins and Schevill 1979, Mayo et al. 1988). Conversely, the strong negative correlations reported here would be expected between the planktiverous right and sei whales and the pisciverous humpback and fin whales.

Competition between whale species

These results, in support of previous studies (Kenney et al. 1981, Payne et al. 1986), suggest that the recent distribution of humpback whales in the Gulf of Maine has been dependent on the spatial distribution of sandlance in that region. These results follow a trend which began in the mid-1970s and, when taken with the results of previous studies (Overholtz and Nicolas 1979, CeTAP 1982, Hain et al. 1982, Mayo 1982, Mayo et al. 1988), indicate that sandlance has been the most important prey item of humpback whales in the Gulf of Maine since at least 1976.

It is also of interest that, while fin whales also closely followed the abundance patterns of sandlance, the overall changes in fin whale abundance fluctuated much less than those shown for the humpback whale. Although both whale species prey on a variety of taxa (Jonsgaard 1966) and have been characterized as generalists in their dietary preferences (Mitchell 1975a), behavioral differences between the two species may result in the ability of fin whales to exploit prey other than sandlance in the study area.

Watkins and Schevill (1979) noted clear differences between the feeding behavior of humpback and fin whales when exploiting the same prey (schooling fish); fin whales lunge horizontally and humpbacks vertically. Humpbacks are also known to produce "bubble clouds or nets" to potentially concentrate prey (Jurasz and Jurasz 1979, Hain et al. 1982, Hays et al. 1985), a feeding method not observed for fin whales. It has also been suggested that the streamlined form and greater speed of fin whales allow them to exploit more widely separated patches of prey than humpbacks (Brodie 1975, Whitehead and Carlson 1988). Thus fin whales may be more independent of local fluctuations in prey availability, explaining why they were located in the study area in 1986, after humpbacks had abandoned it.

Evidence clearly exists to support the belief that competition exists between right and sei whales (Mitchell 1975a, Kawamura 1978). However, Kenney et al. (1986) suggested that competition between right and sei whales in the shelf waters of the northeastern United States is unlikely given their present allopatric distributions (excluding 1986). Perhaps the more important ecological question concerns the reason for the present apparent allopatry. As detailed below, we

believe that this recent distributional change has resulted from differing degrees of interspecific competition between each of the two whale species and sandlance, moreso than from any competition between the whales themselves.

Competition between sandlance and planktiverous whale species

Historically, and in recent times, right whales have been recorded in the Stellwagen Bank region in late winter and early spring (Allen 1908, Allen 1916, Watkins and Schevill 1982, Schevill et al. 1986, Hamilton and Mayo 1990). The species has been virtually absent from the area in summer, when the population's distribution is centered in the Bay of Fundy and on the Scotian Shelf (Kraus et al. 1982, 1986; Mitchell et al. 1986; Winn et al. 1986; Stone et al. 1988; Murison and Gaskin 1989). Therefore, the prolonged residency by a group of right whales in the Stellwagen region throughout summer 1986 may represent the most significant departure from their usual seasonal pattern of occurrence recorded this century.

Is the annual movement of right whales out of the southern Gulf of Maine and into the Bay of Fundy and Scotian shelf areas in early summer related to increased activity and competition from planktiverous fish for calanoid copepods? The question of why right whales generally undertake this northward migration has yet to be resolved. The occurrence of right whales in the Stellwagen Bank area in the summer of 1986 implies that, if certain conditions are met, the normal northward movement is not inevitable for at least part of the population. The occurrence of planktiverous fish (either sandlance, herring or mackerel)—and consequently of increased competition through predation on, or disruption of, copepod patches in spring—may be a major factor in directing the seasonal movement of right whales out of the area to seek more acceptable patches elsewhere in the Gulf of Maine.

Not only are the size and density of copepod patches important to the feeding energetics of right whales, but also the relative proportions of adult copepods within each patch (Wishner et al. 1988). Wishner et al. (1988) described a copepod surface patch (with associated skim-feeding right whales) which contained a regional maximum of copepodite IVs and Vs, the older, energetically richest, developmental stages of copepods (Comita et al. 1966). Although the feeding ecology of right whales is likely more complex than previously thought (Mayo and Marx 1990), these dense aggregations of older, caloric-rich copepods seem to be the required characteristics for energetically successful foraging by right whales (Kenney et al. 1986, Wishner et al. 1988).

The principal diet of sandlance >21 mm is also the larger, older developmental stages of *C. finmarchicus* (Norcross et al. 1961, Scott 1973, Monteleone and Peterson 1986). If the superabundant sandlance are selecting the caloric-rich stages of the copepod population, then there may be insufficient prey available in the remaining developmental stages (independent of abundance) to provide right whales with the required energy densities (as described by Kenney et al. 1986) to meet the metabolic and reproductive demands of the right whale population. Therefore, during those years when sandlance (or ecologically similar planktiverous fish species) are abundant, intraspecific competition may be so intense that right whales may only be achieving basal metabolic needs in the southern Gulf of Maine, precipitating the northward movement of right whales immediately following the period of increased sandlance abundance and activity.

The occurrence of consistent numbers of sei whales in 1986 followed many years in which the species had not been recorded from the study area during any season (Mayo et al. 1988). Jonsgaard and Darling (1977) describe "invasion years" where unusually large numbers of sei whales occur in an area. These years are generally followed by an equally sharp decrease in the number of whales in the same area. Albeit simple, an "invasion year" in response to increased prey abundance accurately describes the occurrence of sei whales on Stellwagen Bank during 1986.

While sei whales seem to prefer planktonic prey (Watkins and Schevill 1979), they have the ability to forage on fish (Nemoto 1959, Nemoto and Kawamura 1977). Despite this, available distributional evidence suggests that sei whales have not exploited the abundant sandlance in the Gulf of Maine to a significant extent. Scant data suggest that sei whales in this region instead subsist primarily on euphausiids and copepods which occur in the waters south of Georges Bank (Kenney and Winn 1987). By remaining on the shelf edge and exploiting a wider range of planktonic (and possibly fish) prey, they may be able to minimize the effect of competition from sandlance for copepods, separating them from the more stenophagic right whales.

Since the early 1950s sandlance populations have fluctuated on remarkably few occasions. Monteleone et al. (1987) described relatively high sandlance densities during 1965–66 (following the depletion of herring and mackerel stocks) and 1978–79 (following the larval sandlance explosion in 1975), and exceptionally low densities of sandlance in 1971–74. Meyer et al. (1979) also reported that adult sandlance were not reported on Stellwagen Bank between 1967–76 and that the mean sandlance catch/10 m^2 in spring 1977 was nine times greater than in spring 1974. Therefore, the two recorded time intervals when sei whales and

right whales were most abundant in the study area (April 1970, reported by Watkins and Schevill 1982; and during 1986) were during periods of documented low adult sandlance densities and observed copepod maxima. The March 1975 observations by Watkins and Schevill (1979) of a sei and right whales feeding together in Cape Cod Bay were also made in the interval between the reduction of planktiverous herring and mackerel stocks and the subsequent population explosion of adult sandlance. These observations further support the theory that planktiverous fish abundance has negatively impacted the occurrence of planktiverous whale species in the region.

In this paper, we have examined species interactions between sandlance (as prey and competitor), *C. finmarchicus* (as prey), and the abundance of four species of baleen whales in the southern Gulf of Maine. The interpretation of these interactions, although largely inductive, provide useful management insights into the relationships between planktiverous finfish and the cetacean community. This interpretation also presents an interesting multispecies-management dilemma regarding finfish and cetacean populations in this region, as well as potential conflicts between single-species recovery plans and two ecologically different groups of endangered whales, pisciverous and planktiverous.

The present abundance of sandlance in the Gulf of Maine followed a long-term depletion of other planktiverous fish species through overfishing (Grosslein et al. 1980). Although it is impossible to reconstruct the extent of competition between finfish (herring and mackerel stocks) and planktiverous whales prior to the mid-1960s, the similarities in prey preference and trophic relationships between mackerel, herring and sandlance (Bowman et al. 1984) certainly suggest that competition between herring-mackerel stocks and planktiverous whales could have existed. We hypothesize that the abundance and distribution of planktiverous fishes have played a significant, perhaps critical, role in structuring (as prey and competitor) baleen whale populations in the Gulf of Maine.

The present, concentrated distribution of humpbacks in the Gulf of Maine is directly related to the distribution and increased abundance of sandlance in that region. Alternatively, the recovery of the stenophagic right whale (historically and at present) may indeed be inhibited in large regions of the northwest Atlantic by competition for its prey by herring, mackerel, and sandlance. Despite decades of protection Schevill et al. (1986) suggested that the [abundance of the] right whale population [now] which passes Cape Cod is "at worst slightly smaller than it was in the 17th century". The abundance and distribution (and continued recovery) of right whales, in contrast to humpback and fin whales, may be contingent upon anomalous disruptions in the occurrence of abundant, ecologically equivalent finfish stocks, which at present are largely human-induced.

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