A review of the status of harbour seals *(Phoca vitulina)* in the Northeast United States of America

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ABSTRACT

We conducted a review of the literature and unpublished databases to describe the distribution, abundance, ecology and status of harbour seals *(Phoca vitulina concolor)* in U.S. Atlantic waters. The harbour seal is the most abundant and widespread seal species in this area. Since passage of the U.S. Marine Mammal Protection Act of 1972, the number of harbour seals observed during the pupping season in this region has increased from about 10,500 animals in 1981 to 38,000 animals in 2001 (uncorrected counts), an average annual rate of 6.6%. This increase has been relatively consistent over the 20 years, and there is no indication that the population size has stabilized. Correspondingly, the seasonal distribution has expanded and interactions between seals and anthropogenic activities have increased.

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INTRODUCTION

Harbour seals *(Phoca vitulina concolor)* have been recorded in the journals and sketches of European settlers in the northeastern U.S. since the beginning of the 17th century (Katona *et al.* 1993, deHart 2002). Historically, harbour seals were killed by fishermen and others as they were considered a nuisance and a competitor for fish (Gilbert *et al.* 2005). New England hunting and bounty programmes resulted in local extinction (Katona *et al.* 1993). However, since 1972 seals have been protected in U.S. waters under the Marine Mammal Protection Act (MMPA).

Following enactment of the MMPA harbour seal studies were initiated along the coast of Maine (Richardson 1976, Wilson 1978). The first studies provided information on distribution, abundance, pupping, social behaviour, and potential impact of seals on fishery resources. Subsequent studies expanded the geographic focus and provided more detailed information on distribution and abundance, fishery by-catch, and diet (Payne and Selzer 1989, Gilbert and Wynne 1984, Barlas 1999, Gilbert *et al.* 2005).

The purpose of this paper is to review available information on distribution, population recovery and growth, fisheries interactions, diet, and strandings of harbour seals in U.S. Atlantic waters (Fig. 1), and to contribute to the NAMMCO goal of summarizing available data on North Atlantic harbour seals.

DISTRIBUTION

In the North Atlantic Ocean, the harbour seal is found in all nearshore waters and adjoining seas from about 30°N to 80°N (Katona *et al.* 1993, Burns 2002). The boundary between the eastern and western Atlantic (EA and WA) populations is unknown (Burns 2002). In the western North Atlantic (WNA), harbour seals are distributed from the eastern Canadian Arctic and Greenland south to New Jersey, and occasionally as far south as the Carolinas (Mansfield 1967, Boulva and McLaren 1979, Katona *et al.* 1993, Teilmann and Dietz 1994, Gilbert and Guldager 1998, Baird 2001). This species is the most abundant and widely distributed phocid seal in Northeast US coastal waters (Baraff and Loughlin 2000, Gilbert *et al.* 2005).

Harbour seals are year-round inhabitants in the coastal waters off Maine and eastern Canada (Katona *et al.* 1993, Baird 2001, Jacobs and Terhune 2000, Harris *et al.* 2003, Hammill *et al.* 2010), and occur seasonally along the Massachusetts to New Jersey coasts (Fig. 1) between September and May (Schneider and Payne 1983, Barlas 1999, Hoover *et al.* 1999, Slocum *et al.* 1999, Schroeder 2000, deHart 2002). A general southward movement in the fall from the Bay of Fundy to north-eastern U.S. coastal waters has been suggested based on concurrent declines in numbers observed hauled out in the Bay of Fundy and increases in numbers observed in southern New England (Rosenfeld *et al.* 1988, Whitman and Payne 1990, Barlas 1999). A reverse movement occurs in the same area prior to pupping. Births occur from May through early June along the Maine coast, and progressively later in eastern Canada (Richardson 1976, Wilson 1978, Gilbert and Stein 1981, Whitman and Payne 1990, Temte *et al.* 1991, Kenney 1994, Bowen *et al.* 2003, Dubé *et al.* 2003; Hammill *et al.* 2010). Overall, the geographic range throughout coastal New

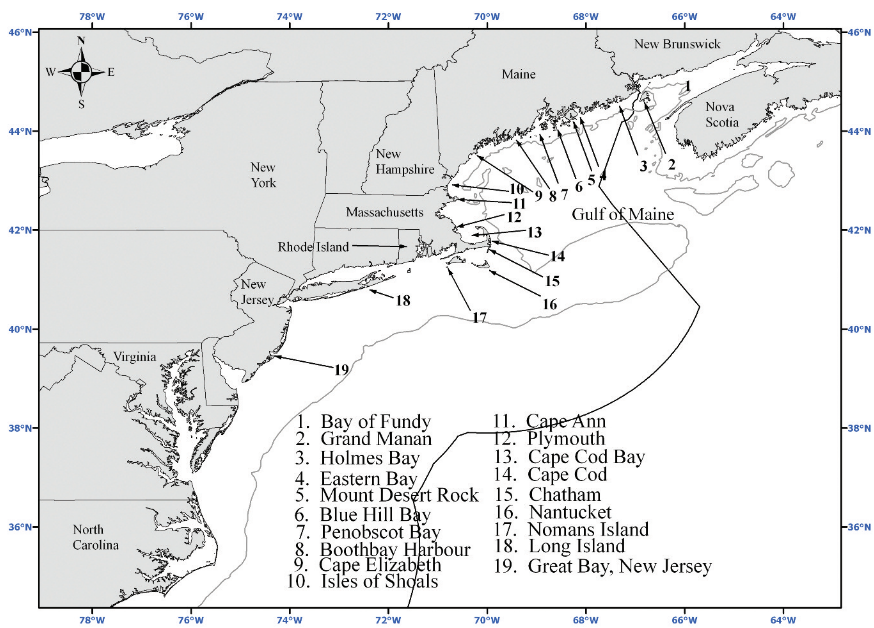

Fig. 1. *Map of Northeast U.S. and adjacent Canadian provinces showing location of place names mentioned in the text.*

England has not changed significantly during the last century (Payne and Selzer 1989).

STOCK DELINEATION

Stanley *et al.* (1996) examined worldwide patterns in harbour seal mitochondrial DNA, which indicate that WNA and eastern North Atlantic (ENA) harbour seal populations are highly differentiated. Further, they suggested that harbour seal females are regionally philopatric; thus population or management units are on the scalof a few hundred kilometres. Although the stock structure of the WNA population is unknown, Temte *et al.* (1991) hypothesized that harbour seals found along the eastern U.S. and Canadian coasts represent one population. Boulva and McLaren (1979) noted some distinction in the numbers and frequency of super-numerary teeth from harbour seals collected at different locations in Eastern Canada, and mitochondrial comparisons by Stanley *et al.* (1996) indicated three distinct groups of harbour seals in Canada (Hudson Bay, Miquelon Islands, and Sable Island). O'Corry-Crowe *et al.* (2003) defined stocks of harbour seals in Alaska at a scale that would lead one to expect some stock structure in the harbour seals in Maine. Wade and Angliss (1997) also note that stock separation could be expected in an area the size of the Gulf of Maine.

POPULATION SIZE AND TRENDS

Colonists and fur traders provided information on species and rough quantities of skins and furs traded (Brown 1913, Quinn and Quinn 1983, deHart 2002). Early explorers described seals as "teeming" along the coast of Maine, and harbour seals were significantly represented in middens of coastal native settlements (Speiss and Lewis 2001). Despite hunting and sub-

Table 1. Summary of 1973 to 1999 uncorrected seasonal counts (see Table 2 for abundance survey counts) of harbour seals in U.S. Atlantic waters, 95% confidence interval are in parentheses.

Location	Date	Counts	Reference
Coast of Maine	summer 1973 & 1974	5,075	Richardson (1976)
Eastern Long Island to Penobscot Bay, Maine	March 1981	2,834	Gilbert and Stein (1981)
	March 1986	5,775	Gilbert pers. comm.
Nomans Island to New Hampshire	January-February 1983	2,858 (172)	Payne and Selzer (1989)
	January-February 1984	2,894 (172)	
	January-February 1985	3,945 (76)	
	January-March 1986	3,870 (300)	
	March 1987	4,194 (255)	
Eastern Long Island & Rhode Island	March 1986	179	
	March 1987	271	
Isles of Shoals to Nomans Island	December 1998 - April 1999	1,667 to 5,010	Barlas (1999)
Nomans Island to eastern Long Island	February & April 1999	1,116 to 1,266	

sequent bounty programmes, no estimates of the historical population are available (deHart 2002, Lelli *et al.* 2009).

Richardson (1976) conducted the first aerial surveys of harbour seals along the coast of Maine. His count of 5,075 seals was an accumulation of counts obtained during the summers of 1973 and 1974 (Table 1). As such, the counts could have been confounded by seal movements and changes in time individual animals spent on land. Following a die-off of harbour seals in the winter of 1980-81 due to avian influenza (Geraci *et al.* 1982), Gilbert counted 2,834 harbour seals in coastal areas between eastern Long Island and Penobscot Bay (Maine) in March 1981 (Gilbert and Stein, 1981). The March 1986 (Table 1) survey covered the coast of Maine, and was coordinated with other surveys conducted in southern New England.

Payne and Selzer (1989) conducted aerial surveys from Nomans Island to the New Hampshire border in winter (1983-1987), and extended their survey to eastern Long Island in March 1986 and 1987 (Table 1). These surveys indicated that several thousand seals were "wintering" in coastal waters between New Hampshire and south-eastern Massachusetts. Barlas (1999) surveyed the same coastal areas during a series of monthly aerial surveys conducted between December 1998 and April 1999 (Table 1). These counts documented anecdotal reports of seasonal increases in the number of harbour seals around Cape Cod and eastern Long Island. For example, winter/spring counts in eastern Long Island Sound averaged 150 and 350, respectively, in the aforementioned studies, and 590 in more recent (2005-2008) surveys (R. DiGiovanni, pers. obs.). In 2000 and since 2005, the National Marine Fisheries Service has been conducting intermittent seasonal (October to April) monitoring surveys from Plymouth, Massachusetts, to Nomans Island. However, these data have not been counted.

Counts of harbour seals along the coast of Maine were also obtained during the pupping seasons in 1981, 1982 (partial), 1986, 1993, 1997, and 2001 to obtain minimum population estimates (Gilbert *et al.* 2005; Table 2). Prior to 1997, replicate counts were not accomplished on any of the aerial surveys. In 1997 three replicate surveys were conducted from late May to early June in a section of Penobscot Bay to evaluate count variability, and the average of these counts was added to other survey regions. Counts during the moulting season were obtained in early August of 1993 and 1997. The 1993 (26,050) and 1997 (19,960) August counts were, respectively, 11.2% and 35.8% lower than the corresponding pupping period counts, therefore spring counts were deemed to provide a better index of population growth. In 2001, the daily counts were corrected based on the fraction of radio-tagged seals relocated (Gilbert *et al.* 2005). Estimation of the correction factor and its variance was accomplished using the approach of Huber *et al.* (2001). Correcting for uncounted seals in the water, the estimated total number of harbour seals in 2001 was 99,340 individuals. Of these, approximately 24.5% (23,722) were pups (Gilbert *et al.* 2005).

Table 2. Counts of harbour seals and pups from surveys along the Maine coast.

	1981 May-June[1]	1986 May-June[1]	1993 May-June[1]	August[2]	1997 May-June[1]	August[2]	2001 May-June[1]	2001 corrected (with 95% C.I.) May-June[1]
Total seals	10,543	12,940	29,538	26,054	31,078	19,956	38,014	99,340 (83,118-121,397)
Pups	676	1,713	4,250		5,359		9,282	23,722 (19,911-28,900)
% pups	0.064	0.132	0.144	na	0.172	na	0.244	

[1] from Gilbert *et al.* (2005)

[2] from Gilbert and Guldager (1998)

The number of harbour seals observed during the pupping season, increased from 10,543 in 1981 to 38,014 in 2001 (Table 2), an annual rate of 6.6%. This increase has been relatively consistent over the 20 years, and there is no indication that the population size has stabilized. However, the increase in harbour seal abundance has not been consistent along the coast of Maine. For example, seal numbers from Eastern Bay to the Canadian border appear to be no longer increasing (Gilbert *et al.* 2005).

LEGISLATION AND PROTECTION

Maine and Massachusetts established bounty programmes in the late 1800s to reduce seal populations and perhaps increase fish landings (Allen 1942, Katona *et al.* 1993, Lelli and Harris 2006). Maine's bounty programme was in place from 1891 to 1905 and from 1937 to 1945 (Lelli and Harris 2006). The Massachusetts bounty was lifted in 1962. By the 1900s, seals in Maine were locally extirpated (Katona *et al.* 1993). Similarly, the Massachusetts programme resulted in local extirpation including a breeding colony in Cape Cod Bay (Katona *et al.* 1993). Lelli *et al.* (2009) estimated that between 72,000 and 135,000 seals (*i.e.*, species composition could not be determined) were killed in the Maine and Massachusetts bounty hunts.

The U.S. Marine Mammal Protection Act (MMPA) provides protection to all marine mammals in U.S. waters (Baur *et al.* 1999, http://www.nmfs.noaa.gov/pr/pdfs/laws/mmpa.pdf). This legislation prohibits any marine mammal "take," which is defined in the MMPA to mean "to harass, hunt, capture or kill, or attempt to harass, hunt, capture or kill any marine mammal". However under Section 101(a) and (b) takes are permitted for scientific research, public display, and incidental to commercial fisheries. The 1994 amendments to the MMPA provided new requirements for monitoring, assessing, and mitigating marine mammal interactions with commercial fisheries (Barlow *et al.* 1995, Baur *et al.* 1999). Under this revised management process, NMFS and the U.S. Fish and Wildlife Service must regularly update stock assessment reports (SAR) for all marine mammal stocks found in U.S. waters (*e.g.* Waring *et al.* 2007). An important component of the SAR is the evaluation of anthropogenic sources of mortality, particularly commercial fisheries, with respect to the species' potential biological removal (PBR) (Wade and Angliss 1997). Should fishery takes exceed PBR, the stock's status is reclassified as strategic and the NMFS is obliged to develop measures to reduce these takes to PBR.

In U.S. waters, both harbour seal and grey seal *(Halichoerus grypus)* stocks appear to be increasing, and the levels of anthropogenic takes have been reduced to well below PBR; as such, these seal stocks are deemed to be MMPA success stories. However, increasing seal populations have raised concerns regarding their ecological role in the marine environment, and particularly their impact on fishery resources. The MMPA generally prohibits, and public policy is opposed to, lethal programmes to address seal-fishery interactions in U.S. waters.

GENERAL ECOLOGY

Reproduction and moulting

Along the Northeast U.S. coast, pupping and breeding normally occur from late May to early June north of the New Hampshire/Maine border (Richardson 1976, Guldager 2001, Gilbert *et al.* 2005; Fig. 1), although breeding/pupping has been reported as far south as Cape Cod in the early part of the twentieth century (Temte *et al.* 1991, Katona *et al.* 1993). In Maine, pups are born on rocky ledges that are used consistently from year to year (*i.e.*, Penobscot Bay, Blue Hill Bay) (Guldager 2001). The peak of pupping occurs in late May (Skinner 2006). Little pupping occurs south of New Hampshire (Payne and Schneider 1984, Barlas 1999), although anecdotal information suggests that in recent years pupping has been occurring at haulout sites near Plymouth, Massachusetts. Occasional strandings of neonates in Massachusetts, Rhode Island and eastern Long Island also imply some degree of pupping south of Maine (NMFS unpublished data).

Moulting occurs during July and August along the Maine coast, generally on outer bay and offshore ledges (Richardson 1976, Gilbert and Wynne 1984). However, no studies have been conducted to precisely define the moulting season in this region.

Habitat

As elsewhere, harbour seals use a variety of terrestrial and aquatic habitats in U.S. waters, and their activities are influenced by regional topography, life history requirements, environmental parameters, anthropogenic activities, prey distribution, and perhaps inter-specific competition with grey seals (Richardson 1976, Gilbert and Stein 1981, Schneider and Payne 1983, Thompson 1989, Payne and Selzer 1989, ,Stobo and Fowler 1994, Barlas 1999, Lucas and Stobo 2000, Schroeder 2000, deHart 2002, Bjørge *et al.* 2002b, Bowen *et al.* 2003, Renner 2005, Robillard *et al.* 2005, Hammill *et al.* 2010). Rocky areas (*i.e.* small islands, isolated rocks, tidal ledges) are the predominant haulout substrate in coastal waters from the Maine-Canadian border south to Plymouth, Massachusetts (Richardson 1976, Schneider and Payne 1983, Harris *et al.* 2003, Gilbert *et al.* 2005, Renner 2005). Rocky substrates are also used during the pupping, breeding and moulting seasons when harbour seals are concentrated in Maine coastal waters (Richardson 1976, Katona *et al.* 1993, Guldager 2001, Gilbert *et al.* 2005). Between Cape Cod and New Jersey (most southern notable haulout sites), the coastal geology is more variable and seals utilize a wider variety of substrates (*i.e.* tidally exposed sand and gravel bars, sand-peat hummock in tidal marshes, sandy beaches and islands, rock outcroppings and stone jetties) (Schneider and Payne 1983, Payne and Selzer 1989, Barlas 1999, Schroeder 2000, deHart 2002). Further, storm events alter the characteristics of or access to "sandy" haulout sites, particularly around the outer portion of Cape Cod and eastern Nantucket Sound. Both harbour and grey seals readily acclimate to newly formed haulout sites (*i.e.* barrier beach breaks, re-emerged sand bars), thus giving the appearance of a "sudden influx" or "population growth" of seal populations in Cape Cod waters.

Seals haul out on nearshore ice (Katona *et al.* 1993), and small groups have been observed on ice floes around Cape Cod in winter when conditions restrict access to traditional (*i.e.* sandy beach) haulout sites (John Prescott, pers. comm., Massachusetts Audubon Society, Wellfleet, Massachusetts).

Movements

Harbour seals are considered to be non-migratory (Thompson 1993, Bowen and Siniff 1999), although along the north-eastern U.S. and elsewhere they undergo seasonal movements that are related to breeding, moulting, and foraging. Information on movements is available from several small-scale tagging projects involving wild-caught animals and rehabilitated seals. In the early 1980s flipper tags, streamers, and VHF radio tags were used to track movements of pups captured during late spring-early summer in Holmes, Blue Hill, and East Penobscot Bays (Gilbert and Stein 1981, Gilbert and Wynne 1983, 1984, 1985, Waring *et al.* 2006; Fig. 1). Most of the resighted animals were located in the same area where they were originally tagged. However, two seals were re-sighted in Nova Scotia: one the same summer and the other the next summer. Four were seen in the Cape Cod-Nantucket area the winter and spring following tagging. Some of the pups tagged by Skinner (2006) were reported from Long Island and New Jersey the following winter.

In early May 1999, four harbour seals were captured and radio-tagged in Western Penobscot Bay (Waring *et al.* 2006; Fig. 1). Aerial search flights were conducted in June and most relocations were within Penobscot Bay. Similar survey operations were conducted in Chatham, Massachusetts and Western Penobscot Bay in early spring 2001. Twelve and 17 seals from Chatham and Western Penobscot Bay, respectively, were tagged and subsequently relocated prior to (1-14 May) and during (16 May-4 June) aerial abundance surveys (Gilbert *et al.* 2005, Waring *et al.* 2006; Fig. 1). Most of the Chatham and Penobscot Bay tagged seals were detected within the greater Penobscot Bay area, suggesting that some of the harbour seals occupying Massachusetts winter haulout sites disperse to mid-Maine coastal waters prior to the pupping season.

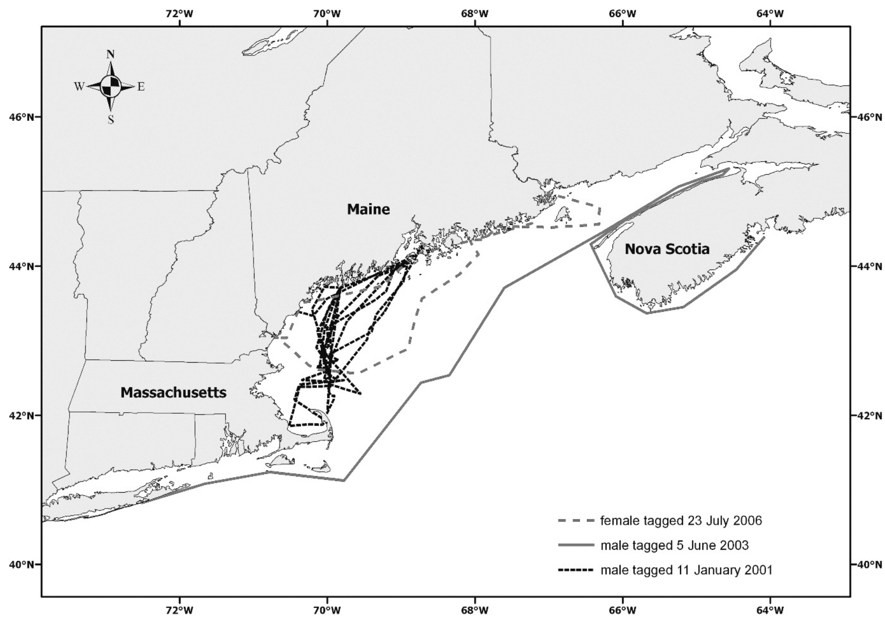

***Fig. 2**. Movement of three satellite tagged juvenile harbour seals from WhaleNet (http://whale.wheelock.edu)*

In 2004, 5 harbour seal pups, all approximately 1 month old, were captured and satellite-tagged in Blue Hill Bay (Bertrand *et al.* 2005). The pups were monitored from June to October when all tags stopped transmitting (Bertrand *et al.* 2005). These pups exhibited a wide range of movements. Two moved north to Nova Scotia, 2 travelled along the Maine coast between Blue Hill Bay and Jeffreys Bank, located ca 50 nm south of Penobscot Bay, and one travelled south to Stellwagen Bank near the tip of Cape Cod (Bertrand *et al.* 2005).

Since the mid-1990s, rehabilitated stranded seals have been satellite-tagged and released in several locations along the northeast U.S. coast, but primarily in Massachusetts and eastern Long Island (WHALENET at http://whale.-wheelock.edu). Data from these animals have provided limited evidence of trans-boundary movements between the U.S. and Canada. Only two of the rehabilitated and tagged seals (n=17) released in coastal waters from Maine to Virginia between July 1997 and December 2007 were detected in Canadian waters. Satellite tracks of 3 seals (Fig. 2) are representative of the movement patterns. One satellite-tagged animal released off Cape Elizabeth, Maine in January 2001 moved into the central portion of the Gulf of Maine, and made some excursions into Penobscot Bay until the signal was lost in late May. Another released off Long Island, New York in June 2003 moved along the Maine coast and into the Bay of Fundy, and then around southwest Nova Scotia where the signal was lost in early August. The third was released off New Hampshire in July 2006 and was detected east of Grand Manan in September. However, a juvenile harbour seal tagged on Sable Island, Nova Scotia stranded on the northern New Jersey coast, a straight line distance of 1,475 km (http://www.-mi.mun.ca/mi net/fishdeve/harbour.htm). Based on these data, harbour seals appear to stay near the coast in relatively shallow waters off the northeast U.S., which is similar to findings in other North Atlantic waters (Thompson 1993, Bjørge *et al.* 1995, Dietz *et al.* 2003, Lesage *et al.* 2004, Robillard *et al.* 2005).

Diet

Information on harbour seal prey species in U.S. Atlantic waters is principally derived from analyses of (a) faecal or "scat" samples collected at haulouts and (b) of stomachs of seals that had been incidentally caught in fishing gear (Payne and Selzer 1989, Ferland 1999, Williams 1999, Slocum *et al.* 2005, Craddock and Polloni 2006). Scat-based information is primarily available from Cape Cod and to a lesser extent from haulout sites north and south of this region (Payne and Selzer 1989, Ferland 1999) (Table 3). Payne and Selzer (1989) determined that American sand eel (lance) (*Ammodytes* spp.) was the dominant

Table 3. Prey items found in harbour seal scat and stomach collections between 1989 and 2005.

Prey species	Region	Sample type	Relative Importance (M, m)[1]	Study
Ammodytes americanus	Cape Cod	Scat	M	Payne and Selzer 1989, Ferland 1999
	Isles of Shoals	Scat	m	Payne and Selzer 1989
	MA north shore	Stomach [2]	M	Ferland 1999
	Gulf of Maine	Stomach [3]	m	Williams 1999, Craddock and Polloni 2006
Clupea harengus	Cape Cod	Scat	m	Payne and Selzer 1989, Ferland 1999
	Maine	Stomach [2]	M	Ferland 1999
	Gulf of Maine	Stomach [3]	M	Williams 1999
	New Jersey	Scat	M	Slocum *et al.* 2005
Brevoortia tyrannus	Cape Cod	Stomach [3]	m	Williams 1999
Alosa pseudoharengus	Cape Cod	Stomach [3]	m	Williams 1999
Scomber scombrus	Cape Cod	Scat	m	Payne and Selzer 1989, Ferland 1999
Gadus morhua	Isles of Shoals	Scat	M	Payne and Selzer 1989
	Cape Cod	Scat	m	Ferland 1999
	Gulf of Maine	Stomach [3]	m	Williams 1999, Craddock and Polloni 2006
Meloanogrammus	Isles of Shoals	Scat	M	Payne and Selzer 1989
aeglefinus	Gulf of Maine	Stomach [3]	m	Craddock and Polloni 2006
Pollachinus virens	Gulf of Maine	Stomach [3]	m	Craddock and Polloni 2006
Enchelyopus cimbrius	Isles of Shoals	Scat	M	Payne and Selzer 1989
	Gulf of Maine	Stomach [3]	m	Craddock and Polloni 2006
Gadidae spp.	Cape Cod	Scat	m	Payne and Selzer 1989
Merluccius bilinearis	Cape Cod	Scat	m	Ferland 1999
	New Hampshire	Stomach [2]	M	Ferland 1999
	Gulf of Maine	Stomach [3]	M	Williams 1999
	Gulf of Maine	Stomach [3]	M	Craddock and Polloni 2006
Urophycis sp.	Cape Cod	Scat	m	Ferland 1999
	Gulf of Maine	Stomach [3]	m	Williams 1999
	Gulf of Maine	Stomach [3]	M	Craddock and Polloni 2006
Urophycis regia	New Jersey	Scat	M	Slocum *et al.* 2005
Sebastes fasciatus or	Isles of Shoals	Scat	M	Payne and Selzer 1989
Helicolenus actylopterus	New Jersey	Scat	M	Slocum *et al.* 2005
dactylopterus	Gulf of Maine	Stomach [3]	M	Craddock and Polloni 2006
Pseudopleuronectes	Cape Cod	Scat	m	Ferland 1999
americanus	New Jersey	Scat	m	Slocum *et al.* 2005
Limanda ferruginea	Isles of Shoals	Scat	M	Payne and Selzer 1989
	Gulf of Maine	Stomach [3]	m	Craddock and Polloni 2006
Hippoglossoides	Isles of Shoals	Scat	M	Payne and Selzer 1989
platessoides	Gulf of Maine	Stomach [3]	m	Craddock and Polloni 2006
Scopthalmus aquosus	New Jersey	Scat	m	Slocum *et al.* 2005
Etropus mirostomus	Gulf of Maine	Stomach [3]	m	Craddock and Polloni 2006
unidentified flounder	Cape Cod	Scat	m	Payne and Selzer 1989

Table 3. *continued*

Prey species	Region	Sample type	Relative Importance (M, m)[1]	Study
skates (*Raja* spp.)	Cape Cod	Scat	m	Payne and Selzer 1989
Illex illecebrosus	Cape Cod	Scat	m	Payne and Selzer 1989
Loligo pealei	Cape Cod	Scat	m	Payne and Selzer 1989

1 Major (M) or minor (m) importance based on report results
2 Stranded animals
3 Fishery by-catch

prey (frequency of occurrence) in the Cape Cod region during the mid-1980s (Table 3). However, the percentage of sand eel in the scat collections differed by season. Other prey species included Atlantic herring *(Clupea harengus* L.*)*, Atlantic mackerel *(Scomber scombrus),* unidentified flounder, Gadidae spp., skates, northern short-finned *(Illex illecebrosus)* and long-finned inshore squid *(Loligo pealei)* (Table 3).

Scat samples collected further north at the Isles of Shoals (Fig. 1) were not dominated by any single prey, but redfish *(Sebastes* spp.*)*, Atlantic cod *(Gadus morhua)*, haddock *(Melanogrammus aeglefinus)*, and four-bearded rockling *(Enchelyopus cimbrius)* made up 44% of the prey (Payne and Selzer 1989, Table 3). Sand eel was represented by a single otolith.

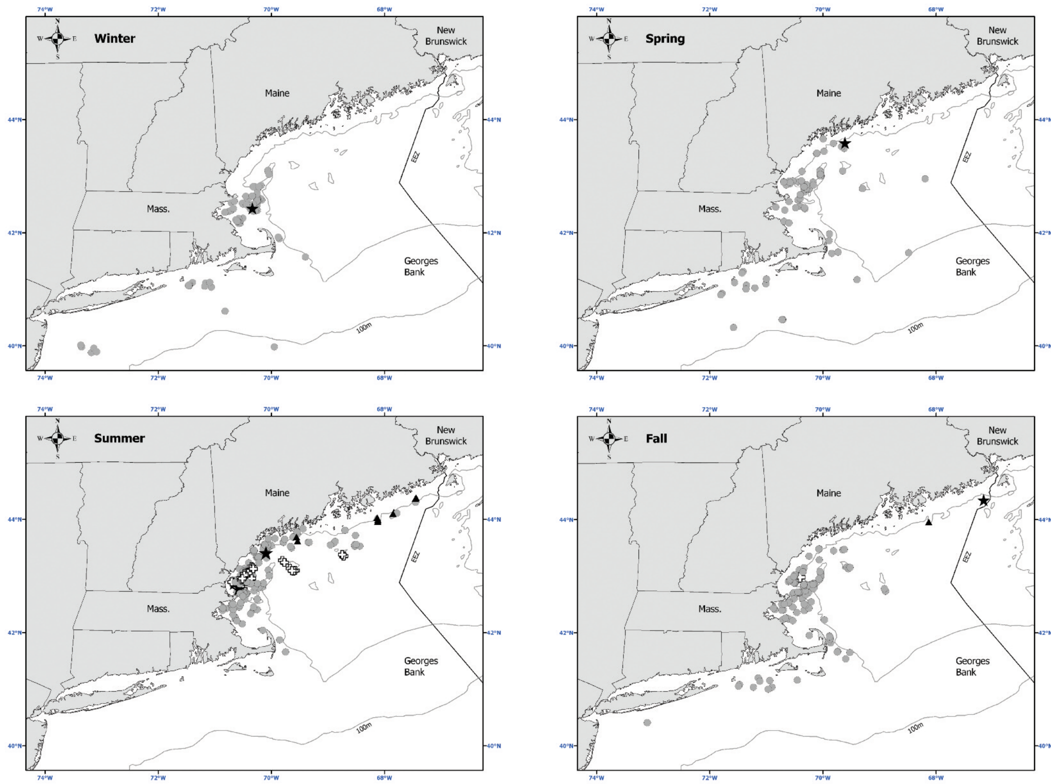

Fig. 3. *Observed harbour seal by-catch by gear and season in U.S. Atlantic fisheries (1989-2006). Star symbols are bottom otter trawl, circles are anchored sink gillnet, crosses are drift sink gillnet and triangles are herring purse seine.*

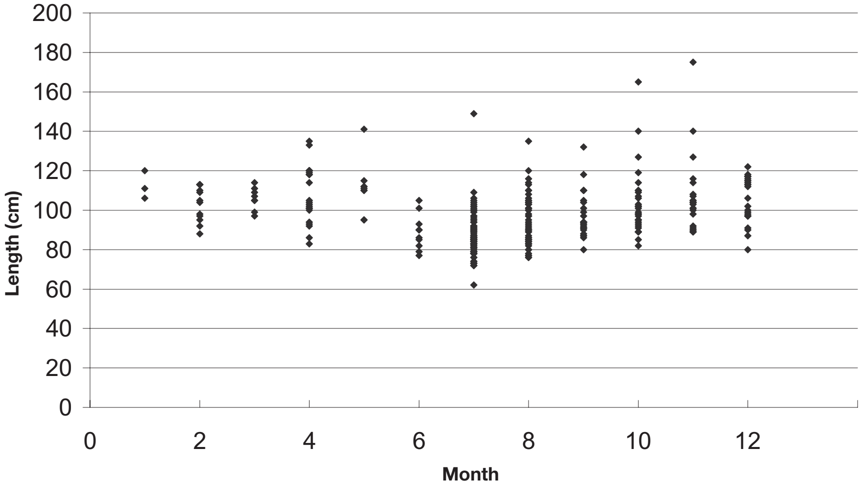

Fig. 4. *Length frequencies of harbour seals by-caught in observed fisheries (1989-2006).*

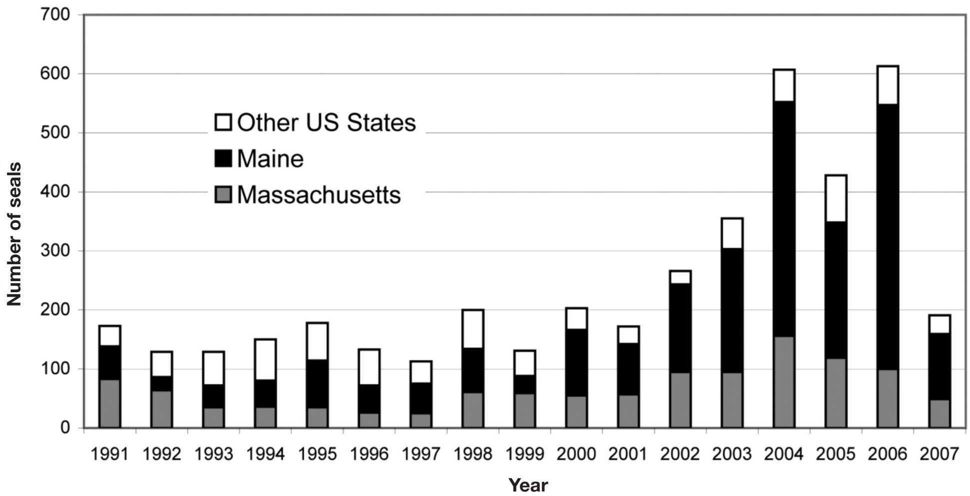

Fig. 5. *Harbour seal strandings for Maine, Massachusetts and all other states (New Hampshire to Florida), 1991-2007, based on data from NMFS national stranding database.*

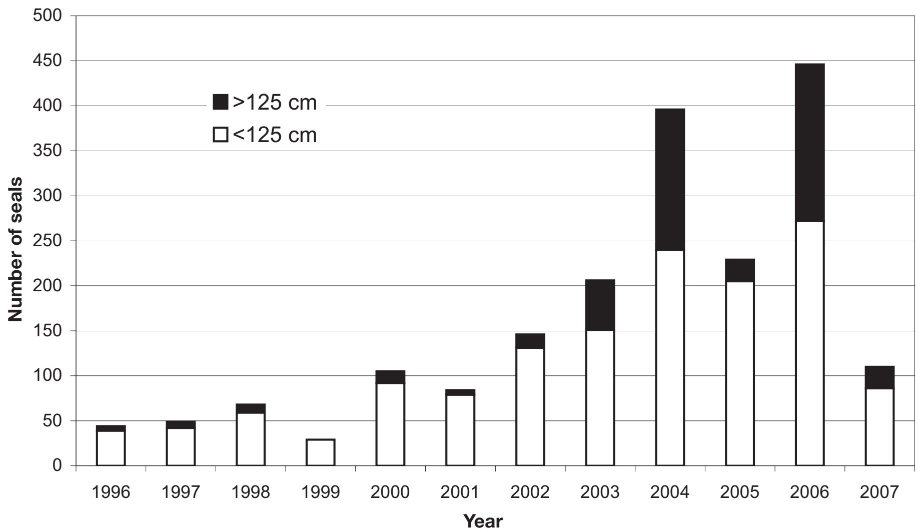

Fig. 6. *Number of adult (>125 cm length) and subadult (<125 cm) harbour seal strandings reported in Maine during 1996-2007, based on data from NMFS national stranding database.*

Ferland (1999) analyzed scat samples collected in winter 1999 on Cape Cod. Based on frequency of occurrence, sand eel (85%) was the dominant prey item, followed by Atlantic cod at 4% (Table 3). Ferland (1999) noted that these findings differed little from the Payne and Selzer (1989) study. Ferland (1999) also examined the stomach contents of 25 seals stranded from Cape Cod to Maine. The majority of the samples (17/25) were from seals entrapped in the intake forebay at the New Hampshire nuclear power plant. Silver hake *(Merluccius bilinearis)* (69%), and red/white hake *(Urophysis* sp.*)* (16%) were the dominant prey items. Major prey items in stomachs in other Gulf of Maine regions were: Atlantic herring (Maine), silver hake (Cape Cod) and sand eel (northern Massachusetts).

Slocum *et al.* (2005) examined scat samples collected over a 5-year period (1996-2002) from a wintering colony in Great Bay, New Jersey. This study provided the first diet data south of New England. Thirteen species were identified, but the two most abundant prey species (71% combined) were spotted hake *(Urophycis regia)* and Atlantic herring (Table 3). Less common species included windowpane flounder *(Scophthalmus aquosus)*, winter flounder *(Pseudopleuronectes americanus)* and redfish.

Williams (1999) examined stomach contents of 75 harbour seals (70% pups, 28% juveniles, and 2% adults) caught in sink gillnets in the Gulf of Maine and adjacent waters from 1991 to 1997 (Table 3). Twenty-four taxa were identified, and silver hake was the most common prey item (52.1% of prey items, and 40.8% of the reconstructed biomass). Silver hake, red/white hake, Atlantic cod, squid and redfish accounted for 77.7% of the reconstructed biomass (% of the total reconstructed mass found in all stomachs) and 87.4% of the prey consumed (Williams 1999). Further, Williams (1999) noted that there was little or no overlap of fish size between prey and commercially targeted fish. Williams (1999) also discerned spatial and temporal diversity in seal diets. Atlantic herring and squid were prevalent in winter samples off Maine, and Atlantic menhaden *(Brevoortia tyrannus)* and alewife *(Alosa pseudoharengus)* were only found in seals caught off Cape Cod. Only a single occurrence of sand eel was noted (Williams 1999).

Craddock and Polloni (2006) analyzed 101 (92% pups) stomachs of harbour seals by-caught in Gulf of Maine sink gillnet fisheries during 1995 to 2004. Ninety-seven (96%) of the samples were from the south-western Gulf. Twenty taxa were identified, with silver hake, Acadian redfish *(Sebastes fasciatus)*, and red/white hake being the three most abundant prey species, (62.4%, 9.2%, and 7.5%, respectively) (Table 3). Atlantic cod, haddock, and pollock *(Pollachius virens)* and rockling *(Gaidropsarus* spp.*)* comprised 5.3% of the prey. Smallmouth flounder *(Paralichthys dentatus)*, American plaice *(Hippoglossoides platessoides)*, and yellowtail flounder *(Limanda ferruginea)* made up only 3.3 % of the stomach contents. Craddock and Polloni (2006) also noted the absence of sand eel in the stomachs.

Harbour seals are opportunistic predators and the diet composition exhibits temporal and spatial preferences (Härkönen 1987, Hauksson and Bogason 1997, Hall *et al.* 1998, Hammill and Stenson 2000, Brown *et al.* 2001, Browne *et al.* 2001, Hammill *et al.* 2010). Likewise, harbour seal diet off the northeast U.S. coast reflects seasonal spatial distributions of prey delineated in NEFSC research trawl surveys (Mountain and Murawski 1992; Garrison 2001). For example, sand eels are abundant on Stellwagen Bank, which is adjacent to a major harbour seal haulout location on the outer portion of Cape Cod, and silver hake is widely distributed in the Gulf of Maine.

INTERACTIONS WITH HUMANS

Fisheries by-catch

Incidental takes of 4 species of phocid seals: harbour, grey, harp *(Pagophilus groenlandicus)*, and hooded seals *(Cystophora cristata)* have been recorded in a variety of fixed and mobile gear fisheries off the northeast U.S. (Gilbert and Wynne, 1985 and 1987, Waring *et* *al.* 2007), but this review is focused on harbour seal by-catch. A study conducted by the University of Maine reported a combined average of 22 seals entangled annually by 17 groundfish gillnetters off the coast of Maine (Gilbert and Wynne 1987). All seals were young of the year and were caught either between late June and August or in early October. Interviews with 5 Cape Cod Atlantic mackerel gillnetters from November 1981 to January 1982 indicated only one harbour seal entanglement. Net damage and fish robbing were not reported to be a major economic c-oncern to gillnetters interviewed (Gilbert and Wynne 1987).

Herring purse-seiners reported accidentally entrapping seals off the mid-coast of Maine, but indicated that seals rarely drowned before the seine was emptied (Gilbert and Wynne 1985). Capture of seals by halibut tub trawls is rare. One vessel captain indicated that he captured one or two seals a year. These animals, all released alive, were hooked through the skin, indicating they were snagged as they followed baited hooks. Infrequent reports suggest seals may rob bait off longlines, although this loss is considered negligible (Gilbert and Wynne 1985).

Table 4. Estimated annual harbour seal by-catch in northeast and mid-Atlantic sink gillnet fisheries, with coefficient of variation in parentheses.[1]

Year	Northeast sink gillnet	Mid-Atlantic sink gillnet
1990	602 (0.68)	-
1991	231 (0.22)	-
1992	373 (0.23)	-
1993	698 (0.19)	-
1994	1,330 (0.25)	-
1995	1,179 (0.21)	0
1996	911 (0.27)	0
1997	598 (0.26)	0
1998	332 (0.33)	11 (0.77)
1999	1,446 (0.34)	0
2000	917 (0.43)	0
2001	1,471 (0.38)	0
2002	787 (0.32)	0
2003	542 (0.28)	0
2004	792 (0.34)	15 (0.86)
2005	719 (0.20)	63 (0.67)
2006	87 (0.58)	26 (0.98)

[1]from Waring *et al.* (2007)

Incidental takes in lobster traps in inshore waters off Maine are rare. Captures of approximately 2 seal pups per port per year were recorded by mid-coastal lobstermen off Maine (Gilbert and Wynne 1985). Seals have been reported to remove bait from inshore lobster traps, especially in the spring, when fresh bait is used. These incidents may involve only a few individual animals. Lobstermen claim that seals consume soft shell shedding lobsters, but there are no data to support this.

Since 1989, NMFS fishery observers have documented harbour seal by-catch in several U.S. Atlantic fisheries, particularly those using anchored sink gillnets (Waring *et al.* 2007). Seals have also been taken in the drift sink gillnet fishery, herring purse-seine fishery, and several bottom trawl fisheries. By-catch has been observed from Maine to western Long Island, and in all seasons north of Cape Cod (Fig. 3). Most of the takes have occurred in the Gulf of Maine, particularly off the Massachusetts coast, across all seasons. During the summer, by-catch extends along the entire Maine coast. By-catches have also occurred from Cape Cod south to Long Island during all seasons except summer. A total of 606 harbour seals were observed taken as by-catch during 1989-2006. By season the by-catch was: winter (n = 80; 13.2%), spring (n = 85; 14.0%), summer (n = 289; 47.7%), and autumn (n = 152; 25.1%). Across all seasons, the majority of takes (winter=90%), (spring=90%), (summer=82%), and (autumn=90%) involved a single animal.

The estimated annual by-catch of harbour seals (CV in parenthesis) in Northeast sink gillnet fisheries from 1990 to 2006 ranged from 87 (0.58) to 1,471 (0.38) (Table 4). These estimates are substantially higher and not comparable to those reported by Gilbert and Wynne (1985), because the earlier study was designed as a pilot project. The declining trend since 2001 is likely due to fishery restrictions (*i.e.*, time/area closures, mesh size, etc.) enacted by the New

England Fishery Management Council, as well as those implemented under the Harbour Porpoise Take Reduction Plan (HPTRP; http://www.nero.noaa.gov/prot_res/porptrp/index.html). The HPTRP requirement for gillnets to be equipped with "pingers" to reduce harbour porpoise by-catch may act as a "dinner bell" or an attractant for seals, as Levine (2000) detected a statistically significant increase in harbour seal mortality in "pingered" vs. non-"pingered" nets in the Gulf of Maine. However, a recent analysis using 1999-2006 data did not indicate a dinner-bell effect (Palka, pers. comm., Northeast Fisheries Science Center, Woods Hole, Massachusetts).

Since 1998, one to two seal mortalities have been observed in mid-Atlantic gillnet fisheries (Fig. 3). The estimated annual mortality (CV in parentheses) attributed to this fishery from 1995 to 2006 ranged from 0 to 63 (0.67) (Table 4).

Two harbour seal mortalities were observed in the Gulf of Maine bottom trawl fisheries, one in 2002 and one in 2005. The estimated annual fishery-related mortality and serious injury attributable to this fishery have not been generated. Bottom trawl vessels were not included in the Gilbert and Wynne (1985; 1987) study.

The Atlantic herring purse-seine fishery was first observed in 2003. No mortalities have been recorded, but 11 harbour seals were captured and released alive in 2004 and 4 in 2005 off the central Maine coast. this fishery was not observed in 2006.

From 1989 to 2006 observers measured 345 by-caught seals. The size of these animals (nose to tail) ranged from 62 to 132 cm (Fig.4). Of the total number, 80.6% (n = 278) were < 107 cm or less, 16.5% (n = 57) were between 108-130 cm, and 2.9% (n = 10) were greater than 130 cm. Williams (1999) aged 69 by-caught seals using cementum annuli in canines, and compared the resulting age/length relationship to New England Aquarium unpublished stranding programme records. Because the age-length relationships were similar and both data sets were dominated by small seals, Williams (1999), classified the aforementioned length groups into three broad age-classes ("pup" (< 1 year), "juvenile" (1-3 years), and "adult" (> 3 years). The predominance of young animals in the by-catch is consistent with findings in other regions (Bjørge *et al.* 2002, NMFS, Alaska Fisheries Science Center, unpublished data).

Strandings

Harbour seals strand each year throughout their seasonal range (Fig. 5), and sporadic extralimital strandings have occurred as far south as Florida (Waring *et al.* 2007). (For the purposes of this review we defined stranded seals as: 1) dead on the beach, 2) euthanized, or 3) animals that died during transport or at rehabilitation facilities.) Stranding data provide insight into some sources of mortality, ecosystem health, and population trends (Becker *et al.* 1994, Geraci and Lounsbury 2005). During the 17-year period (1991-2007), stranding response groups collected an average of 245 harbour seals (range 130 to 600; Fig. 5) annually between Maine and North Carolina (NMFS unpublished data). Overall, Maine (52%) and Massachusetts (27%) accounted for the majority of the recoveries. The frequency of stranding recoveries has increased in Maine from 17% in 1992 to a high of 72% in 2006. Further, recoveries along the coast of Maine increased rapidly between 2001 and 2006. An unknown fraction of the increase is attributed to a concerted effort by a component of the Maine stranding network to actively search for stranded animals.

In 2003, not only did the number of strandings increase, but the proportion of adult seals (>125 cm in length) increased dramatically (Fig. 6). The increase in strandings, and particularly of adults, prompted the declaration of an Unusual Mortality Event (UME) for Maine harbour seals in 2003. The majority of strandings were reported in southern Maine. From May through December 2003, 66 adult harbour seals were reported stranded from Boothbay Harbour south to the New Hampshire border (MMC 2005). No consistent cause of death could be determined for stranded animals in 2003, although most animals were too decomposed for evaluation. The total number of strandings, including adults, increased in 2004. Notably, was the large number (37) of dead animals on, or near, Stratton Island, Maine during 15-26th August 2004. The majority of those seals was found within one small cove on the island, and most were adults. Necropsies were conducted on 15 of these animals, but no consistent cause of death could be determined due, in part, to substantial decomposition of many of the carcasses. The UME was declared over in spring 2005. In October 2006 NMFS declared another UME (MMC 2006) due to the elevated number of seal mortalities (*Morbillivirus* detected in 13 carcasses prior to the declaration) in Maine and Massachusetts. NMFS closed the event in spring 2008, but low level monitoring programmes are ongoing.

Recent increases in strandings in New York (DiGiovanni *et al.* 2000) and New Jersey (Waring *et al.* 2007) suggest that these animals are visiting these areas on a more regular basis. Most of the animals encountered by the rescue programmes are young-of-the-year, although in recent years there has been an increase in the number of subadults and adults recovered (NMFS unpublished data).

ECOLOGICAL INTERACTIONS

Fisheries
Worldwide, seals are perceived as competitors with fisheries for economically valuable resources (Lowry and Frost 1985, Harwood and Croxall 1988, Fu *et al.* 2001, Bjørge *et al.* 2002, Moore 2003, Hansen and Harding 2006). In U.S. Atlantic waters, Williams (1999) provided a direct comparison of the size composition of harbour seal prey and commercial fishery catches in U.S. Atlantic waters. Williams (1999) determined that the average prey size of harbour seals was 222 mm, (ranging from 50 mm to 500 mm), and the smallest and largest fish eaten were silver hake. Small prey (< 100 mm) included silver hake, redfish, red/white hake, Atlantic cod, pollock, and butterfish *(Peprilus triacanthus)*. Large prey (> 350 mm) included silver hake, red/white hake, Atlantic cod, ocean pout *(Zoarces americanus)*, Atlantic wolfish *(Anarhichas lupus)*, and Atlantic mackerel.

The length-frequency distributions of 5 prey species (silver hake, red/white hake, pollock, cod, and redfish) were compared to those eaten by seals, those caught in the covered fishery and kept, and fish that were caught and discarded (Williams 1999). The size of fish consumed by seals was smaller than the size discarded, which in turn was smaller than the catch retained and landed in the fishery. There was very little overlap in the size composition of the fish species consumed by seals and those landed by fishermen. Diet studies in other Atlantic regions have documented varying levels of overlap between prey size and minimum landing size (Brown and Pierce 1998, Hammill and Stenson 2000, Brown *et al.* 2001, Hansen and Harding 2006).

From the species composition within and among samples, harbour seals appeared to feed opportunistically on single large demersal fishes or selectively on small pelagic fishes and cephalopods (Williams 1999).

Interspecific
The limited diet information for all seal species and smaller cetaceans in this region suggests some dietary overlap among species (Recchia and Read 1989, Rough 1995, Gannon *et al.* 1997, Craddock and Polloni 2006). There are no data, however, that suggest that either available prey resources or inter-specific competition is impacting harbour seal population growth.

Competition for suitable haulout habitat likely exists between harbour seals and grey seals. Historical information suggests that grey seal and harbour seal distributions in this region were sympatric (Katona *et al.* 1993). Bounty programmes extirpated grey seals in U.S. waters (Allen 1942), and their colonies were not re-established until the early 1980s (Wood *et al.* 2007). Anecdotal information suggests that grey seals have now expanded back into their former range. Further, some seasonal haulout sites in outer Cape Cod and adjacent areas that were exclusively used by harbour seals in the late 1980s (Payne and Selzer 1989) are currently dominated by grey seals (NMFS unpublished data). However, summer observations of grey seal and harbour seal haulout behaviour on Mount Desert Rock did not reveal significant agonistic interactions (Renner 2005). Studies in other regions, however, have documented habitat displacement of harbour seal by grey seals (Robillard *et al.* 2005).

DISCUSSION

The recent growth and range expansion of harbour seal populations in U.S. Atlantic waters are likely positive responses to both the cessation of bounty programmes and enactment of the U.S. Marine Mammal Protection Act. Furthermore, anecdotal information suggests that limited extralimital pupping may be taking place in Massachusetts waters.

Small-scale and short-term tagging studies of wild caught and rehabilitated stranded seals illustrate a broad range of movements from release sites. This knowledge will need to be incorporated into future studies designed to obtain survey correction factors, examine small scale stock structure, monitor epizootic events, and evaluate impacts of anthropogenic activities like wind farms (Härkönen *et al.* 2003, Koschinski *et al.* 2003, O'Corry-Crowe *et al.* 2003, Bertrand *et al.* 2005, Gilbert *et al.* 2005, Waring *et al.* 2007).

The increase in harbour seal abundance over the past three decades has occurred at the same time as have declines in demersal fish stocks and increases in pelagic fish stocks (NEFSC 2006, Sosebee and Cadrin 2006). Harbour seal prey includes both demersal and pelagic species, but current data are insufficient to evaluate the ecological impact of seals on either group. Similarly, the impact of fishery harvests on harbour seals is unknown. Despite this lack of data, two contrasting opinions exist about the relationship between seals and fisheries in New England: 1) seals are negatively impacting fishery resources, and 2) overfishing is having a detrimental impact on seal populations. Data to address these perceptions will be required for NMFS and regional fishery management bodies to embrace the concept of ecosystem approaches to management of the harvestable and protected resources off the northeast U.S. shelf.

Fishery by-catch is the most important source of anthropogenic mortality affecting harbour seals in U.S. Atlantic waters (Waring *et al.* 2007). The current estimated annual by-catch mortality is 602 harbour seals, which is about 20% of the potential biological removal (PBR) (Wade 1998). This exceeds the MMPA's zero mortality rate goal (*i.e.*, 10% of PBR), but mitigation of this problem is not a high priority because the population is known to be increasing.

The present status of harbour seals in U.S. Atlantic waters indicates that the population is increasing and expanding its range.

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