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Birth, death and taxis: North Atlantic right whales in the twenty-first century

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BIRTH, DEATH AND TAXIS: NORTH ATLANTIC RIGHT WHALES IN THE
TWENTY-FIRST CENTURY

BY

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DISSERTATION

Submitted to the University of New Hampshire

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In

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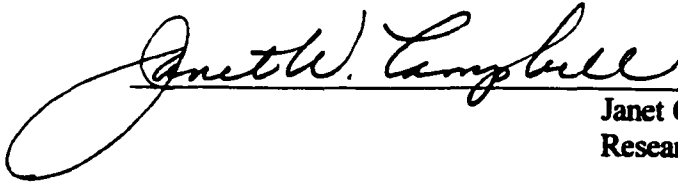
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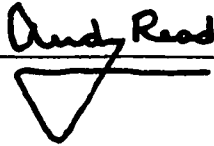
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iii

DEDICATION

This work is dedicated to Peter Scheiber, who taught me that learning was fun; to Steven Katona, who turned me loose in the field, and then helped me make sense of it all; and to John Prescott, who gave me great opportunities long before there was any evidence that this was going to be a good idea...

And to my parents, Sue and Franz, who secretly hoped that someday I'd get a real job, but never pushed me into one...

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TABLE OF CONTENTS

v

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

BIRTH, DEATH AND TAXIS: NORTH ATLANTIC RIGHT WHALES IN THE TWENTY-FIRST CENTURY

By

Scott Douglas Kraus

University of New Hampshire, September, 2002

Twenty two years of North Atlantic right whale data were analyzed. Several measures indicate reproduction in North Atlantic right whales is in a decline. Calving intervals have increased from about 3.3 years in the 1980's to over 5 years, and the age of first parturition is estimated to be 11 years. Females may lose calves before they are detected, artificially increasing the apparent age of first parturition and possibly affecting estimates of calving interval. Northern feeding habitat use patterns do not appear to affect reproduction.

Right whale mortality data was analyzed by age, sex, and habitat use patterns. A total of 46% of all confirmed mortalities are due to human activities. The characteristics of animals presumed dead from long gaps in sighting histories match known anthropogenic mortalities, but not those attributable to natural mortality. Sighting probabilities vary significantly by age, habitat-use pattern and individual. Tag-recapture models of extremely small populations are vulnerable to such heterogeneity, since animals missing for extended periods can create spurious estimates of survivorship, growth rates, and population viability.

An analysis of satellite-tracked movements of two adult female right whales in the Gulf of Maine, one with a calf and one without, examined

relationships between whale movements and sea-surface temperature, distance to front, frontal density, depth, and bottom slope. The cow was primarily influenced by sea surface temperature and the non-calving adult female was primarily influenced by the "distance to fronts". The movements of the cow may reflect the immature thermoregulatory requirements of her calf. In contrast, the movements of the non-calving female appear to be independent of temperature, and may indicate the use of frontal boundaries for navigation and food-finding.

Fishing entanglements and collisions with ships are approximately equally responsible for nearly half of all right whale deaths. There are large gaps in the data that inhibit informed mitigation. Right whales face serious problems, but as a long-lived species, a decadal period crisis does not necessarily spell extinction.

CHAPTER I

BIOLOGY, CONSERVATION, MANAGEMENT, AND SOURCES OF DATA ON THE NORTH ATLANTIC RIGHT WHALE (*EUBALAENA GLACIALIS*)

Appearance and Anatomy

Right whales are large, relatively rotund whales, with square chins and a generally

black coloration with occasional white belly and chin patches. North Atlantic right

whales (*Eubalaena glacialis*, Borowski, 1781) grow to about 16 meters (m) in length,

with adult females averaging about one meter larger than adult males (Allen 1908;

Andrews 1908). A blubber layer up to 8 inches (20 cm) thick serves for both insulation

and energy storage. The head is 25% of the total body length in adults, up to 35% in

juveniles. A strongly arched and narrow rostrum and strongly bowed lower jaws are

characteristic of the species. The skull can be up to 5 m in length and weigh as much as

1000kg, with a distinctive supraoccipital bony shield. The vertebral formula is C7, T14,

and L11 (10-12) (True 1904).

Gray or black thickened skin patches, called callosities, are found on the rostrum,

behind the blowholes, over the eyes, on the corners of the chin, and variably along the

lower lip and jaw lines. The arrangement of callosities is unique to each right whale and

is used for individual recognition (Hamilton and Martin 1999). Callosity patterns appear

light yellow or cream colored due to large infestations of cyamid crustaceans (whale

lice). Callosities consist of spikes of columnar epithelial tissue, appearing barnacle-like,

1

but no barnacles have ever been found on North Atlantic right whales. Baleen plates are black or brown, number 205 to 270 plates on each side, average 2 to 2.8 m in length, and are relatively narrow in width (up to 18 cm) with fine hair-like fringe facing the interior of the mouth. There are no grooves along the throat. The tail is broad (up to 6 m tip to tip) and all black.

In the field, when seen along the axis of the animal, the blow is distinctively V-shaped and can reach 7 m in height. Observations of feeding, when it occurs at the surface, have led to reports of sea monsters, as these whales skim with their mouths wide open, narrow, callosity-covered rostrums raised in the air, and baleen plates partially exposed above the water.

History of Exploitation

The first whaling for right whales started as a shore-based fishery around 1,000 A.D., primarily for oil and baleen, in the Bay of Biscay, off northern Spain and western France. Apparent overhunting led the Basques to extend their whaling activities further afield, first off the British Isles, then as far north as Norway, and east to Iceland. By the early 1500s, the Basques had reached the coasts of Newfoundland and Labrador, where they hunted right whales and bowhead whales (*Balaena mysticetus*) near the Strait of Belle Isle every summer and autumn. Aguilar (1986) estimated a cumulative kill of 25,000-40,000 whales between the years 1530-1610. None of the European whalers ventured farther south than northern Nova Scotia, and right whales in New England waters were not persecuted until the 1600s.

During the late 1600s, colonial hunters developed a small fishery for North Atlantic right whales from shore stations, by launching small boats to pursue and harpoon

2

them. By the early 1700s, North Atlantic right whales were hunted from shore stations from New York to Gloucester, Massachusetts. By the mid-1700s, shore-based whaling had nearly ceased, apparently due to a decline in right whale abundance below economically viable levels (Reeves 2001).

A short-lived renewal in right whale hunting occurred starting in the mid 1800s, with several whale hunting operations along the shores of Long Island, New York, and the Outer Banks of North Carolina (Reeves and Mitchell 1986; Reeves 2001) lasting until the early 1900s. In addition the American pelagic whalers killed right whales at several locations around the North Atlantic until nearly 1900 (Reeves and Mitchell 1986). Although the discovery of petroleum in Pennsylvania in 1859 reduced the demand for whale oil as fuel for lamps and as a lubricant, baleen remained in great demand into the 1900s and right whales were hunted until too few could be found.

There was also a short-lived period of hunting for right whales in the eastern North Atlantic off Scotland and Ireland in the early 1900s. A total of 118 right whales were taken in these coastal fisheries from 1906 to 1922, when they became economically unviable due to a lack of whales.

In summary, it appears that there were several significant reductions in the North Atlantic right whale population. In the first period, the Basques hunted the eastern North Atlantic right whale stock to commercial extinction prior to 1500 A.D. They then reduced the western North Atlantic right whale stock to very low levels by the early 1600s, although probably not to commercial extinction (Barkham 1977). Reeves (2001) suggests that the number of right whales present along the North American coast in the 1680s numbered "well over 1000....". However, colonial whalers effectively reduced this

3

remnant population to extremely low numbers by the end of the 1730s, and North Atlantic right whales were not systematically targeted again until the 1850s. At that time, a coastal fishery and a U.S- based pelagic fishery brought Western North Atlantic right whales down to levels of economic extinction by the early 1900s.

In the eastern North Atlantic, whatever recovery had been experienced by those right whales was negated by the Irish and Scottish whaling in the early 1900s. At the time of international protection for right whales in 1935, estimates for the western North Atlantic stock suggest that fewer than 60 animals were alive (Kenney et al 1995). On the eastern side of the North Atlantic, few sightings have been made in the last twenty years, and this group is not considered viable (IWC 2001).

The original population size will never be known with certainty, although Gaskin (1991) suggested that between 12,000 and 15,000 right whales occupied the North Atlantic before hunting began over one thousand years ago. The history of right whale exploitation shows periodic episodes of drastic reductions followed by prolonged periods of slow recovery. This pattern indicates remarkable resilience in this species' ability to survive population bottlenecks, but it also suggests that recovery, even if facilitated by careful management of human sources of mortality, will be a long process. Both back-counting and genetics data suggest that the population is currently recovering from a low level of a few dozen animals who survived through the early 1900s (Kenney et al 1995; Malik et al 1999).

Systematics, Population Structure, Distribution, and Range

Although the taxonomic status of right whales (genus *Eubalaena*) worldwide has been the subject of mild controversy for over twenty years, most authors accepted two

4

species designations, *glacialis* for the Northern Hemisphere stocks, and *australis* for all

Southern Hemisphere populations, with the North Pacific form sometimes considered the

subspecies *japonica* (see Schevill 1986). A recent review paper by Rice (1998) joined

right whales and bowheads together under the genus *Balaena*, and combined all right

whale species into *B. glacialis*. However, at the 1998 International Whaling Commission

(IWC) workshop on right whales, scientists recommended retaining *Eubalaena* (the right

whales) separately from *Balaena* (the bowhead), and noted that the scientific committee

of the IWC would only consider changing taxonomic status on the basis of published

papers. Rosenbaum et al. (2000) published a review of the genetic data on right whales

worldwide, and concluded that three distinctive populations warranted specific status

within the genus *Eubalaena*. The 2000 IWC Scientific Committee meeting, after

considering genetic and morphological data, decided to accept the proposed

nomenclature, retaining the generic name of *Eubalaena* for right whales, and recognizing

three species, *E. glacialis* for the N. Atlantic, *E. australis* for all southern hemisphere

right whales, and *E. japonica* for the North Pacific.

Stock divisions of right whales within the North Atlantic are poorly understood.

An earlier IWC report provisionally divided North Atlantic right whales into three stocks,

the western, central, and eastern North Atlantic, based upon the sequential depletion of

right whales in the North Atlantic catch history (IWC 1986; Reeves and Mitchell 1986).

Recent photographic matches of individuals moving between Greenland, Norway, with

the cataloged population of the western North Atlantic, suggest that these stock divisions

are unlikely (Knowlton et al. 1992; IWC 2001). As Reeves (2001) points out, the North

Atlantic right whale population could either be a single stock, or two stocks with minimal

5

flow between them. Reeves (2001) and Knowlton et al. (1992) both provide a number of records of right whales outside the well-known habitats in the western North Atlantic, suggesting high mobility and plasticity in right whale habitat use patterns in the North Atlantic.

The range of right whales was historically known to have included a large area along the east coast of North America, including waters of the Gulf of St. Lawrence and Atlantic Canada, east to western Greenland, Iceland, Spitzbergen and Norway, and south along the European coast to the Saharan coast of Africa. Whaling records suggest that some of the eastern North Atlantic stock of right whales wintered near Cintra Bay on the coast of Africa (Schevill and Moore 1983; Reeves and Mitchell 1990), then appeared off the Hebrides and Ireland in early summer, and may have moved to Scandinavian feeding areas later (Collett 1909; Thompson 1928; Fairley 1981). The few recent sightings in British and Irish waters have all occurred between May and September (Brown, 1986). Since the 1920s eastern North Atlantic sightings have been sporadic, coming from the Canaries, Madeira, Spain, Portugal, the United Kingdom, and Iceland (Maul and Sergeant 1977; Brown 1986).

In the western North Atlantic, historical whaling records show right whales were taken in the coastal waters of the U.S. from Florida to Massachusetts, and in and around the Strait of Belle Isle, between Labrador and Newfoundland (Aguilar 1986; Reeves 1988; Reeves et al. 1999; Reeves 2001). The pelagic whaling records indicate a much wider, but sporadic distribution of right whales around the offshore waters of the western North Atlantic, with hints of a summer habitat in the "Cape Farewell Ground", due east of the southern tip of Greenland (Reeves and Mitchell 1986).

6

Contemporary surveys have identified five consistently visited right whale habitats along the east coast of North America (Figure 1.1). Most cows give birth in the coastal waters of the southeastern U.S. during the winter months (Kraus et aL 1986). Males and non-calving females are rarely seen in that area, and their whereabouts during the winter remain unknown (Kraus et aL 1988). In the spring, aggregations of North Atlantic right whales are observed feeding in the Great South Channel east of Cape Cod, and in Massachusetts Bay (Winn et aL 1986; Hamilton and Mayo 1990; Kenney et aL 1995). In the summer and autumn, they are observed nursing, feeding and courting in the Bay of Fundy between Maine and Nova Scotia, and feeding and courting in an area on the Scotian Shelf 50 km south of Nova Scotia (Stone et aL 1988; Kraus and Brown 1992). Several outlying sightings of North Atlantic right whales have been reported, including individuals at Bermuda (Payne 1972), in the Gulf of Mexico (Moore and Clark, 1963), and off Greenland and Newfoundland (Knowlton et al. 1992).

It is interesting that no right whale sightings have been made in the last century in the historical whaling grounds between Labrador and Newfoundland. Also, there is no evidence that there was ever any whaling in three of the contemporary right whale habitats in the western North Atlantic, including the Bay of Fundy (Reeves and Barto 1985), the Nova Scotian Shelf, and the Great South Channel (Reeves and Mitchell 1986). Either right whale distribution has shifted over time, or as Kenney et aL (2001) suggest, the current habitat use patterns seen in right whales represents a remnant of the historic population which only uses the southern periphery of their former range.

7

Figure 1.1. Right whale habitats in the western North Atlantic.

Base Map: Critical Habitats
of the Atlantic Coast

N
W   E
S

Bay of Fundy
Conservation Area

Portland, ME

Roseway Basin
Conservation Area

Boston, MA

Long Island, NY

Great South Channel
Critical Habitat

Cape Cod Bay
Critical Habitat

Baltimore, MD

Figure 5

Bathymetry

0 - 50 Meters

50 - 500 Meters

500 - 1000 Meters

Prepared by J. Donadio Ring
April 2000
Map is unprojected in
decimal degrees.

Wilmington, NC

Charleston, SC

South East
Critical Habitat

8

Current Population Size and Status

The North Atlantic right whale population was probably even smaller in the past than it is today. Malik et al. (1999) found only five matrilines represented in the mitochondrial DNA (mtDNA) from over 200 animals sampled in the western North Atlantic population. Since mtDNA is inherited only from the mother, this suggests that the population did indeed go through a very small "bottleneck" at some time in the recent past. Reeves et al's. (1992) catch history suggests that the population may have been reduced to as few as a dozen animals by hunting by the 1730s. The Malik et al. (1999) result does not imply that only five female North Atlantic right whales existed at some point in the past, because each mtDNA haplotype could have been represented by more than one female.

The population in the western North Atlantic currently numbers about 300 animals (IWC 2001; Kraus et al. 2001), and appears to be recently declining in size (Caswell et al. 1999; Fujiwara and Caswell 2001). The eastern North Atlantic population probably numbers in the low tens of animals and "its future remains questionable" (IWC 2001). Western North Atlantic right whales have been subject to significant losses from anthropogenic mortalities, and have experienced a significant decline in reproductive rates during the last ten years (Knowlton and Kraus 2001; Kraus et al. 2001). In the 1980 to 1992 period, annual estimates of population size back-calculated from data on calving and mortalities showed steady increase from 255 individuals in 1986 to 295 in 1992. The mean net growth from one year to the next was 2.5% (Knowlton et al. 1994). The current growth rate is negative and has led to international calls for immediate conservation

9

management action (Fujiwara and Caswell 2001; IWC 2001). Details on right whale

mortality and reproduction are found in Chapters II and III.

Feeding

North Atlantic right whales migrate into high latitude waters to feed. Their

primary prey is the copepod *Calanus finmarchicus*, especially the larger oil-rich

developmental stages (C-IV and C-V) and adults (Murison and Gaskin 1989; Mayo and

Marx 1990; Kenney and Wishner 1995; Mayo et al. 2001), but other small zooplankton

such as *Pseudocalanus minutus*, *Centropages* spp. and barnacle larvae are eaten at times

(Mayo and Marx 1990). The whales filter feed by swimming continuously with the

mouth open at the surface (skim feeding) or at depth. Feeding bouts at the surface can

last for hours. When feeding at depth (down to 200 m) dives of up to 20 min or more

may be repeated for hours. North Atlantic right whales at times feed very near to the

bottom in the Bay of Fundy, as they sometimes surface with mud on their snouts. Up to

270, long (to 8 ft), finely-fringed baleen plates on each side of the jaw allow the whales

to filter small zooplankton from the water. The mouth is only opened and the baleen

exposed when the concentration of plankton animals in the water is above a threshold

value. North Atlantic right whales observed in Cape Cod Bay did not skim feed unless

more than 1,000 zooplankton organisms/m^3 were present (Mayo and Marx 1990). In the

Bay of Fundy, where observations using sonar have shown whales diving to depths of 90-

150 m in areas of high copepod biomass, whales did not make feeding dives unless at

least 820 copepods/m^3 (170 mg/m^3) were present (Murison and Gaskin 1989).

Kenney et al. (1986) estimated that a North Atlantic right whale must feed in prey

patches containing energy densities of 7.57 to 2,394 kcal/m^3 to support its metabolic

10

requirements. Those values are from 10 to 1,000 times greater than the densest

concentration of zooplankton sampled in the vicinity of North Atlantic right whales in the

Great South Channel. Kenney et al. (1986) suggested that this was the scientists' inability

to sample zooplankton patches as precisely as the whales. Zooplankton organisms are

not homogeneously distributed, but instead usually occur in "patches" in the water

column (Wu and Loucks 1995). The copepods form dense concentrations both vertically

and horizontally where tides, winds, or prevailing currents form convergences or fronts

where water parcels of different temperature, salinity and density meet (Wishner et al.

1988; Kenney and Wishner 1995). Concentration may be further enhanced as the

animals seek preferred intensities of light or other physical factors during diurnal vertical

migration.

Mayo et al. (2001) have recently shown that right whale baleen is well

suited to capture by filtration the most productive size class of zooplankton, that in the

300 to 500 micron range. The baleen filtering efficiency declines with smaller classes of

zooplankton, and the right whale is unable to take advantage of larger more mobile prey

(e.g., euphausiids) because of its "ponderous" feeding method (Mayo et al. 2001). Mayo

and Marx (1990) observed that right whales in a plankton patch with density above the

threshold for feeding swam in convoluted paths, often making abrupt turns. Whales

swimming outside of a patch moved faster and in straighter paths. These observations

are consistent with standard foraging theory across many taxonomic groups.

The four critical habitats where North Atlantic right whales are most frequently

seen are among the few places where extremely concentrated patches of copepods have

been found. Three of them (Browns-Baccaro Bank, Bay of Fundy and Great South

11

Channel) are places where deep basins (approximately 150 m) are flanked by relatively shallow water. Copepods are concentrated by convergences and upwellings driven by tidal and other currents. Upwelling driven by tidal currents also produces the dense patches of plankton in Cape Cod Bay, although no deep basin is present.

Because the summer distribution of North Atlantic right whales is so tightly coupled with their primary prey, *Calanus finmarchicus*, the whales are not seen when copepod populations are abnormally low. During the spring of 1992, hydrographic anomalies in the Gulf of Maine resulted in very low abundance of copepods in the Great South Channel and no right whales were seen there(Kenney 2001). Although Kenney (2001) tested for a variety of factors, only an influx of cold Scotian Shelf water into the Gulf of Maine through the Northeast Channel appears to be linked with the reduced copepod production. The ultimate cause of this influx was unidentified, but may have been associated with decreased temperatures in the Northern Hemisphere caused by the eruption of Mt. Pinatubo or by a high discharge of freshwater from the St. Lawrence River in 1991 (Kenney 2001).

Right whales are, therefore, highly dependent upon a narrow range of prey sizes, which occur in highly variable and spatially unpredictable patches in the Atlantic ecosystem. It is likely that the four northern feeding habitats that have been identified in the western North Atlantic have appropriate hydrographic and oceanographic conditions that are conducive to the creation of highly concentrated patches of copepods. However, there is substantial variability in copepod production and right whale abundance in each of these areas from year to year (Brown et al. 2001; Kenney 2001). Right whales have adapted to this unpredictability with a large caloric buffer in the form of blubber (Moore

12

et al. 2001) and the ability to travel long distances in relatively short periods of time

(Mate et al. 1992; Slay and Kraus 1999; Chapter IV).

Reproduction and Courtship

Although one North Atlantic right whale female was observed to calve as early as

age 6, the mean age at first parturition is currently about 11 years (Chapter II). Except

for post-mortem anatomical examination of the testes, no unequivocal criterion for sexual

maturity in males is available, although there is the potential for measurement of fecal

metabolites of testosterone to shed light on this question (Rolland, pers. comm.). Males

of all ages, including young individuals who cannot possibly be sexually mature, have

been seen in courtship groups (Kraus and Hatch 2001). However, it appears that only

males over 10 years of age can get close enough to a female to have an opportunity for

mating. The age of first reproduction for males will only become known from back-

calculation after analyzing the paternity of calves using genetic techniques. Brown et al.

(1994) used genetics to show that the sex ratio in this population is 50/50.

Courtship is the most energetic and spectacular behavior displayed by this

species. Courtship groups (sometimes referred to as "surface-active groups," or SAGs),

have been described by Kraus and Hatch (2001). SAG's may include 40 animals or

more, as multiple males try to get close enough to the focal female to be able to mate.

Females appear to call males by making groaning sounds resembling the mooing of a

cow, which can be heard underwater for several miles. Males can be seen swimming

quickly in a bee-line for a calling female. Females are usually at the center of these

SAGs, and they appear to avoid copulation by rolling onto their backs with the genital

area out of the water. However, Kraus and Hatch (2001) reported that females roll over

13

to breathe about once a minute, offering males opportunities to mate. Based upon the limited data available, it appears that a female may have intromission frequently during a courtship bout with several different males. Males appear to compete for the "alpha" positions (those next to the female), which are best for taking advantage of each mating opportunity when the female breathes (Kraus and Hatch 2001). Males displace one another from these positions on average every 15 min. There is no evidence of either reciprocity among males for access to females, or of kin selection between related males.

Females appear to be using SAGs as a means of selecting mates who are agile, strong, and good at breath-holding in the context of courtship, perhaps the only arena in which she can exercise mate choice. Male right whales are "sperm competitors" (Brownell and Ralls 1986), devoting energy to gamete production and delivery rather than physical aggression. Sperm competitors typically have large testes and elaborate penises compared to related species that compete in other ways (Parker 1984). Male right whales have the largest testes (up to 975 kg paired weight) and longest penises (up to 11 feet) in the world, and are the largest in both categories relative to body weight and length for all baleen whales (Brownell and Ralls 1986). This mating system is not fully understood, but appears to be the consequence of the prolonged spacing of calves (3-5 year intervals). These calving intervals cause an effective adult sex ratio of one female to every four males, leading to significant male competition for females.

However, the seasonal timing and duration of observed courtship activities, which extends from August through October in the western North Atlantic right whale population, is puzzling. Calving is first observed in December in the waters off Georgia and Florida and extends through early March. The observed courtship is not

14

consistent with Best's (1994) estimate of 12 months for the gestation period in southern right whales. It is possible that courtship in the Bay of Fundy is merely foreplay and successful insemination occurs elsewhere during December. Alternatively, either gestation is longer than 12 months, or implantation of the fertilized egg in the uterine wall is delayed, although this has never been described in cetaceans. The resolution of these questions will require better knowledge about the wintering habitats of right whales, and better methods for evaluating pregnancy in right whales.

Female right whales give birth to a single calf. In 1992, the mean interval between births was 3.67 years (n=86) (Knowlton et al. 1994), with a range of from 2 years to 7 years. However, in the 1990s calving intervals increased significantly to nearly 6 years (Kraus et al. 2001; Chapter II). The increase in calving intervals was associated with increased variability in annual calf production, and a variety of hypotheses have been put forward (Chapter II). At least two females have had calves over a period of 28 years, suggesting that the reproductive lifespan of North Atlantic right whales is at least that long.

Most calves were born in the coastal waters of the southeastern U.S. (Kraus et al. 1992). Since 1990, the number of calves produced each year has varied from 1 to 31, with no apparent trend. Since some cows with newborn calves are missed during the winter surveys off Georgia and Florida, a complete assessment of a year's calf production requires surveys in the northern critical habitats, particularly Cape Cod Bay and the Bay of Fundy.

Mothers and calves migrate north for spring feeding in the Great South Channel and Cape Cod Bay, then on to the only well-defined summer nursery area in the lower

15

Bay of Fundy, where along with juveniles, they feed from late July to mid-October. However, Schaeff et al. (1993) inferred from genetic and photo-identification data that one group of cows does not bring its calves to the Bay of Fundy each year. Therefore, another summer and fall nursery area must exist, although its location is unknown. This unidentified nursery is not in the high use area of the Scotian Shelf near Browns Bank, because cow and calf pairs were seen there only four times in 1,059 sightings over eight field seasons (Knowlton et al. 1995). Knowlton et al.'s (1992) report of a cow and calf off Greenland in 1992, and historical whaling records suggest an area between Greenland and Iceland (Reeves and Mitchell 1986) as a candidate nursery.

Longevity and Demography

Data on mean longevity are not yet available, although back-counting from first birth records suggests that right whales routinely live longer than three decades (Chapter III). A right whale calf observed with its mother was killed in Florida in 1935 and a photograph of the pair was published in the New York Herald Tribune. The cow in the photograph was identified as whale #1045 in the right whale catalog. Whale #1045 was observed in 1959 off Cape Cod by Woods Hole Oceanographic Institution researchers, and then irregularly until the summer of 1995, when National Marine Fisheries Service researchers photographed her near Georges Bank, badly wounded by lacerations from a ship's propeller. If the calf killed in 1935 was #1045's first calf, and if she gave birth at age 10 (the mean age of first calving for North Atlantic right whales; see Chapter II), then whale #1045 would have been 70 years old when last seen, making her the oldest whale of known age in the population (Hamilton et al. 1998).

16

Hamilton et al.'s (1998) work on demographic structure suggests 26% to 31% of the population is comprised of juveniles (< 9.6 years in this analysis), significantly lower than the level observed in other baleen whales, and also much lower than expected from a growing population.

Mortality

Analyses of stranding, entanglement and photographic data have provided estimates of mortality for North Atlantic right whales (Kraus 1990; Kenney and Kraus 1993; Knowlton and Kraus 2001; Chapter III). Mortality is particularly high during the first three years of life, ranging from 5% to 18% based on estimated deaths (Kraus 1990). Mortality rates among adults are very low, probably less than 1% annually, although Fujiwara and Caswell (2001) suggest that adult female mortality rates are much higher, and are the major contribution to the currently declining population (see Chapter III). Details on right whale mortalities, including analyses of known mortalities and animals that "disappeared" from the catalog, are given in Chapter III.

Data from 50 reliably documented right whale deaths between 1970 and 2001 shows that 5/50 (10%) were due to entanglements in fishing gear, 18/50 (36%) were due to collisions with ships, and 27 (54%) were attributed to "unknown causes" or "neonatal mortality". The only "natural" mortality currently recognized is neonatal mortality. The causes of death among the 14 "unknown" mortalities are not known either because the carcass was not retrieved, the carcass was too decomposed to identify a causal factor, or no obvious factor was found despite a detailed necropsy.

Still, over 46% of all confirmed right whale deaths are due to anthropogenic sources, all of which are clearly identified. In the case of shipping collisions, most right

17

whale habitats are also home to major shipping lanes serving the ports of eastern North America (Knowlton and Kraus 2001). In the case of fishing, over 60% of all right whales display scars indicative of entanglements at some time in their lives. Because right whales are coastal animals, they are likely to encounter fishing gear throughout their range, from Florida to Canada. Details of current management strategies for both shipping and fishing are given below, and potential solutions are discussed in Chapter V.

Possible Factors Affecting Population Growth

Shipstrike and Entanglement

Of the possible factors that may be depressing the growth rate of the North Atlantic right whale population, the important ones are strikes by large ships and entanglement in fixed fishing gear. These two factors account for over 46% of all mortality in this population (Knowlton and Kraus 2001). This is a significant factor for reproductive rates if the mortality is biased toward females. Fujiwara and Caswell (2001) suggest that this is exactly what is happening, and that the survival of females in this population is significantly lower than that of other age and sex classes. Given the coastal habits of females when observed with calves, it is believable that adult females are more vulnerable to human activities such as shipping and fishing in and near the coastal waters of North America. However, known mortalities do not reflect a female bias in the last five years. Further, sighting rates for females are significantly lower than the rest of the population (Brown et al. 2001). Chapter III examines this problem in more detail, but Fujiwara and Caswell (2001) provide the first estimates for the potential effect of selective female mortality on the rate of growth of this population.

18

Reproduction

Right whale reproduction has been declining by all measures since about 1990 (Kraus et al. 2001; Chapter II). The potential reasons for this include food limitation (Moore et al. 2001), population and habitat use changes (Kenney et al. 2001), disease and/or marine biotoxins (Rolland, pers. comm.), pollutants (Colborn and Smolen 1996; Weisbrod et al. 2000), genetic factors (Schaeff et al. 1997), and climatic variation (Kenney 2001). Details on these hypotheses can be found in the discussion of Chapter II and in a workshop report on right whale reproduction (Reeves et al. 2001).

Habitat Reduction

Reeves et al. (1978) hypothesized that intensive industrial use of Delaware and Chesapeake Bays by humans since the 1800s had pre-empted their use by right whales, thereby diminishing the potential recovery of the population. Not enough is known about pre-colonial use of those bays by the whales to permit evaluation of this affect. Low-level pollution, ship traffic, ocean dumping, and dredging have all been invoked in recovery plans as factors that could reduce the availability of habitat to right whales. However, no studies on the habitat requirements of right whales have been done, other than those on prey requirements by Mayo and Marx (1990), Kenney et al. (1986), and Wishner et al. (1995). Habitat discussions tend to focus on food as the governing factor in a right whale habitat, although the absence of any evidence of right whale feeding in the southeastern U.S. suggests that at least in that area, other factors are important. Observations of courtship behavior in the autumn in the northern feeding grounds also indicate that factors other than food are important in some locations. If Kenny et al. (2001) are correct, and this remnant population of right whales is only occupying the

19

southern portion of their potential range, then additional habitats suitable for both feeding and courtship may be available to this species in areas north of Nova Scotia. Studies on the habitat requirements for this species are needed, especially to develop predictive models of right whale movements and distribution, for better management of conflicts between humans and whales. At the moment however, all hypotheses on links between habitat quality and reproduction are speculative.

Habitat Degradation Issues

The potential impacts of pollution, habitat, and acoustic disturbance are all complex and related. As the scale of urbanization increases in coastal zones, these factors could become more troublesome. The effects on right whales or any other whale species are unknown, because the few studies that have been done are inconclusive. For example, pollutants are present in measurable amounts in every marine mammal that has been tested, but direct causal links between various compounds and changes in pathology, health, reproduction, or behavior have only been conclusively identified in pinnipeds (Reijnders et al. 1986; DeSwart et al. 1994; Ross et al. 1995). High contaminant levels have been associated with cancers and reproductive dysfunction in the St. Lawrence beluga population (DeGuise et al. 1995) and with reproductive problems in Northwest killer whales (Ross et al. 2000). Contaminants have been associated with potential immune suppression in widespread die-offs of dolphins in the western North Atlantic and with seals in the North Sea (Geraci et al. 1989; Hall et al. 1992). Measuring the responses of populations or of individual whales to pollutants, acoustic disturbance and habitat degradation are difficult problems, partly because baseline data for comparison with the contemporary situation are lacking, and partly because it is difficult

20

to tease apart the multiple potential effects of several variables. Neither the National Marine Fisheries Service (NMFS) nor the Department of Fisheries and Oceans (DFO) have yet articulated a management approach to unknown impacts of this type, although there have been regional efforts to minimize the effects of ocean urbanization.

Whalewatching and Noise

Whalewatching has also evoked concern with regard to right whales. However, since whalewatching only began in the 1970s in New England and in Canada, it could not be a primary cause of the slow recovery of the North Atlantic right whale population. Although whalewatching could potentially have some effect on the whales by distracting them, displacing them from rich food patches, diffusing food patches with wake or propeller wash, it is difficult to imagine this as a significant problem compared to the threats posed by large ships and fixed fishing gear.

It has been suggested that the constant hum of shipping noise in the North Atlantic may have habituated right whales to ship sounds, making them less likely to avoid oncoming vessels. It is also possible that the higher levels of ambient noise in the ocean have reduced the ability of right whales to hear mating calls over large distances, perhaps reducing mating opportunities. Still, there is no evidence that noise from boats or other sources is affecting the reproduction or mortality of right whales at this time.

Current Management Activities

Right whales are protected internationally from hunting by the International Whaling Commission (IWC), and from commercial trading by the Convention on Trade in Endangered Species (CITES). Under the U.S. Endangered Species Act (ESA) and the Marine Mammal Protection Act (MMPA), right whales in U.S. waters benefit from some

21

of the strongest legislative protection measures ever enacted on behalf of rare wildlife. However, North Atlantic right whales travel frequently offshore in international waters, and spend a significant portion of their lives in Canadian coastal waters. Within the U.S., the National Marine Fisheries Service is the responsible agency for the management of right whales. In Canada, the Department of Fisheries and Oceans is the responsible agency for right whale issues.

In the U.S., NMFS has designated three "critical habitats", Cape Cod Bay, the Great South Channel, and the coastal waters of the southeastern U.S between Jacksonville, Florida and Brunswick, Georgia out to 15 miles. In Canada, the DFO has designated two "conservation zones", one in the Bay of Fundy and one on the Nova Scotian shelf. Although all of these habitats have been officially designated, and they appear on nautical charts, there are few restrictions on human activities within them.

The NMFS is issuing an updated Recovery Plan for right whales (NMFS 1991), which will serve as a blueprint for the agency to follow under the ESA and MMPA. Under the recovery plan, implementation teams are given responsibility for taking management actions to ensure the survival of the species. Implementation teams are made up of representatives from the relevant and affected agencies at the federal and state level. These teams have standing advisory boards consisting of scientists, conservationists, and industry representatives. Canada has also issued a recovery plan (DFO 2000) with comparable recommendations to the U.S. plan, but without an Endangered Species Act to drive conservation measures forward, the implementation of Canada's plan may be limited by a lack of legislative power.

22

Under the ESA and MMPA, the NMFS issues annual stock assessments (Blaylock et al. 1995), which include the allowable "potential biological removal (PBR)" from that stock that will not measurably impact its prospects for survival. The current PBR for right whales is zero whales per year. In 2001, two right whales were killed by ships, two died from fishing entanglements, two were probably neonatal deaths from natural causes, and one death occurred offshore from Nova Scotia that was not recovered. In light of this level of mortality, the future survival of right whales probably depends on the speed with which recommendations of the Right Whale Recovery Plan can be carried out in the U.S, and the degree to which DFO can implement recommendations of Canada's recovery plan. A discussion of the effectiveness of these actions, the implementation teams, and additional recommendations, can be found in Chapter V.

A Few Lessons From The History of Right Whale Research and Management

The development of an effective management program requires a comprehensive strategy and sufficient funding to carry out a research program that will provide data for identifying, justifying and evaluating actions for conservation of the species. Good data on habitat use patterns, mortality sources and trends, and population recruitment are especially important, as well as a recognition that many population parameters will not be learned in studies of long-lived species until several decades of work has been completed. Short-term funding cycles have made the long-term data collection efforts extremely difficult and in some cases these limitations have compromised the science (Kenney 2001).

The effectiveness of the recovery efforts for right whales has been dependent upon the cooperation and action from many international, federal, and state agencies and

23

non-governmental conservation groups. Industry stakeholders have also made significant contributions to the development of management strategies.

Finally, the accidental killing of endangered species is much more difficult to regulate than directed take by hunting. In the case of the North Atlantic right whale, the prohibition on hunting has been very effective, but accidental kills from collisions with ships and entanglements in fixed fishing gear could drive this species to extinction. The responsibility for killing North Atlantic right whales has changed from a small number of hunters, to all of us who eat seafood, purchase foreign autos, petroleum, or any other products which arrive on ships, export goods by sea, or benefit from the services of a Navy or Coast Guard. The solutions to these problems are within reach, but will require well-coordinated multi-disciplinary approaches to research and management.

Overview of Data Sources and Research Methods

The data used in this dissertation are the result of studies initiated and conducted by the author since 1980. Since the overall right whale program is oceanwide in scope, it has involved a number of collaborators, and multiple authors have made significant contributions to the field since this program's inception. The foundation of the work described here is a unified North Atlantic Right Whale Catalog (Crone and Kraus, 1990; Hamilton and Martin, 1999), that includes all photographed North Atlantic right whale sightings collected since 1935. The photographic identification and cataloging methods were developed by the author early in the 1980's (Kraus et al., 1986). This catalog is curated at the New England Aquarium under the direction of the author, but it includes photographic data from numerous sources, all of which are acknowledged in the beginning of this document. Permission to use the data for this work was granted to the

24

author through a peer review process by the North Atlantic Right Whale Consortium, the governing body of major photographic contributors that reviews all requests to use the unified catalog for scientific analyses and publications. A summary of the basic data collection methods is given below, and detailed methods are given in each chapter.

Since 1980, North Atlantic right whales have been studied with standardized surveys and photography from boats, ships, airplanes and occasionally blimps to assess distribution, abundance, ecology, and behavior. Shipboard and aerial surveys have been conducted annually in most known habitats of North Atlantic right whales, although offshore areas, including the Great South Channel (southeast of Cape Cod) and the Nova Scotian Shelf were sampled irregularly during the 1990s.

The studies described in Chapters II, III, and V were largely based upon the unified right whale catalog, which is dependent upon the ability of researchers to identify individuals from distinctive natural markings (Payne *et al.* 1983; Kraus *et al.* 1986). Identifications of individuals were made from photographs of the distinctive patterns of raised, rough epidermal tissue (callosities) located on the heads of right whales. Newly collected photographs and associated sighting data have been contributed by researchers working all over the North Atlantic, and matched with archived photographs of individual right whales in the North Atlantic Right Whale Catalog (Kraus *et al.* 1986; Crone and Kraus 1990; Hamilton and Martin 1999). The catalog contained 410 individually identified right whales from the entire North Atlantic Ocean as of January, 2002. The final individual matching of photographs contributed to the Catalog was done under the supervision of the author.

25

The sightings database derived from this photographic data provided information on the age and sex of individuals, movements and habitat use patterns, reproduction, mortality, and the impacts of human activities on the population. Gender identification was made possible from both visual assessments during photographic surveys and genetic studies. Photographic surveys have resulted in approximately two thirds of the population being photographed each year. Of the 25,895 records in the unified catalog, 13,053 (50.4 %) were collected during survey efforts directed by the author.

In work initiated by the author in the late 1980's, collaborators working on genetics and contaminants used a crossbow and hollow-tipped arrow to collect small skin samples from identified individuals (Brown *et al.* 1991). The DNA extracted from the samples has been used to add information on the sex of individuals, compare genetic information with observed patterns of migration and habitat use, and evaluate inbreeding depression (Schaeff *et al.* 1993; Brown *et al.* 1994; Malik *et al.* 1999). The genetic information on each whale is included in the current iteration of the Right Whale Catalog and is updated annually. As of January 2002, over 250 of the North Atlantic right whales have been sampled. Genetic data from these studies were provided by collaborator Dr. Brad White at Trent University in Ontario, are incorporated into all studies of cataloged whales here, and are specifically referenced where appropriate.

Satellite telemetry was used to investigate right whale movements among areas. Tags were attached directly into the blubber layer on a whale's back to provide regular sampling of date, time, and location (Mate *et al.* 1992; Slay and Kraus, 1999; Chapter IV). Remote sensing data were used to evaluate the characteristics of the oceanographic features where some right whales traveled (see Chapter IV), in the hopes that eventually

26

right whale habitat characteristics can be identified with enough accuracy to allow predictions about their occurrence in high-risk locations. However, no satellite tagging efforts have yet been successful in transmitting longer than about six months, apparently because right whale behavior involves a lot of body contact, and the transmitter antennas do not survive this physical trauma.

Other studies linked to this work are summarized below, but the data were not used in any of the analyses here. For example, new methods to assess the causes of reduced reproductive rates in North Atlantic right whales include ultrasonic measurements of blubber thickness from free-swimming whales as a potential measure of body condition (Moore *et al.* 2001) and recent work on fecal steroid hormone metabolites to identify reproductive maturity, pregnancy, and stress hormone levels (Rolland *et al.* in prep.). Fecal sample collection is also being proposed as a method for assaying the potential role of biotoxins, parasites and disease in the reproductive health of right whales (see Chapter II). Other potential assays for pregnancy and stress using skin and blubber samples are also being tested (Mansour *et al.* 2000). Additional research is underway on the acoustic characteristics of right whales and their hearing capabilities. Suction cup tags with acoustic receivers and recorders, as well as movement and depth recorders, are starting to yield insights into right whale behavior underwater (Nowacek *et al.* 2001). Passive recording devices are also being tested as a method for locating right whales within habitats (Clark, pers. comm.). Both research areas may lead to advances in detecting whales and reducing ship strikes.

CHAPTER II

REPRODUCTIVE VARIABILITY AND TRENDS IN THE NORTH

ATLANTIC RIGHT WHALE

Introduction

One of the troubling features of the population biology of the North Atlantic right whale(*Eubalaena glacialis*, Borowski, 1781) is the extreme variation in calf production from year to year. Despite protection for over 60 years, estimates of current abundance for the North Atlantic right whales indicate that only about 300 animals survive today (Kraus et al. 2001). Caswell et al. (1999) and Fujiwara and Caswell (2001) report declining levels of growth in this population, and several studies have shown that anthropogenic sources of mortality are significant contributors to the problem (Kraus 1990; Kenney and Kraus 1993; Caswell et al. 1999; Knowlton et al. 2001).

However, little attention has been paid to the contribution of the right whale population's reproductive parameters to declining growth rates. Mean calving intervals have been increasing throughout most of the study period, although population calving rates have remained stable, probably due to the annual recruitment of small numbers of new mature females (Kraus et al. 2001). During two periods in the 1990s, very low yearly calf production caught the attention of researchers and managers alike. Although no obvious cause was ever identified, these events stimulated the development of several hypotheses that are now being tested in field studies. Potential factors contributing to declining reproductive rates include infectious disease events, inbreeding depression,

28

climatic changes resulting in reduced food availability, sub-lethal effects of toxic contaminants, or the sub-lethal effects of marine biotoxins (Reeves et al. 2001).

Kraus et al. (2001) summarized the available information on reproductive biology of the western North Atlantic right whale population based on data obtained by repeated sightings of photographically identified individual animals through 1998. Additional information has become available since that publication to assess reproductive trends in North Atlantic right whales, the results of which are provided in this Chapter.

Methods

Right whales in the North Atlantic were individually identified and cataloged following methods described by Kraus et al. (1986), Payne et al. (1986), and Hamilton and Martin (1999). Photographic identifications provided repeated records of individual whales, which were used to develop information on reproductive parameters, including annual calf production, calving intervals, age at first parturition, and the number of new cows recruited annually. A supplementary genetics study provided gender information for 270 individuals (Brown et al. 1994).

Annual calf production (c) is presented for all years from 1980 through 2002. Most calves have been probably been reported in this population since 1991 because of intensive survey effort (ca. 90 aerial survey days per year) in the only known calving ground off the southeastern U.S in the winter. However, reliable photo-identification requires that young right whales have fully developed callosity patterns, which do not stabilize until they are 6 months old. Since all cows do not use the same summering habitats, not all calves are photographed between 6 and 12 months, and they therefore remain unidentified. For this Chapter, annual calf counts include all calves, including

29

both those who remained unidentified (but whose mothers were recorded) and those that were known to have died in their first year. Known calf mortalities have been updated to correct errors in Kraus et al. (2001).

Because absolute numbers of calves don't reflect the reproductive health of the population, an index of calves per mature female per year (CMFY) was used. Adult females were classified as mature in two ways; 1) beginning in the year in which they were first seen with a calf (C) , and, 2) based upon the estimated age of sexual maturity (10 years, i.e., the age of first parturition minus 1 year; see results) from all known-age females including those not yet calving (nulliparous adult females, or AFNP). For analyses that required estimating the total number of extant cows, adult females were eliminated from all subsequent counts the year in which they died or the year in which they disappeared, if they became presumed dead (PD) after a six-year hiatus in sightings. This is a departure from Kraus et al.'s (2001) method of counting animals as deceased only after six years from the last sighting. The reason for this is that most of these females disappeared after a significant event in their lives (calving, entanglement, ship strike, or visible deterioration in condition), which in documented cases have been associated with mortalities shortly after the event (Chapter III). One other difference from the Kraus et al. (2001) study is that females not seen in the study period (1980-2002) were excluded from these analyses, so total numbers of adult females will not agree with the earlier publication.

CMFY statistics were derived from the number of calves expressed as a proportion of the total number of extant mature adult females in that year. These

30

estimates were done twice, once with parturient females only, and once with all females over the mean age of sexual maturity as follows:

$$CMFY_{max\ for\ year\ x} = (c)/(C), \text{ and } CMFY_{min\ for\ year\ x} = (c)/(C + AFNP).$$

To account for long term variation in this very long lived animal, an additional calculation was made for the calves per mature female per decade for females born before 1980. These calculations were done for both the 1980s and 1990s, and were divided into two categories by whether the cows were born in the 1960s or 1970s.

All data on calving was used to calculate the age at first parturition. New cows (R) were counted as recruited to the population using data starting in 1985, to try and eliminate recruits who were in fact older cows that had not been observed with calves during the early part of the study period. A review of gaps in the sighting histories of several females indicated they could have given birth earlier than reported, and simply not been seen in those years. These were classified as potentially missed calving events (PMC), and identified as such in the analyses. Females without any gaps in sighting history were identified as "no-missed-calvings" (NMC) females.

In addition, because many mammalian females are known to lose their first offspring at a higher rate than subsequent births (from spontaneous abortion, stillbirth, or neonatal deaths), an analysis to determine potential calf losses (PLC) from these causes was attempted. Previous work had shown most female right whales go to the southeastern U.S. to give birth (Kraus and Kenney 1991). Assuming that most females go to the southeastern U.S. for calving, both non-calving females of at least six years of age (the youngest first calving ever recorded) and non-calving known cows observed there may have lost a calf. To test this, visitation patterns of non-calving females in the

31

region were examined. Any southeastern winter sighting that occurred at least two years before or three years after another calving was considered a potentially lost calf. Because of potential lost calves, the age at first parturition was then recalculated using the minimum age at which a calf could have been born, and these are referred to as PLC primiparous female ages.

To correct for potential lost calves at earlier ages, primiparous no-missed-calves (NMC) female ages and primiparous PLC female ages were combined, and the youngest age from both was selected. These combined data have a range of estimated age of first calving from 6 to14 years. One female who was first observed with a calf at 22 was discarded because her sighting history was represented by only four sightings in the study period.

However, using this method will bias the estimates of first age at parturition downward, since not all females seen in the southeast at age six and seven are likely to be pregnant and lose a calf. So the probability of calving at any given age is the product of the probability of calving at each age times the number of potential calving events.

The probability of calving (P_c) at age (x) was calculated from all primiparous female data where no calves could have been missed (NMC) as follows:

$$P_c = c_x / \Sigma c_{x=6...14}$$

These probabilities were then applied to all primiparous female age data to create a first time calving probability index (I) for each age (x) as follows:

$$I_x = (P_{c \text{ in year } x})(PLC_x + NMC_x)$$

32

Calving intervals were examined for every cow in the population who calved more than once. Mean calving intervals were calculated from the annual totals. Kraus et al. (2001) used all calving intervals of seven years or less to calculate trends in inter-birth intervals, including 21 females with gaps in the sightings data in which there could have been a calving event. This was justified on the assumption that most (19/21: 90%) of those females used the southeastern calving ground to give birth, and if they weren't seen there a calving event was unlikely. Here, an even more conservative approach was taken for the analysis of calving interval trends. In this study, all whales with calving intervals of five years or less with no gaps in their sighting history were regressed on the year of calving.

To determine whether the longer calving intervals could have been due to the loss of a calf, a non-calving winter visitation to the southeastern calving ground was used to estimate potential lost calves (PL(c)) in parturient females. This analysis assumed that no cow had a calf within the first two years after calving or within two years prior to calving. This assumption is based upon the low probability of a two-year calving interval. Of 127 calving intervals recorded since 1980, only one (less than 1%) was two years.

To determine whether reproductive rates and trends might be due to habitat factors, cows were classified by visitation patterns to the Bay of Fundy. Whales that visited the Bay of Fundy once or never in their sighting history, were considered Non-BOF animals (NB), as the Fundy habitat did not play a significant role in their lives. Animals that were sighted in the Bay of Fundy two or more times were considered Bay of Fundy whales (BOF). Analyses of calving rates and intervals, and CMFY statistics were developed for BOF and NB animals separately.

33

Results

Reproductive Females

The number of reproductively active females has increased slowly throughout the study period to 75 in 2002, although the early period growth is probably influenced by the addition of adult reproductively active females that were not identified until calving (Table 2.1 and Figure 2.1). This "discovery" curve is likely to underestimate the total number of reproductive females prior to 1990, at which point the study had been running long enough that any female calves born prior to 1980 would have reached sexual maturity. Throughout the period there were additional females old enough to have calves (age 11, see analysis below), but had never been seen with a calf (AFNP). This number increased through the 1990s, as calves born in the 1980s became sexually mature but calved later than the mean age of first parturition.

The number of new cows recruited to the population ranged from zero to eleven each year, with no significant increase or decline over the period. In both 1996 and 2001, 11 new cows were added to the reproductive female group. These "cohort" additions are partly responsible for the markedly high levels of calving in both years, placing both years well above the mean calving rate (Figure 2.1).

Calving Rates and Losses

The number of calves born per year in 1980-2002 ranged from 1 to 31, with a large level of inter-annual variability (Table 2.1, Figure 2.1). The mean annual calving rate for 1980-2002 was 11.82 calves per year (S.D. = 6.6), with no significant increase (F = 0.9461, p = 0.3418). The calving rate was well below the mean during two periods 1993 – 1995 and 1998-2000.

34

Table 2.1. Reproductive parameters for the North Atlantic right whale population, 1980-2002.

Year	M	R	PD(C)	AFNP	TotAF	Tot(c)	Mort(c)	CMFYmx	CMFYmin	PL(c)
1980	16		0	3	19	7		0.3750	0.3157	
1981	21	5	0	3	24	9	1	0.4285	0.3750	
1982	27	7	1	3	30	13	2	0.4815	0.4333	
1983	33	6	0	3	36	9		0.2727	0.2500	0
1984	35	5	3	3	38	12		0.3428	0.3158	3
1985	37	2	0	3	40	11		0.2973	0.2750	1
1986	39	6	4	3	42	13		0.3333	0.3095	1
1987	43	5	1	3	46	12	1	0.2791	0.2609	1
1988	45	2	0	3	48	8	1	0.1777	0.1666	1
1989	47	3	1	3	50	18	2	0.3829	0.3600	10
1990	47	2	2	4	51	13	1	0.2766	0.2549	5
1991	50	4	1	4	54	17		0.3400	0.3148	2
1992	51	3	2	4	55	12		0.2353	0.2182	1
1993	47	2	6	5	52	8	2	0.1702	0.1538	7
1994	51	4	0	6	57	9		0.1765	0.1579	6
1995	51	2	2	6	57	7		0.1373	0.1228	2
1996	60	11	2	7	66	24	3	0.4000	0.3582	12
1997	64	7	2	10	74	20	1	0.3125	0.2703	3
1998	62	0	2	12	74	6	1	0.0967	0.0811	6
1999	63	1		14	77	4		0.0635	0.0519	7
2000	62	0	1	18	80	1		0.0161	0.0125	8
2001	73	11		19	92	31	4	0.4247	0.3369	
2002	75	2		20	95	18		0.2400	0.1895	

Key:

(C) = Cows
R = Recruits (First time cows)
PD(C) = Presumed Dead Adult Females
AFNP = Adult Females (Nulliparous)
TotAF = M + AFNP

(c) = Calves
CMFY = Calves/Mature Female/Year
PL(c) = Potentially lost calves
(undetected mortalities)
$(C)_{year\,x} = (C)_{x-1} + R_x - PD(C)_x$

35

Figure 2.1. Right whale reproduction, 1980-2002[1]
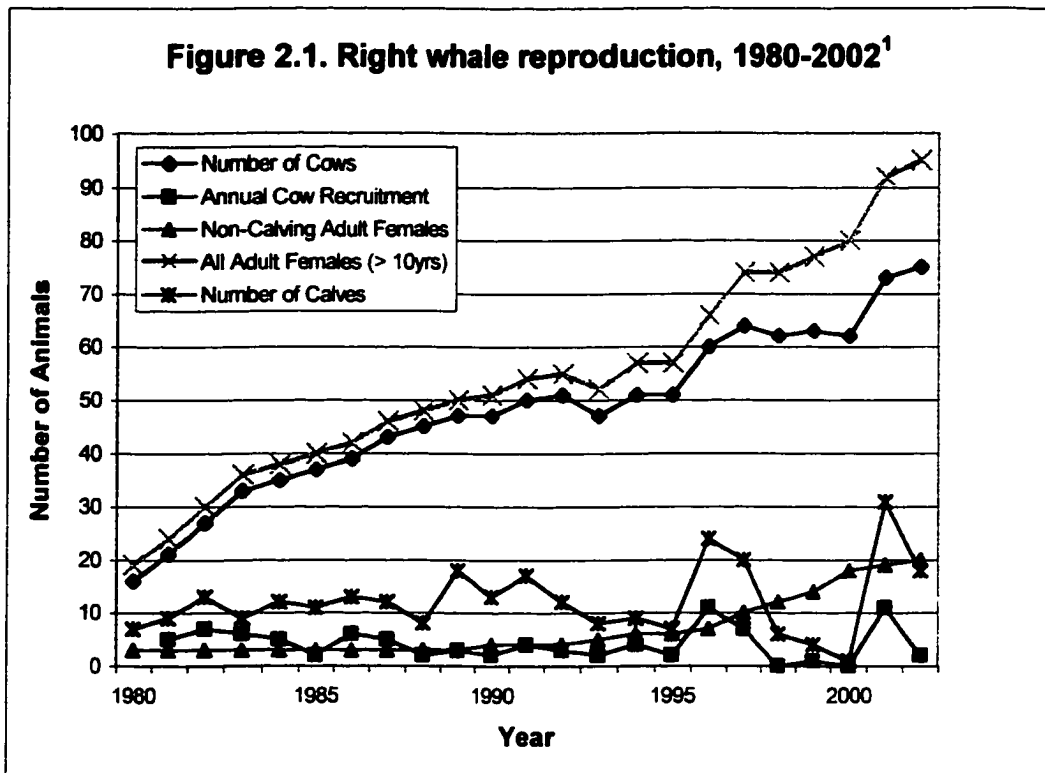
The potential lost calves are shown in Figure 2.2 with both total calving counts and calf mortality. Although the data are sparse, the known mortality in calves appears to correspond with higher levels of potential lost calves, suggesting an environmental effect on the population.

[1] Data on sex from Brown *et al.*, 2001, and from the right whale catalog (Hamilton and Martin, 1999)

36

Figure 2.2. Calving, calf mortality, and potential lost calves. [2]

Number of Animals

— + — Calves (Alive)
— ▲ — Dead Calves
— ■ — PLC's

35
30
25
20
15
10
5
0

1980   1985   1990   1995   2000
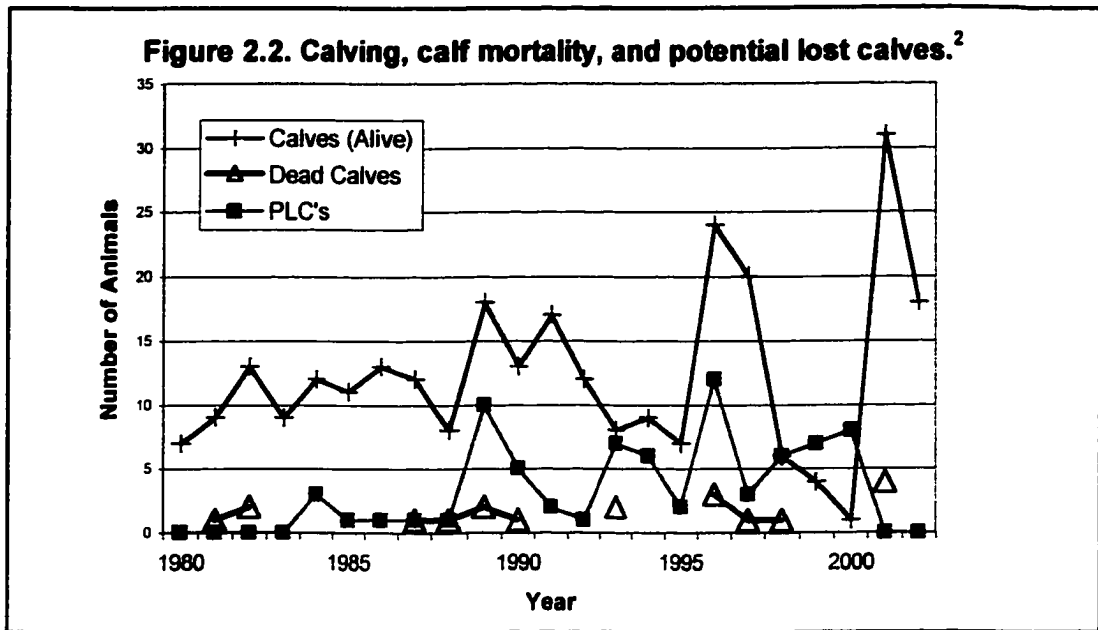
Year

Calves Per Mature Female Per Year

CMFY statistics were calculated for all females over the age of 10, and for parous females only. The first statistic, $CMFY_{Max}$ represents the smallest number of females, and so will maximise the ratio of calves to adult females. The statistic $CMFY_{Min}$ includes both females that have calved and females age 10 or older. The mean $CMFY_{Max}$ for the period was 0.2722 (s.d. = 0.1234). The mean $CMFY_{Min}$ was 0.2428(s.d. = 0.1101). The annual variation in CMFY values is high, ranging from 0.0125 to 0.4815, but the average rates suggest that about one adult female in every four is calving annually. A summary of the CMFY statistics is given in Table 1.1 and in Figure 2.3. Figure 2.3 suggests an estimated decrease in CMFY over the study period. However, early CMFY data are biased upwards by the "discovery" of calving females during the first five years. Also,

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[2] Data on sex from Brown et al., 2001, and from the right whale catalog (Hamilton and Martin, 1999)

37

the data before 1990 is biased upwards on the CMFY$_{Min}$ curve by the fact that some identified females had not yet reached ten years of age. A regression of the CMFY data from 1990 – 2002 shows no decline over time (F = 0.3067, p = 0.59) but the high levels of variance confound the test. A regression on three year moving averages shows a significant decline in both the CMFY$_{Min}$ (F = 6.0098, p = 0.0321) and CMFY$_{Max}$ (F =533, p = 0.0092).

Figure 2.3. Calves per mature female per year, 1980-2002.[3]
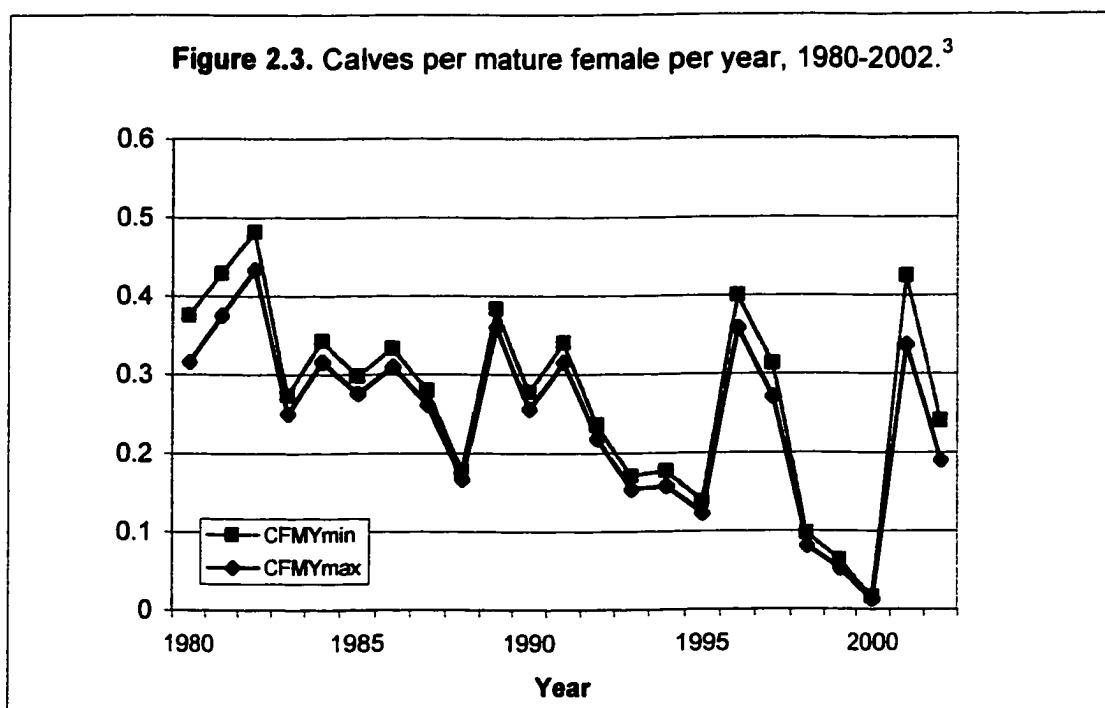
One alternative approach to assessing reproductive success in this long-lived population is to look at calving rates on a decadal scale. A quick review of older cows that were mature in the 1980s and 1990s and were born in the 1960s and 1970s is given in Table 2.2 below.

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[3] Data on sex from Brown *et al.*, 2001, and from the right whale catalog (Hamilton and Martin, 1999)

38

Table 2.2. Calves per mature female per decade (CMFD) for cows born before 1980.

	Decade	N	# (c)	CFMD
C born in 1960's	1980's	15	32	2.133
	1990's	12	18	1.5
C born in 1970's	1980's	35	62	1.771
	1990's	29	47	1.621

Calving Intervals

A total of 165 intervals between calving events have been recorded since 1980. Calving intervals have increased across the population of repeatedly calving females during the study period (Table 2.3, and Figure 2.4). Knowlton et al. (1994) reported a mean calving interval of 3.67 years (SE = 0.11; n = 86; range = 2-7 years). The most frequently observed interval at that time was three years, with 53 observations (61.6%). The most frequently reported interval in the last two years of the study period was five years (n = 16/34, 47%).

Because whales are not seen every year, some cows with longer calving intervals may have had calves during a year in which they were not sighted. Annual mean calving intervals given in Table 2.3 were calculated from all intervals of seven years or less to minimize the potential for missed calves. This approach follows methods and a rationale given in Kraus et al. (2001).

Knowlton et al. (1994) also reported an apparent trend toward increasing calving intervals with time, though it was not statistically significant. Kraus et al. (2001) reported that the calving interval increase was significant through 1998, although half of the females with long calving intervals were not seen in years during which they could have had a calf. Here calving intervals were analyzed only from cows without any potentially missed calving events, including all intervals less than six years (Figure 2.4).

39

Only data from 1986 onward was used to capture all possible five year intervals in the study period. Calving intervals have increased significantly since 1986 ($F = 40.05$, $p < 0.0001$, $df = 102$).

Table 2.3. Distribution of calving intervals by year for North Atlantic right whales. Mean intervals are calculated from annual totals, with intervals longer than seven years excluded because of inconsistency in the sighting records. Longer intervals given in parentheses.

| | Calving Intervals In Years | | | | | | | |
	2	3	4	5	6	7	8+	Mean Interval
1980	-	1	-	-	-	-	-	3.0
1981	-	-	1	1	-	-	-	4.5
1982	-	1	-	1	-	-	-	4.0
1983	-	2	1	-	-	-	-	3.3
1984	-	7	-	-	-	-	-	3.0
1985	1	6	-	2	-	-	-	3.1
1986	-	5	2	-	-	-	-	3.3
1987	-	4	-	1	-	1	-	4.0
1988	-	2	1	1	1	-	-	4.2
1989	-	7	2	4	-	-	-	3.8
1990	-	7	1	1	1	-	-	3.6
1991	-	4	3	3	2	1	-	4.5
1992	-	7	1	-	1	-	-	3.4
1993	-	-	3	1	-	-	-	4.3
1994	-	-	3	1	-	-	-	4.3
1995	-	1	1	1	1	-	1(13yr)	4.5
1996	-	-	1	6	2	1	-	5.3
1997	-	2	1	2	3	3	1(13yr)	5.4
1998	-	-	1	-	3	1	-	5.8
1999	-	-	2	-	-	1	-	5.0
2000	-	-	1	-	-	-	-	-
2001	-	-	1	10	1	2	5(8,8,8,10,10)	5.28 (6.21*)
2002	-	1	2	6	2	2	2(13, 9yrs)	5.15 (5.93*)
Totals	1	57	28	41	17	12	9	(n = 165)

* Mean annual calving interval if all calving data included.

Figure 2.4. Calving interval by year, 1986-2002, eliminating all potential missed calvings.[4]
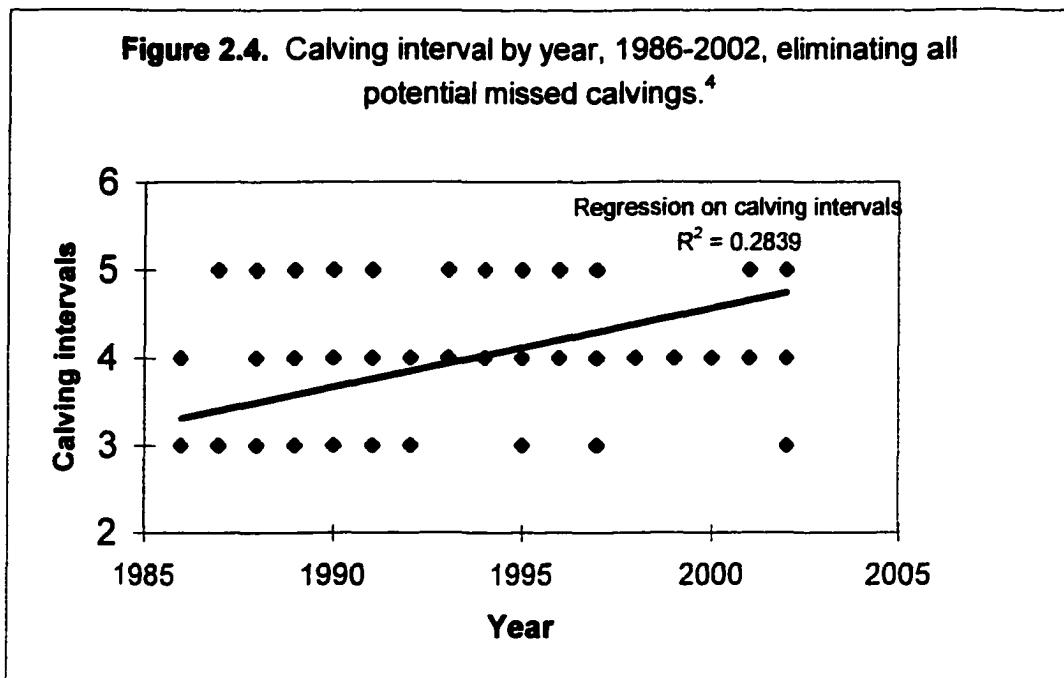
Age at First Parturition

Knowlton et al. (1994) reported a mean age at first calving of 7.57 years (SE = 0.63). With additional data and a longer time series, Kraus et al. (2001) estimated the mean age at first calving at 9.53 years (S.D. = 2.32). In this study, there were 30 females of known age that gave birth for the first time in the study period. The mean age of first calving for all primiparous females was 12.2 years (s.d. = 3.84) and the mode was 11 years (Figure 2.5).

However, missed sightings of cow and calf pairs or early fetal or calf mortality will lead to overestimates of the age of first calving. Several of these females had either sighting gaps in their pre-calving history, or had been seen in the southeastern U.S

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[4] Data on sex from Brown *et al.*, 2001, and from the right whale catalog (Hamilton and Martin, 1999)

41

without a calf in an earlier year. Figure 2.5 shows all primiparous females by category, including females without any possible missed calves (NMC), potential missed calves from gaps in their sighting history (PMC)(n=13), and potential losses of calves due to spontaneous abortions, stillbirths, or early neonatal mortality (PLC)(n = 16). The probability of missing calves is probably minimized by the habitat visitation patterns of those females with sighting gaps – 12/13 (92.3%) of these females when first observed with a calf were seen in the southeastern U.S. No other calving ground has been identified in the North Atlantic, and heterogeneity in sighting probabilities of all right whales is well documented (Brown et al. 2001; Kraus et al. 2001, Chapter III). For this reason, the sighting gaps in pre-calving females were not considered a significant factor in estimating the age at first parturition, and PMC female ages were not analyzed further. However, nine of the 13 females with missing sighting gaps were also seen in the southeastern U.S. indicating a potential lost calf, and those females ages were included in the subsequent PLC female analysis.

No previous studies have attempted to estimate the effects of early fetal or calf mortality on estimates of first parturition. In the data shown in Figure 2.5, a relatively large contribution to the mode comes from animals that potentially lost earlier calves.

Figure 2.5. Age at first calving, 1980-2002, including potential missed calves and lost calves.[5]
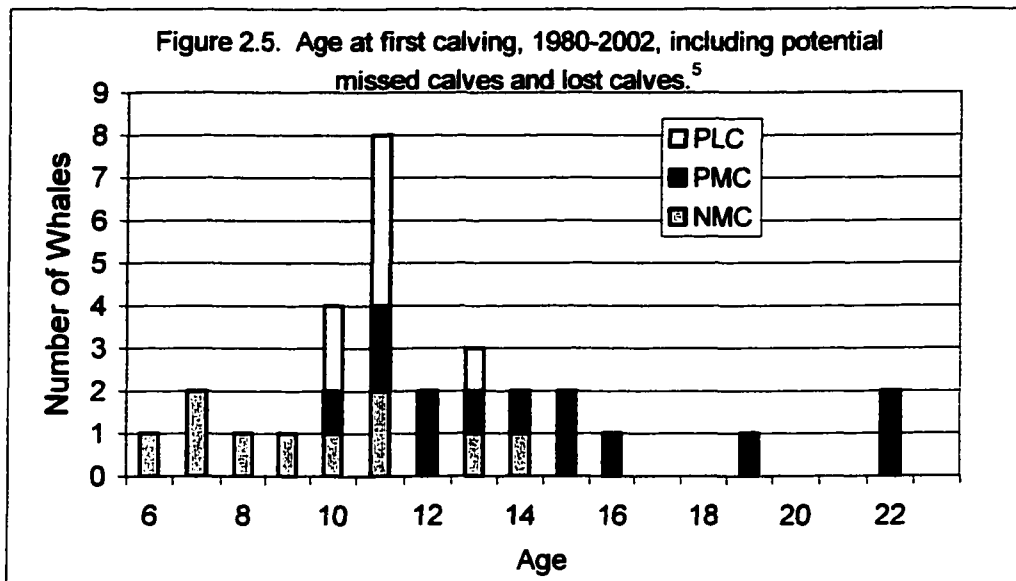
Using the correction method combining PLC and NMC primiparous female ages, the range of estimated age of first calving is from six to 14 years. One female who was first observed with a calf at 22 was discarded because her sighting history was represented by only four sightings in the period. If the assumptions about lost calves are correct, this method indicates that the mean age of first calving is 10.03 years (s.d.=3.09). The age of first calving using the combined PLC and NMC female ages is shown in Figure 2.6.

To remove downward bias in the method above, a probability index of first calving was calculated and the results are displayed in Figure 2.6. The probability index estimates the probability of first calving at a given year by correcting for lost calves. It shows the highest probability of first calving at age 11, higher than the mean of 10 years

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[5] Data on sex from Brown et al., 2001, and from the right whale catalog (Hamilton and Martin, 1999)

43

taken from the minimum estimate of first calving, and lower than the mean of all

uncorrected first calving data (12.2 years).

Figure 2.6. Estimated age at first calving including PLC and NMC females.[6]
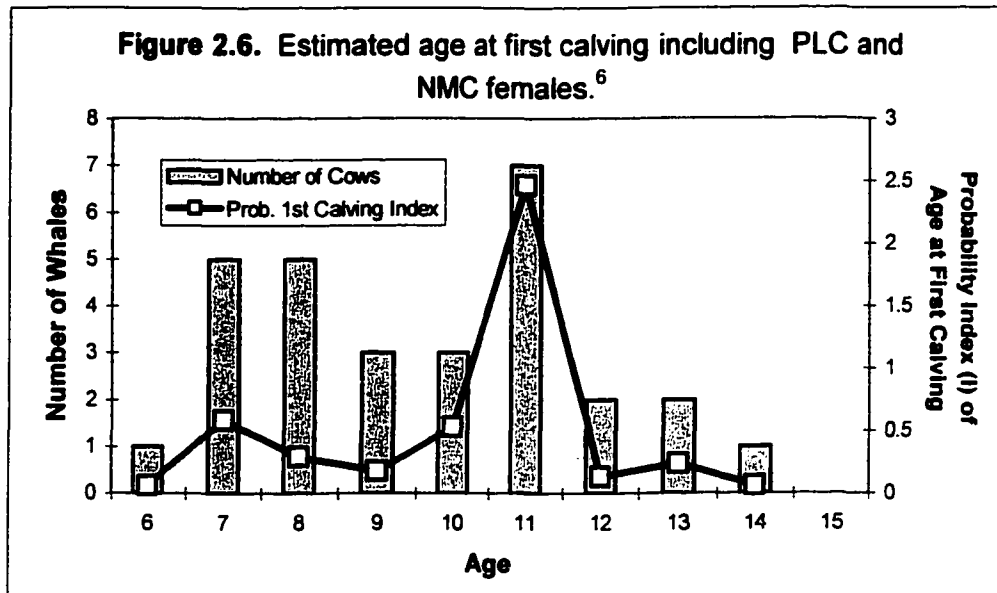
An analysis of trends in the age of first parturition indicated an increasing trend

over the study period (Figure 2.7). However, few known-age females at or near the age

of sexual maturity were available prior to 1993. A regression on the data from 1993

through 2002 using all NMC and PLC female ages indicates that the apparent overall

trend is an artifact of the short study period, as the slope is insignificant (F= 2.354, p =

0.1398, df = 22).

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[6] Data on sex from Brown *et al.*, 2001, and from the right whale catalog (Hamilton and Martin, 1999)

44

Figure 2.7. Age at first parturition, 1980-2002.[7]

Age of Primaparous Females

◆ NMC Females
■ PLC Females

15
13
11
9
7
5

1980   1985   1990   1995   2000   2005

Year
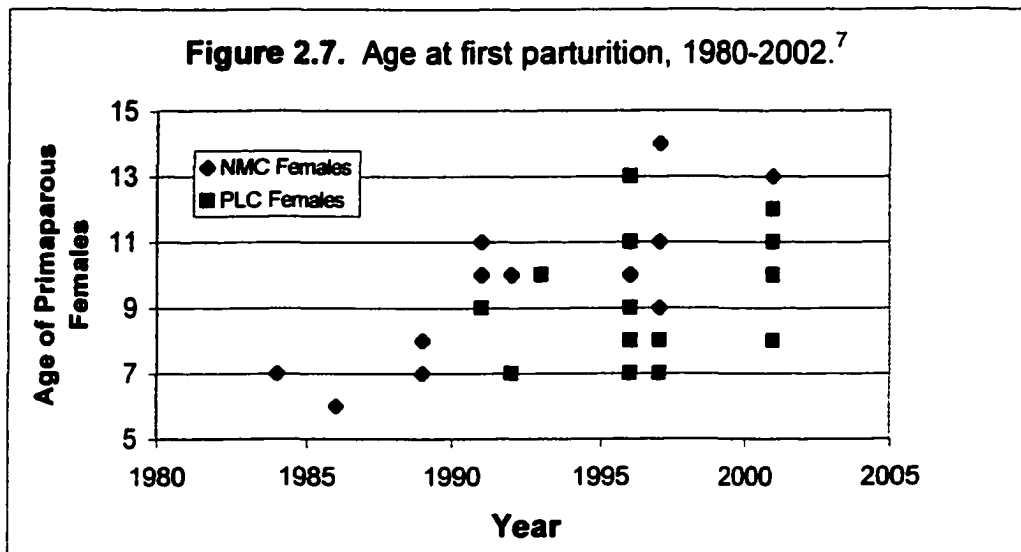
Effects of Differences in Habitat Use on Reproductive Parameters

A summary of the reproductive statistics for BOF and NB animals is given in Table 2.4.

The NB cows comprise about one third of the total number of cows in the population.

Annual calving rates for both groups of animals are given in Table 2.4 and shown in

Figure 2.8. The BOF whales have a mean of 7.7 calves per year (s.d. = 5.87) and the NB

whales have a mean of 3.52 calves per year (s.d = 1.50). The variances of calf production

between the two groups are significantly different ($F = .0655$, $p < 0.001$, $df = 22$).

However, when calving rates are corrected by applying CFMY statistics, there is no

significant difference between the groups ($F = 0.9419$, $p = 0.4448$).

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[7] Data on sex from Brown et al., 2001, and from the right whale catalog (Hamilton and Martin, 1999)

45

Table 2.4. Reproductive parameters by northern habitat use pattern, 1980-2002.

Yr	B(c)	B(C)	B(CMFY)	NB(c)	NB(C)	NB CMFY	ID(c)	Tot(C)
1980	3	10	0.4000	3	6	0.5000	6	16
1981	7	14	0.5000	1	7	0.1428	8	21
1982	8	20	0.4000	3	7	0.4286	11	27
1983	4	22	0.1818	5	11	0.4545	9	33
1984	11	25	0.4400	1	10	0.1000	12	35
1985	5	25	0.2000	6	12	0.5000	11	37
1986	7	27	0.2593	6	12	0.5000	13	39
1987	8	29	0.2759	3	14	0.2143	11	43
1988	4	29	0.1379	3	16	0.1875	7	45
1989	12	33	0.3636	4	14	0.2857	16	47
1990	9	34	0.2647	3	15	0.2000	12	47
1991	12	35	0.3429	5	15	0.3334	17	50
1992	7	36	0.1944	5	15	0.3334	12	51
1993	5	32	0.1563	1	15	0.0667	6	47
1994	5	35	0.1429	3	17	0.1765	8	51
1995	4	35	0.1143	3	17	0.1765	7	51
1996	16	42	0.3810	5	18	0.2777	21	60
1997	15	45	0.3330	4	19	0.2105	19	64
1998	1	44	0.2273	4	18	0.2222	5	62
1999	0	44	0.0	4	19	0.2105	4	63
2000	0	43	0.0	1	19	0.5263	1	62
2001	26	54	0.4815	4	19	0.2105	30	73
2002	11	56	0.1964	6	19	0.3158	17	75

Key: (C) = Cow   (c) = calf

B = Bay of Fundy Whale   NB = Non-Bay of Fundy Whale

ID(c) = Photographically identified calf

46

Figure 2.8. Right whale calving by northern habitat use pattern.[8]
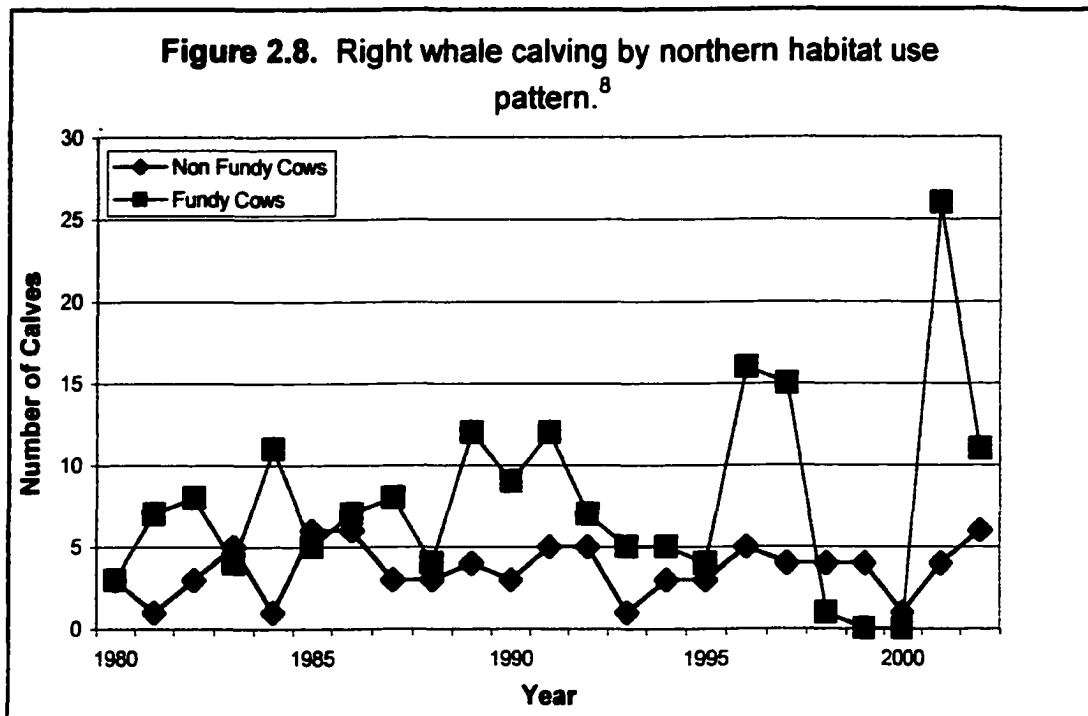
The marked variability in the CFMY statistics could mask any trend, so a three

year rolling average was computed, and results are shown in Figure 2.9. The BOF and

NB CFMY are highly correlated (Spearman rho = 0.749). Regressions on both BOF and

NB CFMY averages for the 1990s show a slight decline, which is not significant in the

BOF females (F = 2.56, p = 0.138), and slightly significant in the NB females (F = 5.67,

p = 0.036).

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[8] Data from the right whale catalog (Hamilton and Martin, 1999)

47

Figure 2.9. Three Year Moving Average CMFY, 1982-2002[9]

CFMY 3yr Average

0.5
0.45
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0

BOF
NonBOF

1982   1987   1992   1997   2002
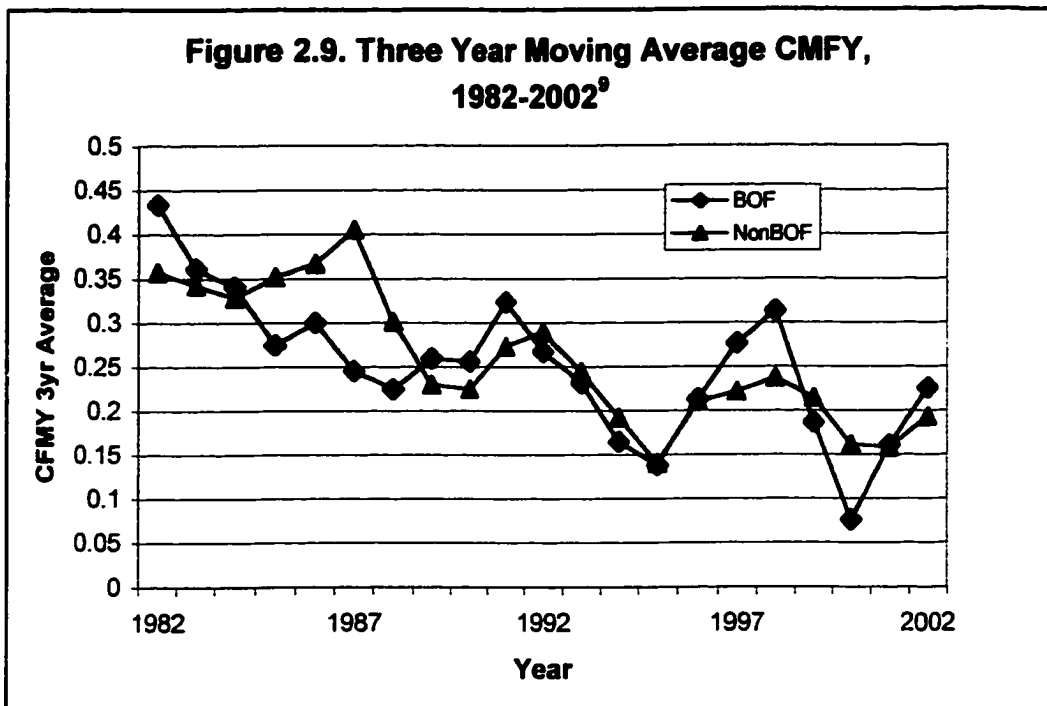
Year

Discussion

Annual right whale calf production shows large variability, ranging from a record

low of one calf to a record high of 31 calves during the study period, around a mean of

11.8 calves per year. The surprising feature of calf production is that it has not increased

over time, despite a slow increase in the number of mature females. The lack of

increasing calf production appears to be the result of a combination of features of right

whale reproduction in the 1990s, including a proposed increase in lost calves, a decline in

calving per mature female, and an increase in calving intervals. It stands in sharp

contrast to South Atlantic right whales, whose populations appear to be growing at 6.9 %

to 7.1 % (Best et al. 2001; Cooke et al. 2001).

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[9] Data from the Right Whale Catalog (Hamilton and Martin, 1999)

48

Analysis of the CMFY statistics is confounded in the 1980s by the addition of

cows that could be animals that are either newly mature or newly identified due to rare

visitation patterns. The use of data after 1990 should eliminate this effect, and in the

averaged CMFY analyses for the latter period, there is a significant declining trend.

CMFY statistics can be confounded by females with extreme sighting heterogeneity,

which in this case removes animals from the available cow pool if they have not been

seen for a period of six years or more. If they are still alive, but do not visit the highly

surveyed areas, the CMFY will be artificially inflated, as there are actually more females

with fewer calves. Based upon the sighting heterogeneity analyses provided in Chapter

III, this may be a significant factor in the 1990s CMFY statistics.

CMFY statistics could also be affected if females were giving birth in areas where

the detection of their calves was unlikely. It is possible there is another calving ground,

but the sightings data do not support this conclusion. Regardless of the northern habitat

use pattern, most females appear to use the southeastern U.S coastal waters as a calving

ground. Calves in that habitat were probably missed due to limitations in right whale

survey and detection methods (Hain et al. 1999) rather than their absence in the region.

Calving intervals have increased significantly over the period, with most of the

increase occurring in the 1990s. Despite calf production well above the mean in the last

two years, the calving interval remains above five years for multi-parous calving females.

The large calf numbers may obscure some underlying slowdown in right whale

reproduction, which is detectable through the monitoring of the inter-birth interval. No

definitive causes for the increase exist, and hypotheses to account for it are discussed

below. Possibilities not examined here include large numbers of senescent mothers

49

and/or an unstable age structure. However, this work and the analysis conducted by Hamilton et al. (1998) of age structure in this population do not support either hypothesis.

Estimating the age at first parturition for large whales is made difficult by sighting heterogeneity and the potential for missing calves that are lost due to stillbirths, late-term abortions, or early neonatal mortality. Here a probabilistic method was applied that indicates the mean age of sexual maturity for right whales is 10 years, with age at first parturition of 11 years. The method is weakened by the low sample size of primiparous females that could not have lost a calf or been missed prior to their first recorded calving event. Further data will strengthen this approach over time. The results are comparable with the southern right whales in Argentina, which have an estimated mean age of first calving at 9.1 years (Cooke, et al. 2001). It is possible that North Atlantic females mature more slowly than their southern hemisphere cousins, or as Cooke et al. (2001) suggest, that the southern right whale estimate is still low.

Researchers have long speculated that right whale reproduction is being affected by some combination of genetics, pollutants, food limitations, disease and loss of critical habitat. If so, than some of these factors may be related to where animals feed and how they use available habitats. The non-Fundy females comprise about a third of the total population of calving females so analyses on this subset are compromised by small sample sizes. Nevertheless, NB females show a slightly greater decline in CMFY statistics over the latter half of the study period than the BOF females. The NB and BOF CMFY rates are highly correlated, indicating that the cause of reproductive decline in this population is not related to whether or not the cows use the Bay of Fundy as a habitat. These analyses do not shed light on the potential for other habitat use patterns to affect

50

reproduction, but they do suggest that the cause is due to something affecting all females. It could be due to a commonly shared habitat (e.g., the southeastern U.S calving ground), or it could be an ocean-wide environmental or anthropogenic phenomena. The differences in the calves per mature female per decade suggest that animals born in the 1970s produce fewer calves than those born in the 1960s. A discussion of the hypotheses potentially causing the reproductive slowdown in this population is given below.

Genetic Factors, Including Potential Inbreeding

The small size of the North Atlantic right whale population has raised hypotheses that "inbreeding depression" might be retarding its recovery. It is unlikely that consistent effects of inbreeding alone could account for the wide variation and recent decline in reproduction. However, reduced genetic diversity in critical areas of the genome that control for immunity (the MHC complex), ontogenesis, or for other areas of reproduction, could be contributing to reproductive vulnerability through synergistic effects with disease, contaminants, or temporal and spatial food reductions.

Schaeff et al. (1991) demonstrated from the nuclear DNA (which is inherited from both parents) that the proportion of genetic material shared among unrelated North Atlantic right whales is significantly higher than that shared among unrelated right whales (*Eubalaena australis*) in the South Atlantic. Correlating this reduced genetic diversity with actual effects on reproduction or mortality will not be easy. To date, no such effects have been identified, although field studies on the effects of inbreeding in the wild have lagged behind such studies on mammalian populations in captivity. Further research on the reduced genetic variability of this species and its potential effects is needed.

51

Potential Effects of Pollutants

Two major pathways of pollutant exposure could impact right whales. First, chemical contaminants are known to enter whale tissues via their food, including calves through lactation (Woodley et al. 1991; Weisbrod et al. 2000). The low trophic level on which right whales feed might minimize the effects of bio-concentration (O'Shea and Brownell 1994), although this does not address the potential effects of short- term acute exposures. Second, non-food items or chemical contaminants might be ingested directly during feeding. Right whales feed in convergence zones and slicks where surface currents concentrate anything that floats or is neutrally buoyant, including not only prey items, but also oil, plastics, tar balls, and contaminants or debris associated with the surface microlayer (Carr 1985).

An analysis of blubber samples from biopsied right whales revealed measurable levels of DDT, other organochlorine pesticides, and PCBs (Woodley et al. 1991), but the reported levels were considered low relative to those of other marine mammals (see also O'Shea and Brownell 1995). Weisbrod et al. (2000) identified comparable levels of organochlorine compounds in right whale tissue, and also discovered that relatively high levels of PAH's (poly-aromatic hydrocarbons) were present in some areas. The variability of contaminant distribution within the blubber layer and within other tissues, as noted by Aguilar and Borrell (1994) and recognized by Woodley et al. (1991), is still an issue needing more investigation.

Further, there may be risks to reproduction posed by a newly identified suite of contaminants (e.g., organotin anti-fouling agents leaching from commercial ship hulls;

52

phthalates, plasticizers that are persistent and widely distributed in the marine environment; polybrominated diphenyl ethers, used as flame retardants; alkylphenol ethoxylates, used as surfactants and dispersants in detergents and pesticides and widely present in sewage effluents), all of which have been shown to be endocrine disruptors (Colborn et al. 1993; Meerts et al. 2001) and are present in marine animals (Kannan et al. 1997; Lye et al. 1997; DeBoer et al. 1998; Tanabe et al. 1998). None of these compounds have been analyzed in right whale tissues.

Food Supply Limitations and/or Reduced Carrying Capacity

Possible reduction in the abundance of copepods, caused either by competition or oceanographic changes, has been hypothesized as a cause of reduced reproductive rates. Females require adequate lipid supplies for both reproduction and lactation, and a diminished food supply could cause a reduction in calving rates (Moore et al. 2001). Mitchell (1974) hypothesized that competition from sei whales (*Balaenoptera borealis*) may have limited the ability of right whale populations to increase. Payne et al. (1990) considered competition from sei whales less important than potential competition from planktivorous fishes, such as sand lance (*Ammodytes americanus*), herring (*Clupea harengus*), basking sharks (*Cetorhinus maximus*) and others. Kenney (2001) has shown that temporary, large scale hydrographic changes in the Gulf of Maine probably altered currents and temperatures and prevented the formation of dense patches of copepods in the Great South Channel during 1992, a year when right whales were absent. The importance of very dense patches of plankton prey to North Atlantic right whale feeding patterns has been well established (Mayo and Marx 1990; Mayo et al. 2001). The identified feeding habitats in the northern portion of the range are areas where those types

53

of zooplankton concentrations have been recorded during oceanographic sampling (Murison and Gaskin 1989; Wishner et al. 1995).

However, data indicating that North Atlantic right whales are food-limited are not convincing. While competition or oceanographic changes may locally and temporarily limit the food intake of right whales, the abundance of planktivorous fishes suggests that copepods, on which North Atlantic right whales primarily feed, are far too plentiful to be limiting this population to fewer than 300 individuals. Planque and Fromentin (1996) and Lambert (1998) both suggest a decline in *C. finmarchicus* over the last decade in the North Atlantic, and point out that the Gulf of Maine represents the southern limit of this species distribution. It is possible that Gulf of Maine *Calanus* abundance is vulnerable to climatic shifts and the North Atlantic Oscillation, and there is some evidence that the regional shifts in right whale distribution are related to this (Kenney, 2001). Nevertheless, it appears unlikely that the 10 year reproductive decline in North Atlantic right whales is due exclusively to food limitation. It has also been suggested that the current population, which was estimated to be 300 whales in 1998 (Kraus et al. 2001), may represent the approximate carrying capacity (K) for right whales in today's environment. The historical records of right whale abundance suggest that between 10,000 and 25,000 animals inhabited the North Atlantic before whaling. As imprecise as these estimates are, the reduced carrying capacity hypothesis does not appear likely.

Infectious Diseases and Biotoxins

A number of infectious diseases could be affecting reproduction (including the death of fetuses and/or neonates) in ways that are consistent with the observed variability in calving, and the increase in calving intervals. For example, brucellosis and

54

leptospirosis are bacterial diseases that are known to cause spontaneous abortions and reproductive dysfunction in domestic animals, and both have been found in free-ranging cetaceans (Smith et al. 1974; Miller et al. 1999). Further, a variety other viral diseases that could cause neonatal mortality, such as influenza, herpes virus, and calicivirus, have all been found in cetaceans (Van Bressem et al. 1999). Although none of these have been identified in right whales, all have been isolated from pinnipeds or dolphins, and all are known to affect either reproduction or survivorship in domestic and wild terrestrial mammals. At the current time, the tools for diagnosis of infectious diseases in free-swimming large whales do not exist.

Recent data indicate that right whales in the North Atlantic are passing PSP toxins (paralytic shellfish poisoning, *Alexandrium spp.*) in fecal samples collected in the Bay of Fundy (Doucette and Rolland pers. comm.). The effects of such toxins on right whales are unknown, but other biological toxins such as brevitoxin (from *Gymnodinium brevi*) are known to have both developmental and reproductive effects on mammals (Kimm-Brinson and Ramsdell 2001). PSP and other toxins such as domoic acid and brevitoxin have been demonstrated to kill humpback whales, manatees, and sea lions through neurological pathways (Scholin et al. 2000). However, the potential sub-lethal effects of these toxins have not been well studied.

55

Prospects for Understanding Right Whale Reproduction

North Atlantic right whale reproduction has clearly slowed in the last decade, in stark contrast to South Atlantic right whales. The reasons for this are unclear, and studies to determine potential causes are needed in several areas.

Food limitation hypotheses are partly being tested by comparative studies of blubber thickness between North Atlantic and South Atlantic right whales (Moore et al. 2001). To provide additional information on the potential effects of food limitation on right whale reproduction, analysis of historical prey abundance relative to the history of calving is needed. In addition, reviews of temporal and spatial changes in oceanographic conditions such as those done by Kenney (2001) for the Great South Channel are needed. Shifts in right whale distributions can provide natural experiments for the assessment of habitat use requirements, and should be linked with historical data on prey and oceanography (Reeves et al. 2001). Further, studies on nutrients of prey species, and the application of stable isotope analysis to right whale baleen from necropsies can help illuminate whether there have been changes in right whale diet in the last 20 years.

Genetic studies are continuing, and the program is collecting samples from calves and previously unsampled right whales to complete the population assessment of potential genetic effects (White, pers. comm.). Tests of the effects of inbreeding, particularly in the MHC complex which codes for immunity, may reveal whether right whale with less genetic diversity may be more prone to disease or poor reproductive success. Further, the completion of paternity analyses for this population will allow the testing of male reproductive success relative to genetic diversity, contaminant burden, external assessments of health, and habitat use patterns.

56

No studies on pollutants are currently underway. However, because ambient levels of certain endocrine disruptors have been found to affect reproduction in a variety of organisms, studies on still untested compounds are needed. Levels and types of contaminants should be evaluated across all females to determine if there are correlates with reproductive success. Further, as the genetic studies on paternity advance, it will be worthwhile conducting the same analyses correlates with male reproductive success.

Reproductive cycles are still poorly understood in right whales. Preliminary analyses of fecal samples for the metabolites of reproductive and stress hormones show remarkable promise for identifying the reproductive status both males and females (Rolland, pers. comm.). The analysis of stress hormones from feces should be used to determine the non-lethal effects of entanglements, ship traffic, pollutants, biotoxins and perhaps habitat disturbance factors on health and reproductive cycles (Reeves et al., 2001). Fecal analysis of biotoxins in right whales should also be developed to assess potential non-lethal reproductive or health effects.

The effects of diseases on right whale are unknown. Evidence of skin lesions and the results of a population-wide visual health assessment suggests that right whales are subject to unknown pathologies that affect health (Pettis, pers. comm.). Biopsy samples should be tested with PCR for pox, herpes, and other viruses using appropriate genetic primers. Histopathology and electron microscopy could provide additional information on skin lesions. Blowhole exudate, and possibly feces, should be evaluated to test for microbial infectious agents. Further development of analytical methods for antigen detection from skin biopsies, respiratory fluids, or fecal materials, may allow the evaluation of disease effects on right whales in the future. Also, a rapid response to

57

neonatal mortalities that ensured the recovery of fresh tissues and fluids could provide materials for conventional laboratory detection methods. As new technologies provide new disease and pathology data, multivariate analyses should test individual reproductive histories against the potential factors affecting reproduction. Disease or pathology data should also be tested against genetic features of individuals.

In the long term, reproductive success in right whales may best be measured in calves per mature female per decade. Long-lived mammals are certainly subjected to short-term variation in their environment, and analyses from short-term studies (relative to the total life span of the study subject) by short-lived researchers have limitations. When the subject animal is endangered, it is necessary to take declines seriously. In this population, the management focus on the population's decline has been on anthropogenic causes of death. It is important to realize that the elimination of all human-caused mortalities will make no difference if anthropogenic causes of reproductive failure are occurring. Right whale researchers and managers must not lose sight of the need to determine whether the current reproductive decline in right whales is short-term or long-term, and whether it is due to human activities, or to normal environmental variation over which we have no control.

58

CHAPTER III

MORTALITY RATES AND CAUSES IN NORTH ATLANTIC RIGHT WHALES AND THE EFFECTS OF SIGHTING HETEROGENEITY ON ESTIMATES OF SURVIVORSHIP

INTRODUCTION

One of the problems in evaluating the population status and trends in the North Atlantic right whale(*Eubalaena glacialis*, Borowski, 1781) population is the heterogeneity of sighting probabilities within the survey and photo-identification data. In some cases, animals are not observed for several years, and the researcher is left wondering whether they are dead, have moved elsewhere, or have just been missed because of bad weather, poor effort, or some inherent "boat shy" behavior. Cows are known to "disappear" more frequently than expected in the years before calving (Brown et al. 2001), and many whales exhibit philopatry (Schaeff et al. 1993), which means their chances of being re-sighted are not random with respect to the known habitats. Further, survey effort has not been consistent across all known habitats and years, and at least one winter and one summering habitat for right whales remain unidentified in the North Atlantic (Malik et al., 1999). Even within known right whale habitats along the east coast of North America, distribution patterns have shifted over time (Kenney 1994; Kenney 2001).

59

The sighting heterogeneity problem for right whales has been addressed by several researchers in recent years (Hain et al. 1999; Brown et al. 2001; Wade and Clapham in press). Several population modelers have attempted to correct for hetereogeneity in a variety of ways (Caswell et al. 1999; Fujiwara and Caswell 2001; Wade and Clapham in press). All of these models show a recent decline in population size, although there is disagreement on the magnitude of the decline. Caswell et al. (1999) applied a correction to account for poor survey effort and unequal capture probability between "inshore" and "offshore" components of the population. Fujiwara and Caswell (2001) applied corrections for survey effort differences between the northern and southern habitats. Wade and Clapham (in press) used cluster analysis to identify groups of animals that showed specific habitat use patterns and then adjusted sighting probabilities for each group in their model.

The models have led to a better understanding of the population dynamics of right whales in the North Atlantic, and have helped identify the significant gaps in our knowledge about this species. However, all of these models depend upon capture/recapture statistics to estimate the mortality parameters. In a small population, a very few animals can skew both the parameters and the transition probabilities between different model stages. Indeed, Fujiwara and Caswell (2001) state, "...prevention of just two female deaths per year would suffice to increase λ (the asymptotic growth rate) to 1." Thus the tag-recapture estimators are vulnerable to the sighting, travel, and ecological characteristics of merely two animals per year. None of the models have looked explicitly at the characteristics of the known and estimated mortalities to determine

60

whether these factors may be affecting the results.

Here, the characteristics of the "disappearing" right whales were examined. This included those animals that appear as "presumed dead" in Knowlton et al.'s (1994) paper, and the animals that become "dead" in capture/recapture models when they were not recaptured. By analyzing the demographic structure of the known mortalities, and comparing them with that of the estimated mortalities, the probability that the "presumed dead" were actual mortalities was determined. The sighting records for "disappearing" animals were also used to determine the likelihood that re-sightings might occur after x period of years. Comparative analyses of natural versus anthropogenic mortalities were also conducted. Finally, a detailed examination of sighting probabilities was conducted to determine the impact of sighting heterogeneity on estimates of mortality.

METHODS

Stranding and Mortality Data Collection

Since 1985, all right whale strandings on the east coast of North America have been examined by New England Aquarium researchers to collect basic anatomical data, identify individual whales, and if possible determine the cause of mortality. Necropsy procedures follow standard large-whale protocols, with several additional features specific to right whales. These additional methods include flensing of the entire animal to look for evidence of broken bones from ship collisions, measurements of blubber to assess health and condition (Moore et al. 2001), and photo-identification or genetic sampling procedures to identify the individual. Internal examinations have proven of limited value, primarily because post-mortem autolysis is rapid and widespread, possibly due to the well-insulated carcasses or an active gut fauna, or both.

61

All confirmed mortalities are classified as attributable to "natural causes", "anthropogenic causes", or as unknown causes. Most anthropogenic mortalities are relatively easy to identify, since propeller cuts, collision fractures, and entangling fishing gear leave significant measurable evidence behind. Most of the whales classified as "natural causes" mortalities are calves, and these deaths may be due to premature births, birth defects, failure to thrive, starvation, or disease. However, because of the rapid decomposition of internal organs, mortalities for which there is no external or skeletal evidence of anthropogenic injury are usually classified as unknown. Infectious disease diagnosis requires fresh tissues and fluids for histological or culture detection, and are therefore unlikely to be available from a stranded right whale. Since infectious diseases are known to cause mortalities in every wild mammalian population for which there is good data, it is likely that the right whale mortalities classified as unknown cause, are primarily due to natural causes. Therefore, in this Chapter, I have classified the deaths in the unknown category as attributable to natural causes, and combined these data in subsequent analyses.

Individual Right Whale Identification, Survey Effort, and Habitat Use Definitions

Right whales in the North Atlantic have been individually identified and cataloged since the 1950s using callosity patterns and scars found on their heads and bodies (Kraus et al. 1986; Payne et al. 1986). Right whale identification photographs have been obtained through both aerial and shipboard surveys over the last twenty years. Although there has been significant variation in effort from year to year, photographic surveys for right whales have been done annually in the southeastern U.S. wintering ground since 1984, in Cape Cod Bay since 1982, and in the Bay of Fundy since 1980.

62

Right whale surveys started in the Great South Channel in 1979, but there were several years in the early 1990's with no effort. Surveys on the Nova Scotian Shelf started in 1983, and have been continued sporadically to the present. For this Chapter, photographic identification records of individual whales provided information on the age and size of right whales at death, sighting rates, gaps in sighting histories, reproductive parameters and life stages, and the status of animals affected by human activities, based upon the North Atlantic Right Whale Catalog (Hamilton and Martin, 1999). A supplementary genetics study provided gender information for 250 individuals (Brown et al. 1994; 2001).

Work by Malik et al. (1999) demonstrated population sub-structuring by habitat use patterns, and several modelers have attempted to correct for the sighting heterogeneity introduced by this sub-structuring (Caswell et al. 1999; Wade and Clapham in press). Schaeff et al. (1994) also suggested that female philopatry was responsible for most of the habitat use patterns observed, and that calves brought to the Bay of Fundy in their first year, tended to return there in subsequent years. Calves not brought to the Fundy habitat in their first year are rarely seen there subsequently. For this Chapter, right whales were divided into Fundy and non-Fundy categories based upon their presence or absence in the Bay of Fundy at any time in their entire sighting history. Although a crude measure of habitat use patterns for this population, it matches the "offshore" animals in Caswell's 1999 paper remarkably well, and adds some animals that were not strictly "offshore" in the Caswell definition. The rationale for this approach is that the Bay of Fundy has been surveyed consistently since 1980, so this definition is less dependent

63

upon sighting probabilities that other habitats, all of which have had highly variable effort over the same period.

Mortality Analyses

To estimate the age of mortality, age-length curves were created from the stranding data where animals of known age had been accurately measured on the beach. Then, the age at death of unidentified right whales was estimated from necropsy measurements gauged against the curves derived from known age versus length data. This information was used cumulatively to identify the ages of whale mortalities caused by anthropogenic and natural or unknown causes for comparative purposes.

A second analysis was conducted on the survivorship of calves, by evaluating the sighting records for animals over the 20-year study period. This exercise cumulatively summed survivorship by year class to estimate age specific mortality rates. These rates were also compared to the known mortality curves derived from stranding data above.

The right whale catalog curators have adopted "presumed dead" as a term to classify animals that have not been seen in six years (Knowlton et al. 1994). Because the use of "presumed dead" status has come under criticism for its statistical weakness, analyses were conducted to determine the probabilities of re-sighting animals after sighting gaps of varying lengths of time.

Further, the characteristics of the "disappearing" right whales were examined, particularly with regard to entanglement injuries, antecedent sighting histories, as well as the effects of changes in survey effort that occurred in the early 1990s. Right whales that appear as "presumed dead" (Knowlton et al. 1994) are also animals that become "dead"

64

in capture/recapture models when they are not re-sighted. Using the age-length curves generated from known mortalities, the demographic structure of the known mortalities was determined, and a comparative analysis was conducted to determine whether the age and life stage characteristics of the "presumed dead" are consistent with known mortalities.

Fundy and non-Fundy "presumed dead" were analyzed to identify differences in demography of the disappearing whales. Comparative analyses of natural versus anthropogenic mortalities were also conducted to determine if the "presumed dead" might be attributable to either anthropogenic or natural causes.

To determine whether individual or yearly sighting rates could affect tag-recapture analyses, or the determination of "presumed dead", an additional series of analyses were conducted on the sighting rates of all right whales known to be alive, by year and by individual over the study period. Sighting rates were calculated for all individuals in the population that were known to be alive in 2000, based upon sightings of those individuals seen in either the year 2000 or the two previous years. Right whales known to be alive (by these criteria) were selected to eliminate probabilistic estimates of mortality from the analysis, and to evaluate the contribution of individual whales to the apparent mortalities. Sighting rate comparisons then were conducted by year, age, sex and reproductive state for the entire population known to be alive.

Because both the Caswell et al. (1999) and the Fujiwara and Caswell (2001) papers identified a significant decline in reproductive females, special attention was paid to analyzing their sighting histories. Calving intervals have increased throughout the 1990s (Kraus et al. 2000; Chapter II), and sighting probabilities of cows are significantly

65

lower when pregnant or resting than when lactating (Brown et al. 2001). The hypothesis suggested by this relationship was that increased calving intervals would lead to decreased sighting probabilities of cows during the 1990s, therefore artificially creating the appearance of increasing mortality. Analyses were conducted on the relationship between calving interval and sighting rate both before and after calving events, as well as comparisons of sighting gaps of cows over time through the study period.

The results from the tests conducted above suggested that a few individual right whales were significantly affecting most analyses. An examination of the data showed a cluster of animals with sighting probabilities below 50%, and these were subject to a detailed analysis of sighting probability by age, sex, haplotype, matriline, and Fundy/non-Fundy pattern. Genetic data were provided by Dr Brad White of Trent University.

RESULTS

Confirmed Right Whale Mortalities

A summary of all known right whale mortalities between 1970 and 2001 is given in Table 3.1. There have been 50 confirmed right whale deaths since 1970. The causes of mortalities are given in column 7 of Table 3.1, and are categorized by "natural" (N), "unknown" (U), ship strike (SS), and entanglement (E). Natural and unknown causes were combined in subsequent analyses. A total of 46% (23/50) of all confirmed right whale mortalities were due to anthropogenic causes.

66

Table 3.1. Confirmed right whale mortalities in the North Atlantic, 1970-2001.

ID#	Date	Sex	Length	Stage	Location	Cause	Age
	1/26/70	F	439	C	FL	N	1
	9/1/71	U	1200	J	NY	U	4
	1/30/72	U	600	C	TX	SS	1
	1/12/74	M	407	C	SC	N	1
	5/13/75	M	1030	J	MA	U	2
	4/15/76	U	760	C	MA	SS	1
	11/5/76	U	1100	J	ME	SS	2
	3/5/79	U	1100	J	NY	SS	2
	12/10/79	F	1550	A	FL	U	25
	12/30/81	M	464	C	GA	N	1
	2/20/82	F	457	C	GA	N	1
	4/19/82	F	900	C	DE	U	1
1128	2/21/83	M	1100	J	NJ	SS	2
1504	8/7/86	F	1090	J	MA	SS	2
	5/22/87	U	1200	J	MA	U	4
	7/9/87	M	800	C	NS	SS	1
	1/17/88	M	438	C	FL	N	1
	3/15/88	U	1500	C	NFLD	U	23
	11/17/88	U	U	J	NB	E	2
	1/3/89	M	425	C	GA	N	1
	1/26/89	U	488	C	FL	N	1
1219	9/8/89	F	1200	A	FL	U	7
	9/10/89	U		C	FL	U	1
	10/17/90	M	1675	A	ME	U	30
1907	3/12/91	F	1005	J	FL	SS	2
1223	9/5/92	F	1360	A	NB	SS	12
	1/5/93	M	581	C	FL	SS	1
	1/15/93	F	473	C	FL	N	1
	12/6/93	M	1400	A	VA	U	10
	12/6/93	F		J	VA	SS	3
	7/9/94	M	1155	J	NS	U	2
2366	7/17/95	M	1009	J	RI	E	2
2250	10/20/95	M	1270	J	NS	SS	3
	1/2/96	F	478	C	FL	N	1
1623	1/30/96	M	1415	A	GA	SS	11
	2/8/96	F	1100	J	FL	U	2
	2/19/96	F	513	C	FL	N	1
	2/22/96	M	U	C	GA	N	1
2220	3/10/96	M	1350	J	MA	SS	4
	1/9/97	M	417	C	FL	N	1
2450	8/19/97	F	1259	J	NB	SS	3
	1/10/98	F	455	C	GA	N	1
	10/7/98	M	1460	A	NC	U	20
1014	4/20/99	F	1370	A	MA	SS	24
2030	10/20/99	F	1350	A	NJ	E	10
2701	1/10/00	F	N/A	J	RI	U	2
	3/17/01	M	771	C	VA	SS	1
	6/18/01	F	910	C	NY	SS	1
1102	9/12/01	M	U	A	GOM	E	22
1238	10/29/01	M	1455	A	GSL	E	19

67

The measurement data from all known age right whale mortalities were plotted

against age, and a natural logarithm curve was fitted to the length measurement data

(Figure 3.1). The formula was $y = 186.95Ln(x)+945.76$ with an R^2 of 0.959.

Figure 3.1. Age-length curve from known-age right whales.
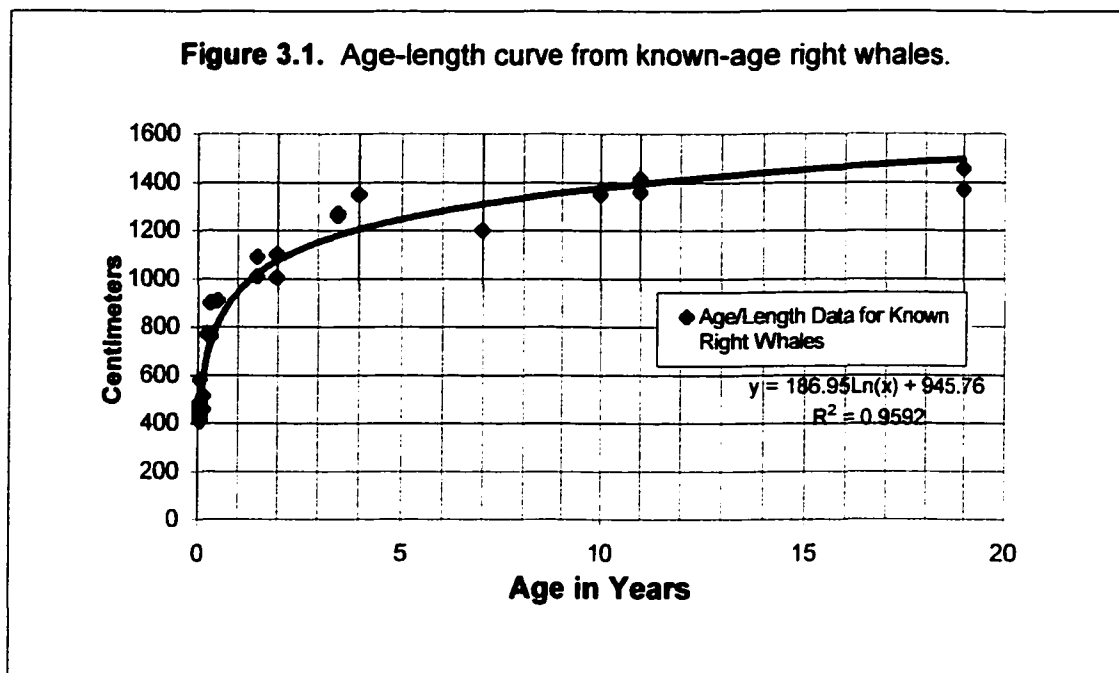
From this curve, ages were estimated for right whale mortalities with

measurements but without known histories from which to determine age. Both estimated

and known ages are given in the last column of Table 3.1. From these age

determinations, whales were classified as calves (0 to 1 year), juveniles (1-9 years), and

adults (10 yrs and older). These life stage classifications were combined with data on

sexes to create the demographic profile of mortalities in North Atlantic right whales

68

given in Table 3.2. Mortalities were approximately equal between males and females, and mortality rates decreased with increasing age, as expected for most mammals (Caughley 1966). An examination of the confirmed right whale mortalities by cause, sex, and age-class shows that nearly half of all confirmed mortalities are due to anthropogenic causes, with ship kills accounting for most of those deaths (Table 3.3). A summary of all confirmed mortalities by known age and cause is given in Figure 3.2.

Table 3.2. Demographic profile of confirmed right whale mortalities, 1970-2001.

Sex	Adult	Juvenile	Calf	Totals
F	5	6	8	19
M	6	6	9	21
U	0	5	5	10
Totals	11	17	22	50

Table 3.3. Right whale mortalities by sex, life stage, and source, 1970-2001.

Sex	Stage	Natural	Unknown	Entanglement	Ship Kill	Total
Females	A		2	1	2	5
	C	6	1		1	8
	J		2		4	6
F Total		6	5	1	7	19
Males	A		3	2	1	6
	C	6			3	9
	J		2	1	3	6
M Total		6	5	3	7	21
Unknown	C	1	2		2	5
	J		2	1	2	5
U Total		1	4	1	4	10
Grand Totals		13	14	5	18	50

Key to Tables 3.2 and 3.3.
A = Adult   J = Juvenile
C = Calf   F = Female
M = Male   U = Unknown

69

Figure 3.2. Confirmed right whale mortalities by age and cause, 1970-2001

Number of Mortalities

■ Natural   □ Anthropogenic

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Natural	15	4		2			1			1										1			1		1					1
Anthropogenic	6	7	3	1						1	1	1							1				1		1					

Minimum Age
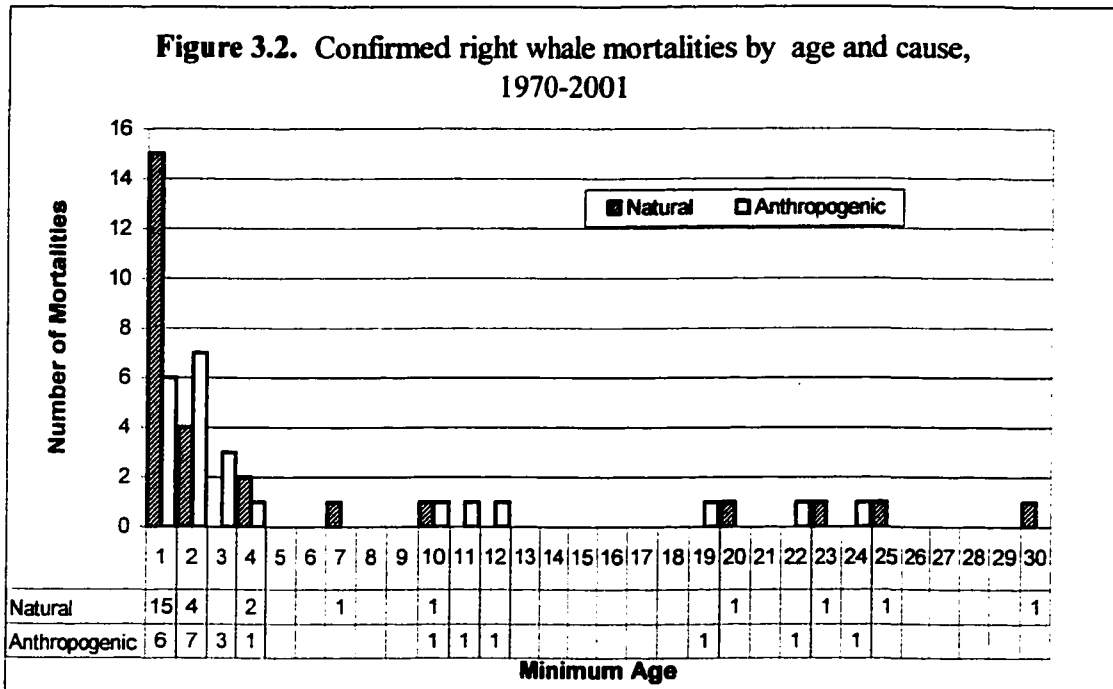
The distribution of the mortality data by age is consistent with normal mammalian mortality curves for a variety of long-lived species (Caughley 1966). The data in Figure 3.2 include both anthropogenic and natural sources of mortality, separated to show the differences in age structure, which are significant ($\chi^2 = 35.394$, p = 0.002). Anthropogenic mortalities appear to affect two and three-year-old whales more than other ages, effectively doubling death rates in those years. Anthropogenic mortalities also double overall death rates for adults, although the effect is not as statistically significant because it is distributed across two or more decades.

Age-Specific Mortality Rates

The mortality rates in right whales first identified as calves were estimated from sighting records for the period 1980-2000, by summing all cohorts by age. Survivorship

70

was calculated as the total number of whales sighted in a given year (or in any subsequent year) divided by the total number available to be sighted (Table 3.4). The inverse of the survivorship data represent mortality rates, which are more comparable to the strandings and presumed dead analyses, and these are given in Figure 3.3. Two mortality rate analyses were done, one for the whole dataset, and one for animals only up through 1996, to eliminate the apparent increase in mortality at the end of the time series (Figure 3.4). The longer intervals between sightings at the end of the study period, which are common in this population, appear as mortalities in both this analysis and in tag-recapture models.

Table 3.4. Survivorship table for right whales first identified as calves. Survivorship rates are given for all animals by the age shown in the first column. The rates in the last column are derived from all whales born from 1980 through 1995. The rates in the third to last column include all whales born from 1980 through 1999, and may underestimate survivorship in the last four years because of the probability of subsequent re-sightings. Data from Right Whale Catalog (Hamilton and Martin, 1999).

yrs	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	n	80-99	N	<1996
1	3	8	9	7	11	8	11	11	7	15	10	12	8	5	7	3	13	12	1	0	161	0.6909	135	0.7584
2	3	8	8	6	10	6	10	11	5	15	8	11	8	4	6	3	12	11	1	0	146	0.9068	119	0.9015
3	3	8	8	6	10	5	10	11	5	13	8	10	7	4	6	3	12	9	1		139	0.9521	108	0.9557
4	3	7	8	5	10	5	9	11	5	12	8	10	7	3	6	2	12	9			132	0.9565	11	0.9615
5	3	7	8	5	10	5	9	10	5	11	8	9	7	3	6	2	11				119	0.9675	90	0.9677
6	3	7	8	5	10	4	9	10	5	11	8	9	6	3	6	2					106	0.9815	80	0.9876
7	3	7	8	5	9	4	9	10	5	10	8	9	6	3	6						102	0.9808	70	0.9722
8	3	6	8	5	8	4	9	10	5	10	8	9	5	3							93	0.9688	58	0.9666
9	3	6	8	5	8	4	9	10	5	10	7	9	5								89	0.9888	53	1
10	3	5	8	5	8	4	9	10	4	10	7	9									82	0.9762	42	0.9767
11	3	5	8	5	8	4	9	10	4	10	7										73	1	33	1
12	3	5	8	5	8	4	9	10	4	9											65	0.9848	29	1
13	3	4	8	5	8	4	9	8	4												53	0.9464	20	0.9523
14	3	4	8	5	8	4	9	7													48	0.9796	15	1
15	3	4	7	5	8	4	9														40	0.9756	7	1
16	3	4	7	5	8	3															30	0.9677	3	
17	3	4	7	4	7																25	0.9259		
18	3	4	7	4																	18	1		
19	3	4	7																		14	1		
20	2	3																			5			
21	1																				1			

71

Figure 3.3. Inferred annual mortality rates in right whales tracked from birth[10]
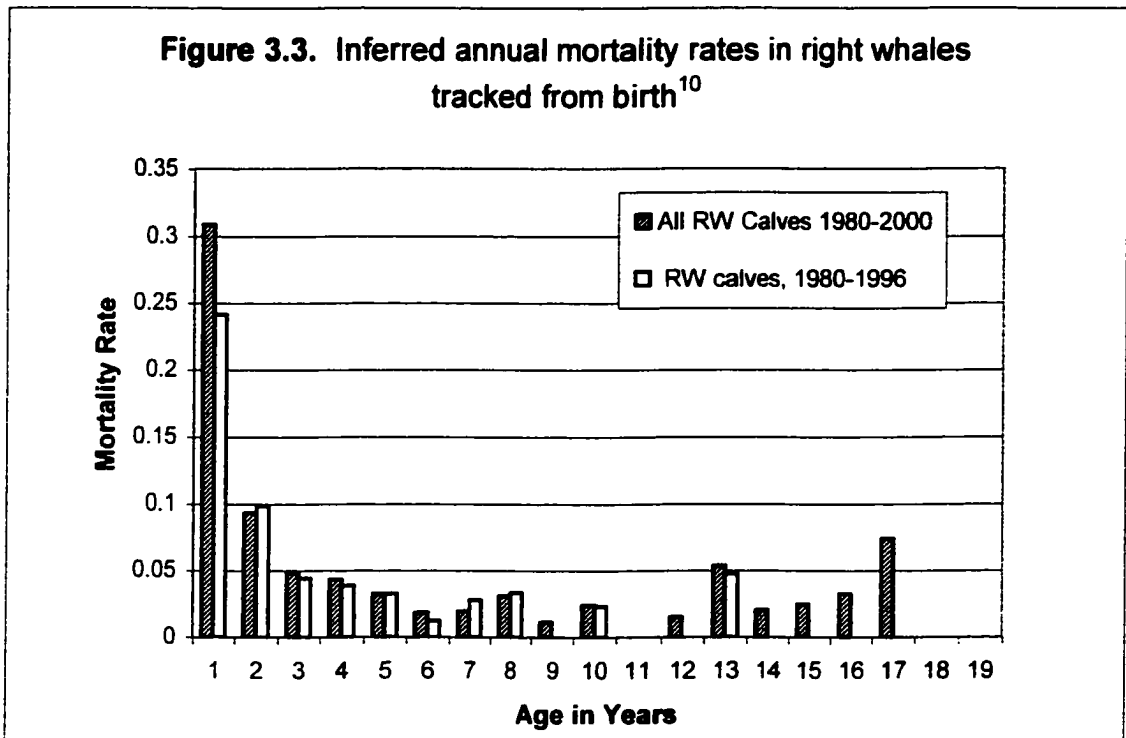
Right Whales that are Presumed Dead

To test the validity of the "presumed dead" category, the gaps in the sighting histories of all right whales known to be alive between 1980 and 2000 were summed by the number of years, and are shown in Figure 3.4. Because these are animals known to have been alive during this period, the probability of a whale being sighted in the year after each interval is 1 minus the probability of that interval occurring within the population, plus the probability of all intervals less than that one.

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[10] Data from the Right Whale Catalog (Hamilton and Martin, 1999)

72

Figure 3.4 shows that the probability of a right whale being re-sighted after a gap of x years decreases rapidly after x is greater than three years, diminishing to about 0.05 at 4 years, and 0.01 at eight years. For the six year sighting gap whales that Knowlton et al. (1994) called "presumed dead", the probability of re-sighting those individuals is 0.0259. No right whale has ever been re-sighted after a sighting gap of 12 years.

Thus one can be 95% confident that a whale not seen in 4 years will never be seen again. Researchers using the presumed dead criteria can be 97.41% confident that a whale missing for six years will never be seen again, and 99% confident that an eight year gap in sightings will never be seen again. In 2000, there were 99 animals "presumed dead" in the catalog, and all but 13 had been missing for eight years or more. Almost half (45) had been absent for 12 years or more.

Figure 3.4. Occurrence of gaps in the sighting history and the cumulative probability of re-sighting after each interval in right whales, 1980-2000[11]
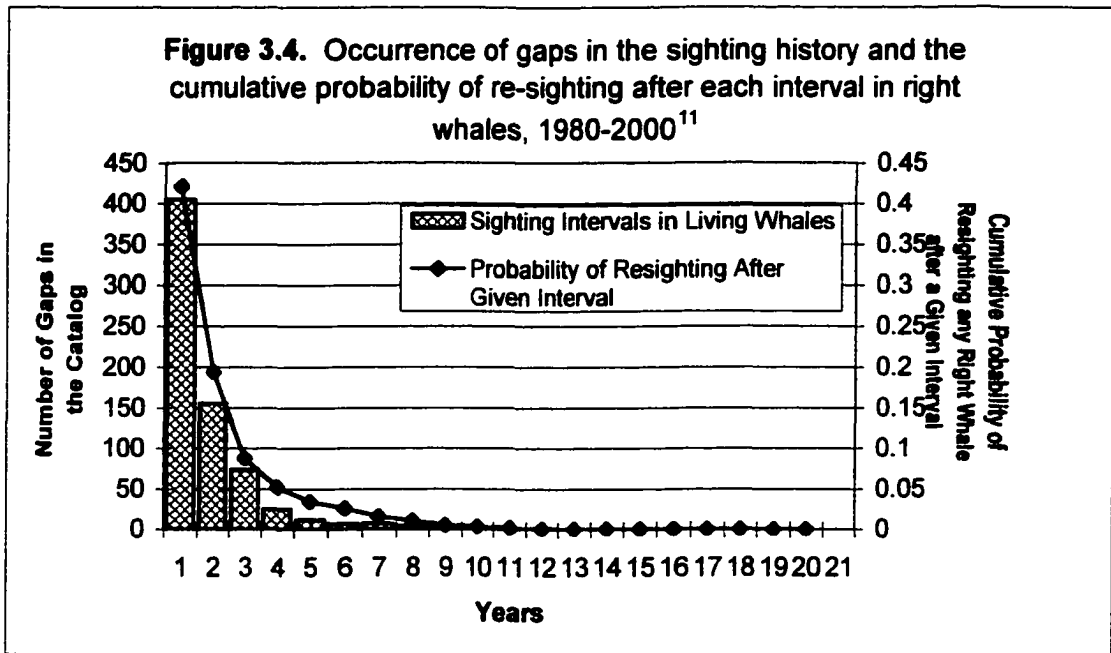
Right whales presumed dead by the six year criteria were analyzed by sex, age, and Fundy/non-Fundy habitat use patterns. There were no significant differences in the frequency of sexes in the presumed dead. However, when presumed dead were analyzed by age-class and habitat pattern, there were significantly more adults and juveniles in the non-Fundy group than expected compared to Fundy group (Figure 3.5) (χ^2 = 10.432, p = 0.015). This group is comparable to the "offshore" groups that Caswell et al. (1999) identified and accounted for in their best-fit model. As Caswell et al. (1999) point out, the "offshore" animals had an increasingly negative effect on sighting rates in the 1990s, as effort in the offshore (non-Fundy) areas declined or ceased. In this case then, the

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[11] Data from the Right Whale Catalog (Hamilton and Martin, 1999)

74

presumed dead category may have been increased by the reduction in effort and

concurrent reduction in sighting probabilities for non-Fundy whales.

Figure 3.5. Presumed dead by habitat preference[12]

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Fundy	13	7	5	2	3	2	3	5	3	4	2	2	4	1	4	1	2	1	1	1	0	1	1	0	0
Non-Fundy	1	1	1	0	2	5	1	2	5	3	1	1	0	1	0	1	0	0	0	0	0	0	1	0	3
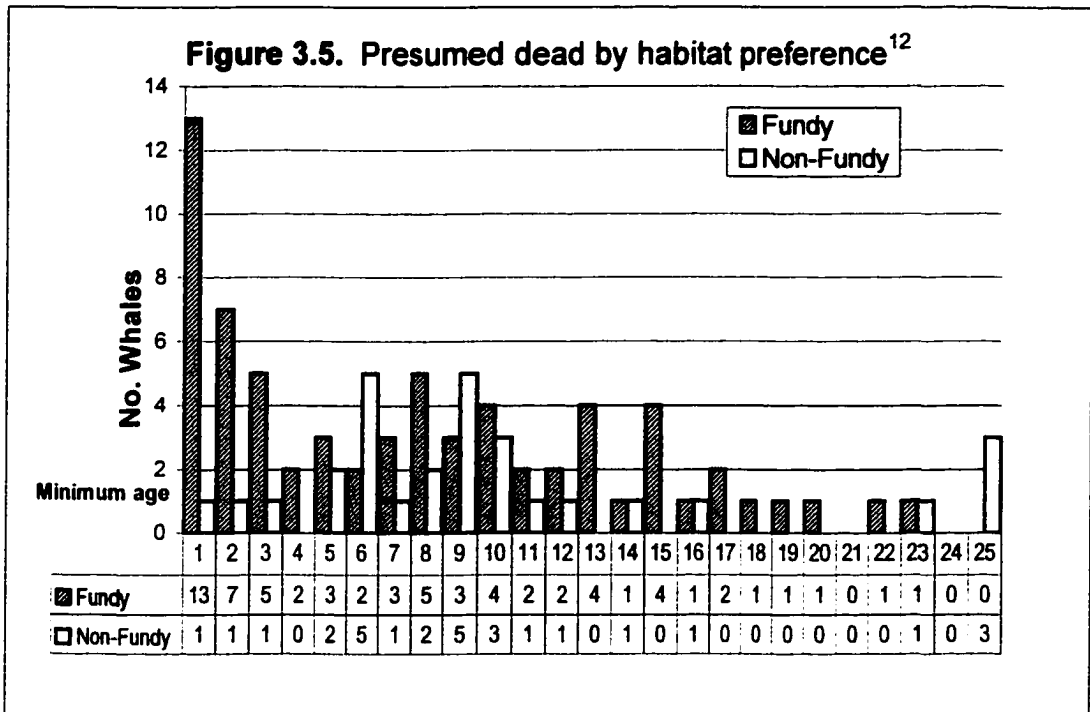
Comparisons of the presumed dead with the confirmed mortalities were made to

determine demographic characteristics of the missing whales (Figure 3.6). A comparison

of age-classes between presumed dead and those whales that died of natural causes (from

Figure 3.2) showed the demographic characteristics of the two groups were significantly

different ($\chi^2 = 22.491$, p< 0.001). A subsequent comparison of the demographic

characteristics of the presumed dead and known anthropogenic deaths showed no

significant difference ($\chi^2 = 2.5$, p = 0.475). This suggests that the demographic features

[12] Data from the Right Whale Catalog (Hamilton and Martin, 1999)

75

of the missing and presumed dead right whales are closely similar to those found in the anthropogenic deaths, but not in those due to natural causes.

Figure 3.6. Presumed dead and confirmed natural mortality by age[13]

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Presumed Dead	14	8	6	2	5	7	4	7	7	7	3	3	4	2	4	2	2	1	1	0	0	1	1	0	2	2
Natural Mortality	15	4		2		1			1											1			1		1	1

Minimum Age at Disappearance or Death
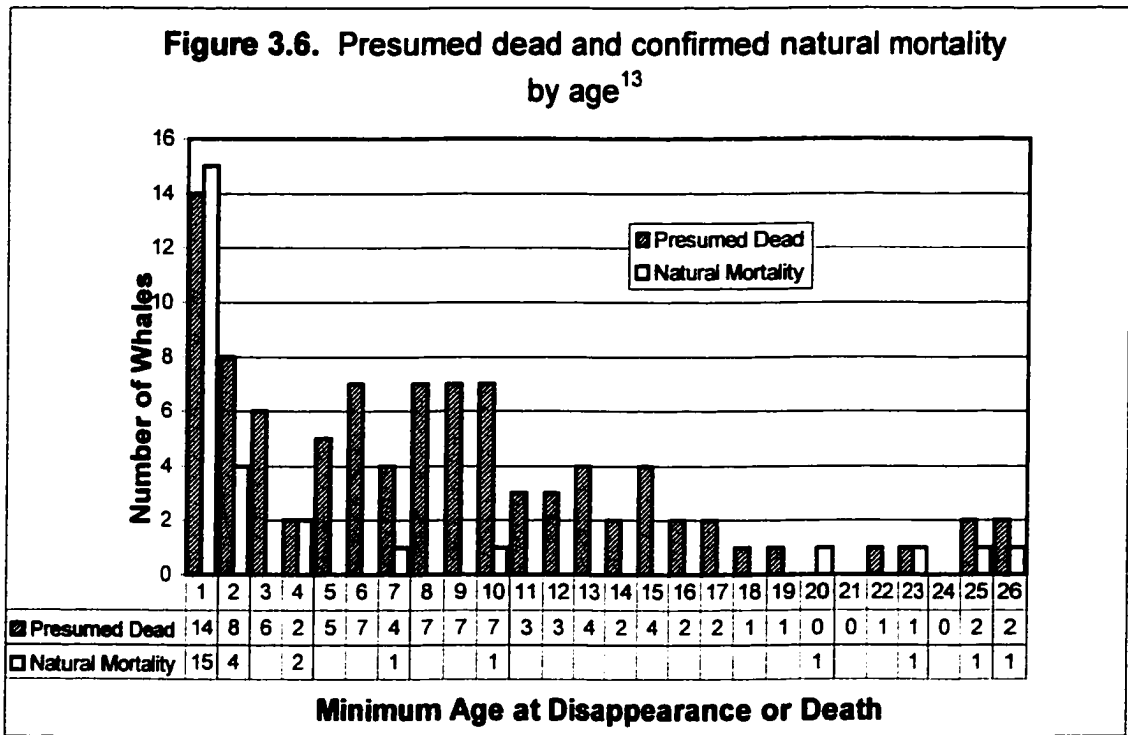
An analysis of the presumed dead data was conducted to identify trends and variation in the study period. Because of the steep discovery curve in the first six years of the study period, this analysis only included animals starting in 1987. A regression on the number of presumed dead versus year was calculated for the period 1987 through 1997, based upon the year in which an animal was last seen. This provides a worst case scenario, as animals that were last seen in 1997 may be re-sighted within the next few years, although the sighting probability analysis suggests that only 5% of them will be

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[13] Data on age from the Right Whale Catalog (Hamilton and Martin, 1999)

76

seen again. Nevertheless, although there was a slight increase in presumed mortalities

through the period, it was not significant (F = 1.0698, p = 0.3232) (Figure 3.7).

Figure 3.7. Trend in presumed dead, 1985-1997[14]

Year of Disappearance
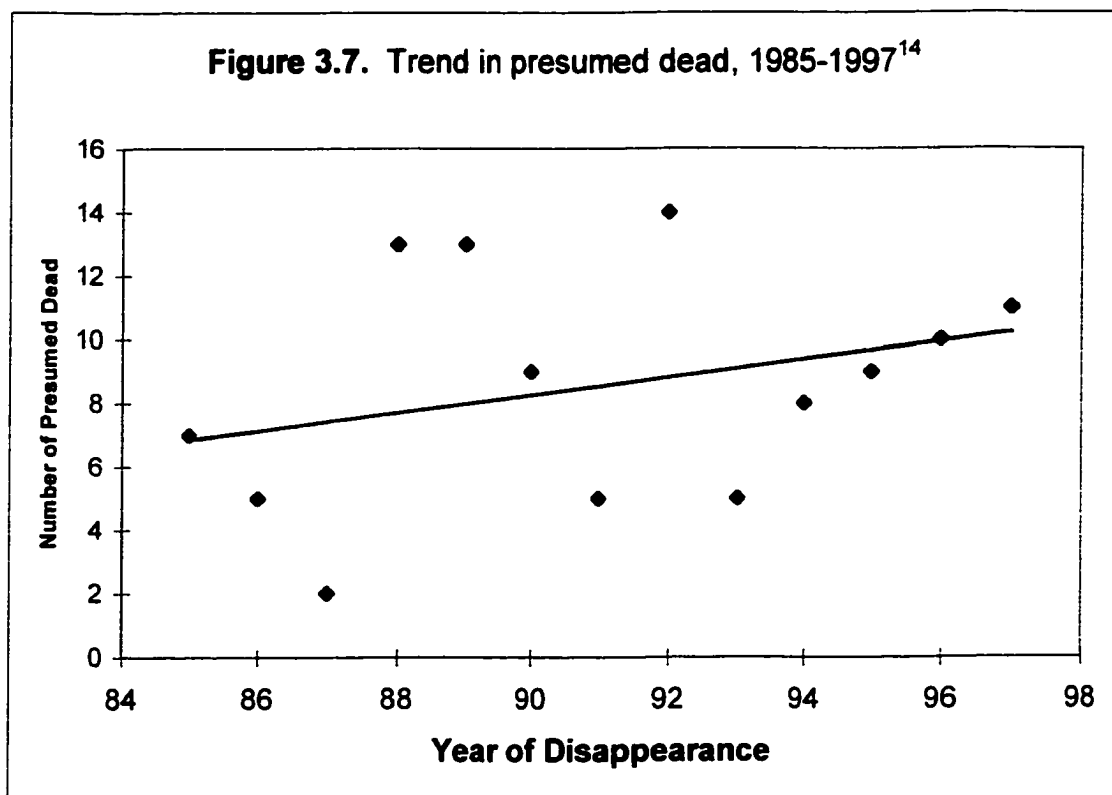
Potential Causes of Mortality in Presumed Dead Right Whales

Confirmed mortalities have provided data on the causes of death associated with

human activities (Knowlton and Kraus 2001; Chapter V). From work on right whales

through 2001, there were 56 serious injuries caused by human activities, 25 from

collisions with ships, and 31 from entanglements in fishing gear. Deaths were confirmed

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[14] Data from the Right Whale Catalog (Hamilton and Martin, 1999)

77

from these injuries in 18 of the ship strike events and 5 of the entanglements. A follow-up on the injured whales believed to be survivors at the time revealed that 10 of the entanglement-injured whales were never seen after the entanglement event, and 2 of the ship-struck whales were never seen again after being observed with a significant injury attributable to a ship. Since more than six years has passed on most of these animals, it is 97% probable that these animals are dead. Their disappearance immediately after a significant injury strongly suggests cause and effect. Thus the total number of right whale deaths from shipping was probably 20 animals, and the number of mortalities from fishery entanglements was probably 15 animals for the period 1970 – 2001. These numbers are much higher than whale deaths previously estimated for the fishing industry.

Sighting Probabilities

Because both population models and the presumption of death in the catalog depend upon individual sighting probabilities, these were calculated for all right whales known to be alive in 2000. These probabilities were calculated by year, sex and reproductive life stage, following the definitions by Fujiwara and Caswell (2001). The results are shown in Figure 3.8, and are mostly consistent with the data shown by Fujiwara and Caswell for all right whales. Cows between calving events are seen significantly less than juvenile females. They are also seen significantly less than cows with calves, but sighting probabilities of parturient mothers are always 1 by definition – if they aren't seen with a calf, they don't exist. This may be a problem, if cows are giving birth that are not detected, although the data to date do not suggest that many calves are missed in current survey efforts. In addition, a comparison between Fundy and non-

78

Fundy right whales known to be alive in 2000 showed that non-Fundy right whales had significantly lower sighting probabilities than those that went to the Bay of Fundy (mean Fundy = 0.7559, mean non-Fundy = 0.3974; $t = -10.6547$, $p < 0.001$). This supports the correction provided by Caswell et al. (1999) for "offshore" whales, the set of which will include the non-Fundy whales identified here.

Generally, the sighting probability patterns reflect an increase in survey effort starting in 1986 (with the formation and funding of the Right Whale Consortium). The second increase in the early to mid-1990s probably reflects the shift in distribution of many right whales from the Nova Scotian shelf habitat to the Bay of Fundy, where effort has remained consistent for 20+ years. The increase in sighting probabilities of non-calving cows in the late 1990s may be attributable to an increase in the survey effort by NMFS in offshore areas during this period.

The increase in sighting probabilities for all categories of right whales alive throughout the period matches the data shown for all right whales by Fujiwara and Caswell (2001) for all right whales, suggesting the decline in survivorship shown by them is not an artifact of reduced sighting rates for any particular class of animals. However, probabilistic deaths (disappearances of animals for extended periods from the sightings database) would have the effect of reducing survival in the models.

Figure 3.8. Sighting probabilities for adult right whales known to be alive[15]
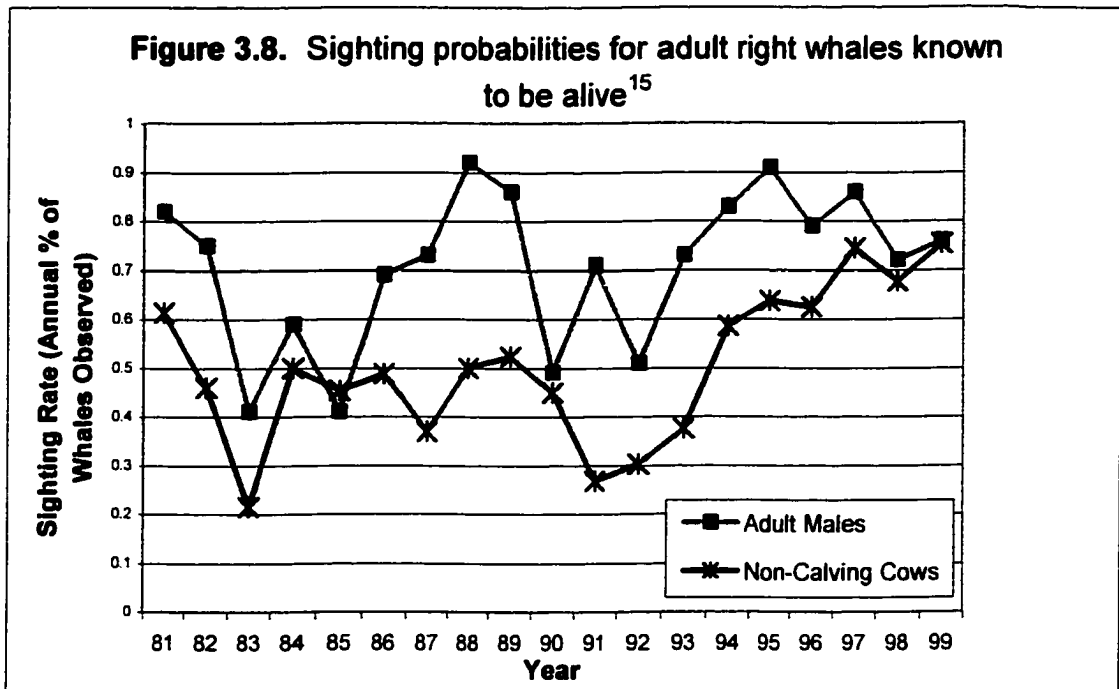
To test this, a regression of the length of sighting gaps against the year in which

those sighting intervals ended was run on all right whale cows known to be alive in 2000

(Figure 3.9). The results show a small but significant ($F = 10.717$, $p< 0.0013$) increase in

sighting gap size over the study period, but this increase might have been due to two

animals with sighting (and calving) intervals of nine and 12 years, respectively, late in the

study period. A stepwise regression eliminating these two whales still showed a

significant increase in the length of sighting gaps ($F = 10.2552$, $p < 0.0016$) (Figure 3.9).

A review of the data points in Figure 3.9 reveals a cluster of animals with longer sighting

gaps than usual in the period 1994 through 1998. Since the Fujiwara and Caswell models

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[15] Data on sex from Brown *et al.*, 2001, and from the Right Whale Catalog (Hamilton and Martin, 1999)

80

both ended in 1996, some of these animals should have been accounted for as survivors, so sighting gaps can only partly explain the apparent decline in survivorship.

Figure 3.9. Distribution of sighting gaps in cows known to be alive in 2000[16]
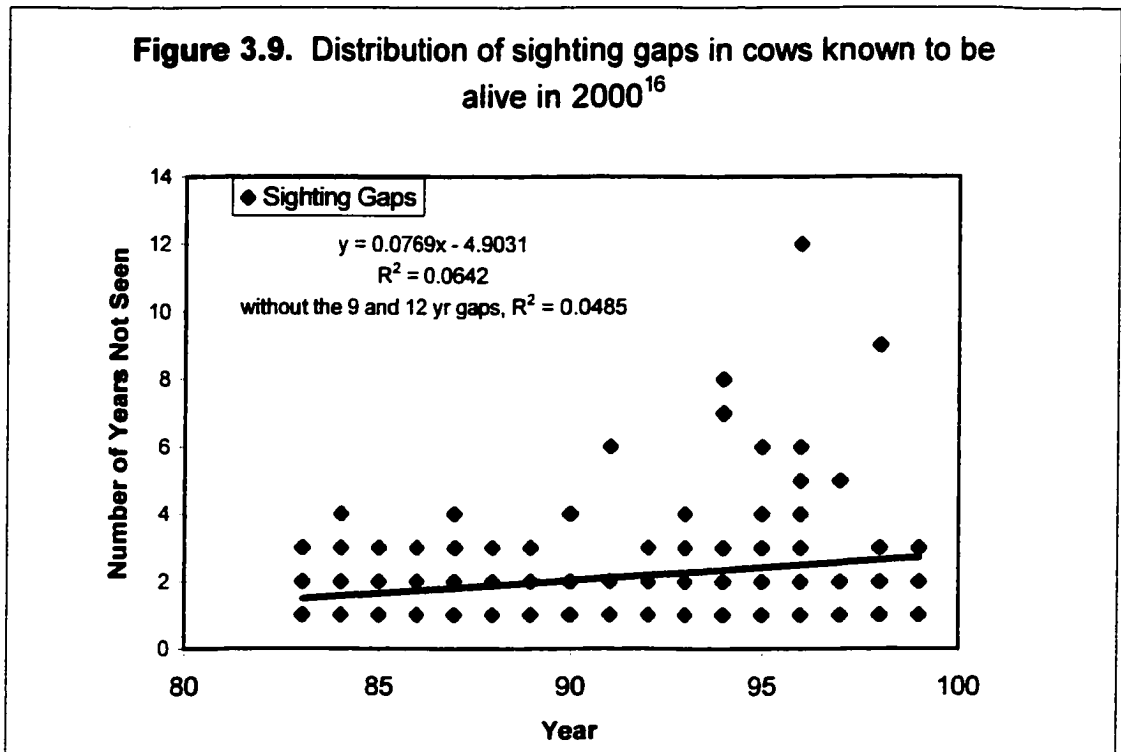
A regression on males showed no significant change in sighting intervals over the period ($F = 0.4037$, $p = 0.5262$)(Figure 3.10).

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[16] Data from the Right Whale Catalog (Hamilton and Martin, 1999)

81

Figure 3.10. Sighting gaps in adult male right whales known to be alive[17]
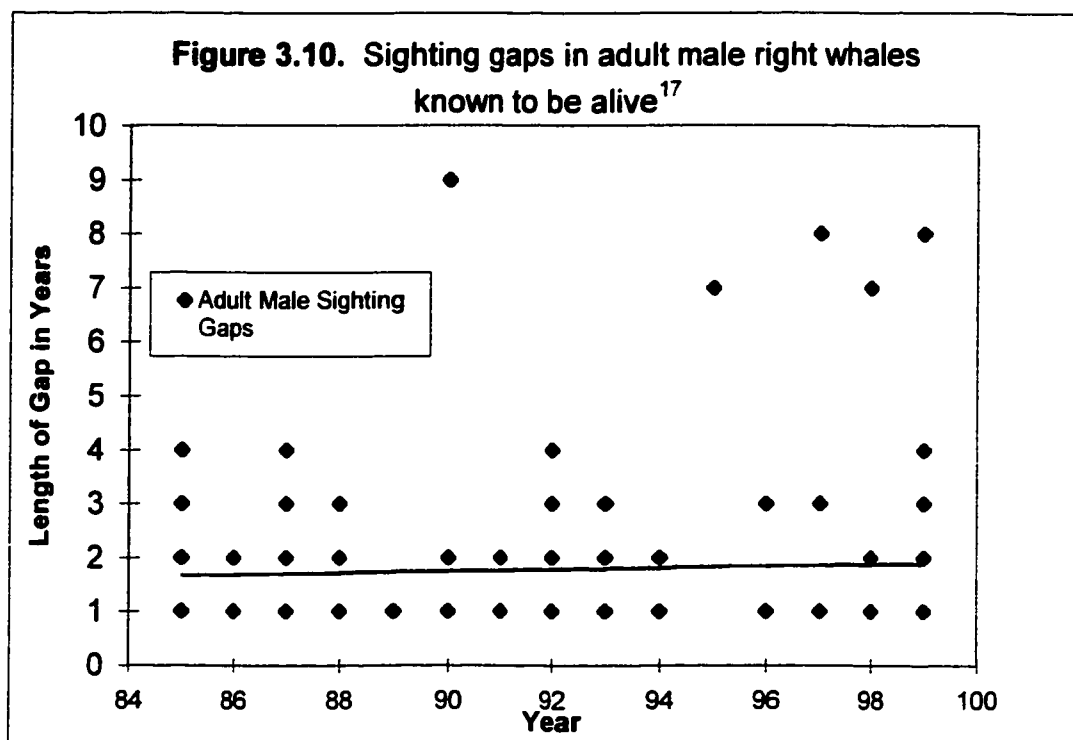
The increase in sighting gaps of cows raised the possibility of a link with the increased calving intervals previously documented (Kraus et al. 2001). Analyses of associations between sighting gaps and the intervals both before and after a calving event were conducted, and showed no significant relationship. There was also no significant difference between sighting gaps in cows following a calving event versus cows observed without a calf. Finally, there was no significant difference between sighting gaps before and after a calving event. The results of these analyses indicated the gaps in sightings of cows are not linked with the increased calving interval, and that a prior gap in sighting history is not a good predictor of future gaps.

To determine if the age of a right whale played a role in the variation in sighting

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[17] Data on sex from Brown *et al.*, 2001, and from the Right Whale Catalog (Hamilton and Martin, 1999)

82

probabilities, analyses were conducted on the characteristics of animals with known ages, unknown ages, and ages estimated from sighting histories. Sighting probabilities in animals of known ages were summed across year-class by sex, and are given in Figure 3.11. Both males and females show a significant increase in sighting probability in the first fifteen years of life (females: $F = 11.5459$, $p = 0.0053$, males: $F = 7.7261$, $p = 0.0166$).

Figure 3.11. Young right whale sighting probabilities by age[18]
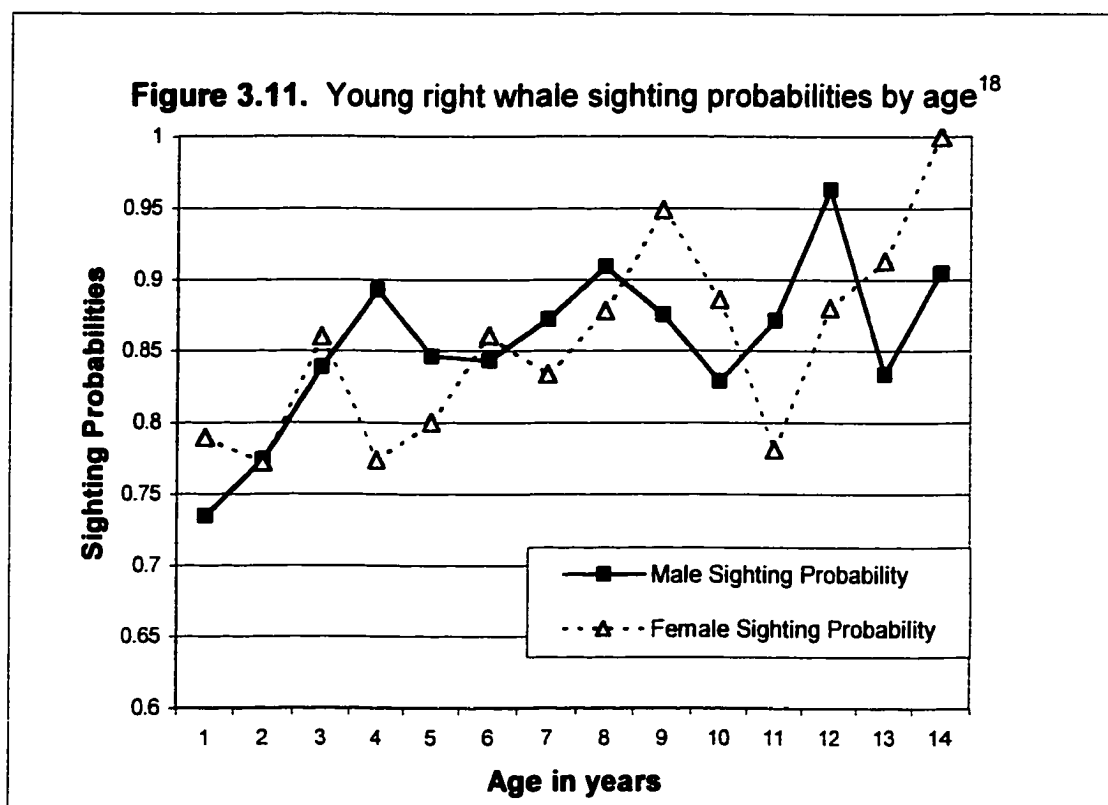
[18] Data on sex from Brown et al., 2001, and from the Right Whale Catalog (Hamilton and Martin, 1999)

Females reach sexual maturity between six and 22 years of age, with a mean of age of first parturition reported at 9.53 by Kraus et al. (2001). However, new data and the re-analysis in Chapter II indicate the mean age at first parturition is currently 11 years, with several females having first calves well into their teens. Thus the data shown in Figure 3.11 primarily represent animals that are sexually immature.

To evaluate sighting probabilities after first calving, the sighting probabilities of mature cows of known age were regressed on their age, and the results are shown in Figure 3.12. The data on animals older than the length of the study were available by back-calculating cow ages from their first sighting with a calf and assuming an average age of sexual maturity of ten years. This yielded estimated minimum ages for 30 cows in their 20s and 30s known to be alive in 2000. The decline in sighting probability with age is significant (F = 19.2817, p < 0.0002).

Precise data on male sighting probabilities by age is only available from whale first observed as calves, as there is no reliable way of back-calculating minimum ages from first sightings. Although photographic examination can identify the difference between calves, one-year old juveniles, and animals older than two, it is impossible to estimate age more precisely due to the difficulty of size estimation in the field. This limits the male dataset to animals first identified at the beginning of the study period, plus one or two years if well photographed. Sighting probabilities for known age males increase at least until sexual

84

Figure 3.12. Age versus sighting probability of cows alive in 2001[19]

$y = -0.0209x + 1.1242$
$R^2 = 0.5173$
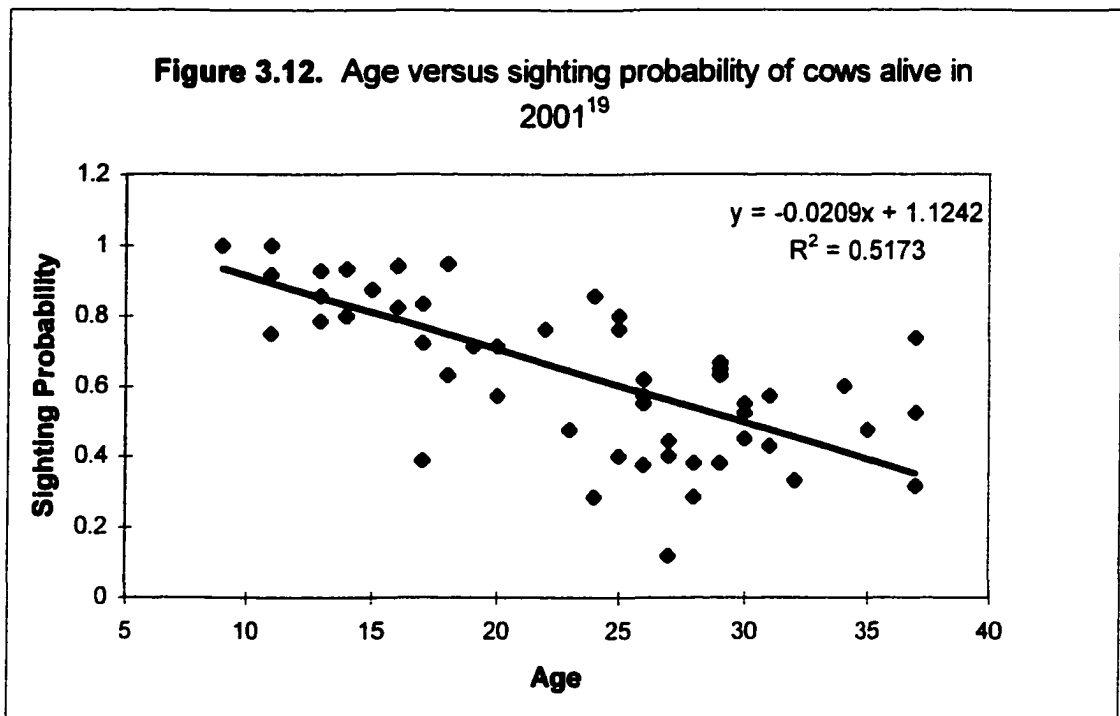
maturity (Figure 3.11), so a comparison of the sighting probabilities of all whales of

known age with those whose ages are not known was conducted. This showed that adult

whales with unknown ages have significantly lower sighting probabilities than those with

known ages (t = 9.405, p < 0.001). Whales with known ages were animals first identified

as calves, so all were younger than 21 years of age. Adult whales with unknown ages

were never seen as calves, and were classified as adults after a sighting history of 10

years or more, so all were over 10 years of age. These results show that sighting

probabilities are a function of age as well as life-stage, and are not constant throughout an

animal's life.

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[19] Data on age and sightings from the Right Whale Catalog (Hamilton and Martin, 1999)

85

The low sighting probabilities of a few animals appeared to influence many of the tests conducted above. Because cows appear to be most affected by increased mortality, a histogram of the mean sighting probabilities for those known to be alive in 2000 was created to evaluate the variation in sighting probabilities (Figure 3.13).

Figure 3.13. Sighting probabilities for cows known to be alive in 2000[20]
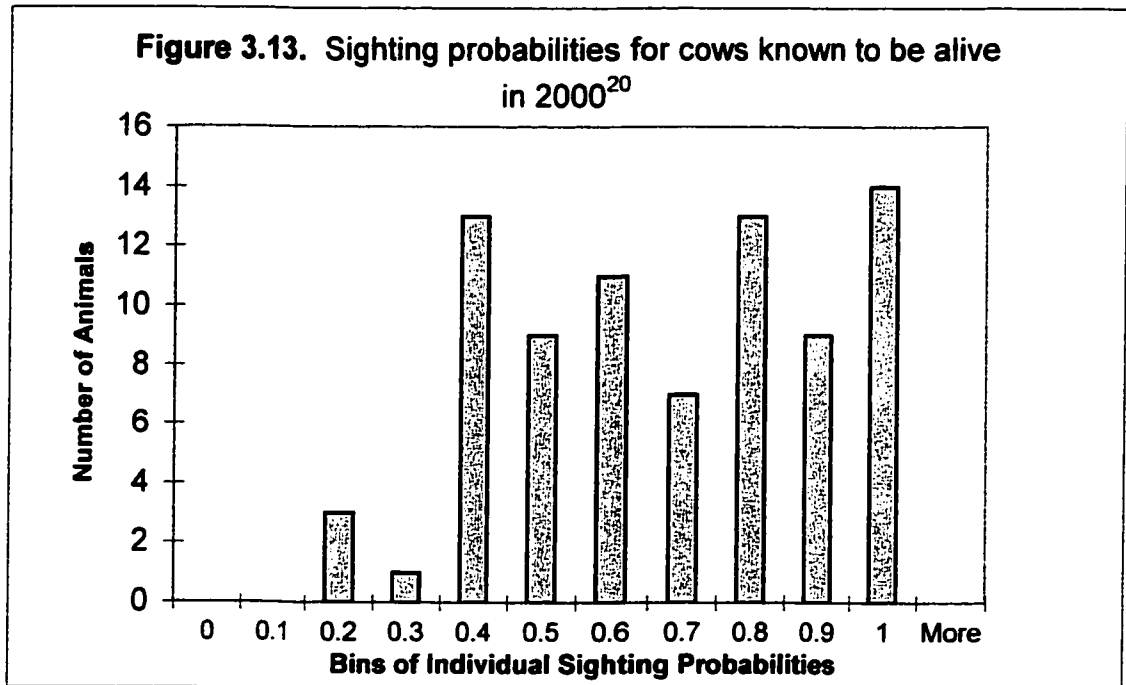
Mean sighting probabilities were calculated for all individuals by sex, matriline, haplotype, and the presence of a sighting gap of six or more years in an animal's history (the "resurrected" category, as classified by the catalog curators). The mean sighting probability for all females was 0.6988 (S.D. = 0.2499), for all males was 0.7655 (S.D. = 0.2137), and for animals of unknown sex, was 0.5772 (S.D. = 0.2796). Right whales of

[20] Data from the Right Whale Catalog (Hamilton and Martin, 1999)

86

unknown sex (n = 38) had significantly lower sighting probabilities than both females (p < 0.0098) and males (p < 0.0002).

Tests for differences in sighting probability between the three matrilines identified by Schaeff et al. (1994) showed no significant difference between them. Analyses of the sighting probabilities between the current matrilineal definition of five haplotypes (Malik et al. 2000) showed no significant differences between any of them. A comparison of the right whales with long sighting gaps (> 6 yrs) against the rest of the population showed a significantly lower sighting probability (mean of resurrected = 0.3112, mean of population = 0.7555, t = -17.3519, p < 0.0001). This is not terribly surprising, in that one would expect animals with long hiatuses in sighting history to have lower sighting probabilities.

Whales with Extreme Sighting Heterogeneity

An examination of Figure 3.13 shows a group of females with sighting probabilities lower than 0.5 (much lower than known males, females, or animals of unknown sex), which probably includes the group of resurrected animals identified discussed above. Because the Fujiwara and Caswell (2001) model appears sensitive to the survival of just two cows per year, a close examination of all the animals with low sighting probabilities was undertaken. As Fujiwara and Caswell (2001) note, "if sighting probability was heterogeneous, the survival probability of mothers toward the end of the study period would be underestimated." The bins of cows with low sighting probabilities in Figure 3.13 represent high levels of capture heterogeneity in a few animals.

There were 56 right whales known to be alive in 2000 with mean sighting probabilities below 0.5, defined here as "rare" whales. These 56 whales, included 26

87

females, 18 males, and 12 whales of unknown sex. A total of 32 were observed at least once in the Bay of Fundy, while 24 never were seen in this habitat. In males, females, and unknown sex whales, there are representatives of every matriline and haplotype. All of the animals in this group are over 10 years of age, and the mean minimum age of the female group is 26 years. The average age for the males is 17.8 years and for those whales of unknown sex it is 17.5 years. In these analyses, there does not appear to be any characteristic that would explain the low sighting probabilities alone, although age appears to be a significant factor.

With the benefit of hindsight and a longer study period, we can now re-examine the apparent decline in cow survivability at the end of Fujiwara and Caswell's (2001) model study period. Among the 26 "rare" females whose sighting probability is below 0.5, eight were missing for at least three years at the end of the model run in 1996, all of which were subsequently re-sighted. Because the logistic function of survival probability approximates the survivorship curve in Figure 3.4, the model estimated that females missing for three years were dead with over a 90% probability. Thus survivorship in this small population of females known to be alive in 2000, showed an apparently dramatic decline at the close of 1996. Fujiwara and Caswell (2001) point out that the "prevention of just two female deaths every year would suffice to increase λ (the asymptotic population growth rate) to 1 (no decline or growth). The resurrection of eight whales to the model in the period 1997 through 2000 does exactly that.

The correction to the model may even be greater. Of the 12 "rare" unsexed whales known to be alive in 2000, six (50%) had been missing for at least six years

88

straight in the period prior to 1997. Although Fujiwara and Caswell (2001) are not explicit in their paper about how they dealt with animals of unknown sex, they apparently divided them randomly and equally between the males and females (Fujiwara, pers. comm.). This would add at least three additional resurrections to the model's estimate of female survivorship. Of the "rare" males known to be alive in 2000, only five out of 18 (27.7%) had sighting gaps prior to 1997, supporting the Fujiwara and Caswell (2001) model that shows higher male survivorship. These findings suggest that the "rare" animals in this population are problematic for estimates of survivorship, population viability, and growth rates, when based upon models that depend upon grouped estimates of sighting probabilities.

Discussion

Understanding the details of mortality in right whales is critical to ensuring the North Atlantic population's survival in the long-term. The data provided here on the causes and rates of death by age, sex, and habitat use patterns can provide a guide to best target management actions. A total of 46% of all confirmed mortalities are due to human activities. The confirmed mortality data provided the first age-length curve developed for this species, and the derived estimates of age then allowed demographic comparisons between natural and anthropogenic mortalities. The fact that human sources of mortality are nearly doubling the death rate in this population represents a crisis for the species, but it is a probably a manageable one.

An analysis of estimated mortalities in right whales first seen as calves indicates first year mortality ranges from 26% to 31%, second and third year mortalities are 10% and 5%, respectively, and rates range from 1% to 4% for ages 4 through 10. These data

89

are consistent with the confirmed mortality data on strandings from natural causes. However, the demographic characteristics of animals presumed dead because they were missing from the database six years or more, match those characteristics of anthropogenic mortalities, but not those attributable to natural mortality. This suggests that the disappearances of younger animals are probably due to natural mortalities, but that the high percentage of the missing older animals may be dead from anthropogenic causes. This is supported by the entanglement data presented in Chapter V, where nine out of the 50 right whales observed entangled in fishing gear have never been seen after the entanglement event.

Analysis of animals that disappear from the sightings database over time showed that 99% of the animals not seen for eight years will never be seen again, and that 95% not seen for four years will never be seen again. There was no significant trend in the number of animals presumed to be dead annually between 1985 and 1997. While this is a simple-minded approach to estimating changes in mortality rates, it has the advantage of being robust to variations in sighting probabilities over time and age. Since the analyses above show that sighting probabilities of right whales known to be alive in 2000 vary significantly with age and habitat use pattern, these variations could affect estimates of mortality in this population.

However, the most significant problem in estimating mortality appears to be due to a group of 56 rarely seen whales, whose sighting probabilities are less than 50%. Because the sighting probability analyses shown here were conducted only on animals known to be alive in the year 2000, it explicitly excludes animals whose fates are unknown. Both the Fujiwara and Caswell (2001) model and the analysis shown in Figure

90

3.4 provide probabilistic estima tes of mortality for animals missing from the sightings database over x number of years. However, the 56 "rare" whales identified above appear to represent the extreme problem of heterogeneity in sighting probabilities. Not only is the likelihood of sighting one of these whales lower than 50%, 26 of them have had sighting gaps of six years or more. Such gaps will probabilistically be defined as dead in mark/recapture models, and when such gaps occur at the end of the study period, survivorship will always appear to be declining.

Population models of extremely small populations are vulnerable to such heterogeneity, since animals missing for extended periods will appear in logistic functions as dead when they are not. In such cases, a few animals with low recapture probabilities will create spurious estimates of survivorship, growth rates, and population viability. Refined models that account for extreme sighting heterogeneity are needed to deal with a population such as this one. Even so, it seems unlikely that such models will provide near real-time estimates of population growth, viability, and survivorship. The lack of any predictive feature of the rare whales makes it difficult to determine when a particular whale will go missing from the sightings database, even if still alive. The analysis that showed that pre-calving sighting gaps were not predictors of post-calving sightings gaps is not hopeful either. A model that estimates the rare whale survivorship on the basis of the sighting probabilities of the identified rare whale group may still fail, as it appear that animals can enter this category in an unpredictable fashion. However, as the study progresses, further information should help refine the characteristics of group and age related changes in sighting probabilities that are likely to play a role in any future model development.

91

In right whales, there are serious problems due to anthropogenic mortality and a declining birth rate, but as a long-lived species capable of reproducing over periods of 30 years or more, decadal range crises do not necessarily spell extinction.

92

CHAPTER IV

THE FEASIBILITY OF LINKING NORTH ATLANTIC RIGHT WHALE MOVEMENTS WITH OCEANOGRAPHY

Introduction

Large ocean animals have life history challenges similar to terrestrial ones; locations for feeding, breeding, and the production of young require appropriate conditions (temperature, depth, visibility, acoustic characteristics, and adequate food density) for their specific trophic and social requirements. Oceanic prey species are either mobile or seasonably variable, and concentrated in relatively small patches, so large predators must be capable of occasionally traveling great distances to find food. Breeding and young-bearing habitat requirements are poorly known for most large marine predators, but endotherms must deal with potential thermoregulatory constraints upon their young, which usually requires shifting to warmer waters. As examples, the pupping of seals and the egg-laying of turtles requires that both groups must make seasonal visits to land, although their prey is sometimes far at sea. Therefore, large marine animals must move from place to place, seeking appropriate conditions for different needs and life history stages.

On an ocean basin scale, this involves long-distance migrations, usually between feeding grounds and breeding or calving grounds. Examples in the cetaceans include humpbacks (Stone et al. 1990; Stevick et al. 1999) and gray whales (Swartz 1986). Comparable long-distance migrations occur in sea turtles (Renaud and Carpenter 1994;

93

Morreale et al. 1996), bluefin tuna (Lutcavage et al. 1999) and seals (McConnell and Fedak 1996; Boyd et al. 1998). Once within a habitat, animals may engage in smaller scale movement patterns, either seeking food patches or mates (LeBoeuf et al. 2000). In any region with a heterogeneous distribution of resources, animals will have to search for those resources. For large scales, animals engage in far-field search patterns characterized by low turning rates and relatively rapid movements. When a resource is found, movement rates drop, and animals make acute angled turns more frequently (Stevick et al. 2002).

Satellite tagging has offered marine mammal scientists an opportunity to examine movements of animals over thousands of square miles of ocean. If quantified appropriately, movement patterns derived from tagged animals may elucidate habitat use patterns by the same animal in different areas and help identify biological and oceanographic cues that influenced the changes in movement patterns (Brill and Lutcavage 2001). To test this hypothesis, satellite tracking data from two North Atlantic right whales (*Eubalaena glacialis*, Borowski, 1781) were tested with new analytical methods to evaluate their movement patterns relative to remotely sensed oceanographic features.

Right Whale Biology Related to Movements

Distribution and Seasonal Habitat Use. The long-term study of identified individuals and the use of satellite-monitored radio tags have supplemented historical records to provide considerable information on seasonal patterns of distribution and movements of the northwestern Atlantic stock of right whales (Kraus et al. 1986; Mate et al. 1997; Kenney et al. 2001). Seasonal distribution and movements show some

94

segregation by sex (Stone et al. 1988; Brown et al. 1994). Most cows give birth in the

coastal waters of the southeastern U.S. during the winter months (Knowlton et al. 1994).

These mothers and calves are frequently seen within five to 10 miles of the coast,

sometimes within one mile of the beach in very shallow water. Males and non-calving

females are rarely seen in that area, and their whereabouts during the winter remains

unknown (Kraus et al. 1988).

In the spring, aggregations of North Atlantic right whales are observed feeding in

the Great South Channel east of Cape Cod, and in Massachusetts Bay (Winn et al. 1986;

Hamilton and Mayo 1990; Kenney et al. 1995). In the summer and autumn, they are

observed in the Bay of Fundy between Maine and Nova Scotia, and in an area on the

Scotian Shelf 50 kilometers (km) south of Nova Scotia (Stone et al. 1988; Kraus and

Brown 1992). Schaeff et al. (1993) inferred from genetic and photo-identification data

that another summer and fall nursery area must exist, although its location is unknown.

Tracking of individual North Atlantic right whales equipped with satellite-

monitored radio tags has revealed excursions of surprising speed and distance (Mate et al.

1997; Slay and Kraus 1999). One mother and her calf traveled more than 3,764 km

during a 42-day period (Mate et al. 1997).

Feeding Ecology and Whale Movement Patterns. In northern feeding areas,

right whales moving from place to place may frequently be seeking food. Kenney et al.

(1986) used estimates of body weight, metabolic rate, assimilation efficiency, time spent

feeding, mouth size and swimming speed to calculate that a North Atlantic right whale

must feed in prey patches containing energy densities of 7.57 to 2,394 kcal/m^3 to

maintain itself. Zooplankton usually occur in dense spatially discrete "patches" (Wu and

95

Loucks 1995), where the animals are aggregated vertically or horizontally at convergences or at fronts where different water masses meet (Wishner et al. 1988; Kenney and Wishner 1995). Copepod concentrations may be further enhanced during diurnal vertical migrations.

The northern feeding habitats where North Atlantic right whales aggregate in the spring, summer and fall, are among the few places where extremely concentrated patches of copepods have been found. Three of them (Browns-Baccaro Bank, Bay of Fundy and Great South Channel) are places where deep basins (approximately 150 m) are flanked by relatively shallow water. Upwelling driven by tidal currents also produces the dense patches of plankton in Cape Cod Bay, although no deep basin is present. In the Great South Channel right whales were significantly associated with the 100 m isobath and associated thermal fronts (Brown and Winn 1989). Because the northern distributions of North Atlantic right whales appear tightly coupled with their primary prey, *Calanus finmarchicus*, the whales are not usually seen when copepod populations are abnormally low (Murison and Gaskin 1989; Mayo and Marx 1990; Kenney 2001).

Mayo and Marx (1990) observed that right whales in a plankton patch with density above the threshold for feeding swam in convoluted paths, often making abrupt turns. Whales swimming outside of a patch moved faster and in straighter paths. This is the context in which the principal hypothesis of this Chapter was tested. It was assumed that right whales would travel widely in search of food patches, and that the discovery of a food patch would lead to longer periods of residence in a feeding location. Satellite tracking of individuals allows the testing of differences in movement patterns that might relate to this, but the lack of synchronous field sampling for potential prey prevents

96

determinations of the causes at this time.

Reproductive Behavior and Movement Patterns. One other motivation for right whales to move between locations is to engage in reproductive activity. Right whales give birth to a single calf every three to five years, so receptive adult females are rare relative to males, leading to strong male-male competition (Kraus and Hatch 2001). In this case, females will be the resource over which males compete, and males may be motivated to travel long distances to search for those females. Previous records of satellite-tagged male right whales do show rapid and long-distance movements (Mate et al. 1997).

Courtship behavior has been observed in nearly every month of the year, in spite of a narrow range of winter calving times. If Best's (1994) estimate of 12-13 months for the gestation period in southern right whales applies to northern right whales, it suggests that courtship in right whales has a social function and successful insemination occurs somewhere from November to January. Alternatively, gestation in this species could be longer than 12-13 months. Nevertheless, courtship occurs throughout all northern feeding grounds. In courtship groups, which may include 40 animals or more, males try to get close enough to the focal female to be able to mate repeatedly. Females appear to attract males by making sounds, which can be heard underwater for several miles. Males have been seen swimming toward courtship groups with calling females at speeds up to seven knots from eight km away (Kraus and Hatch 2001), and it is likely in this mating system that only males will be motivated to move large distances for sexual activity.

Missing Information

There is still a lack of information on right whale movements, habitat use

97

patterns, the location of missing summer and winter habitats, and trends in biological and oceanographic changes within those habitats. Some of these gaps in information impede our understanding of the status of this species, and prevent the development of a comprehensive management and recovery plan. For example, identifying the habitat requirements of an endangered species is the critical first step in habitat protection. Second, the apparent decline in reproduction in North Atlantic right whales over the last 10 years may be habitat or food related, but developing testable hypotheses around reproduction may depend upon a better understanding of habitat use patterns. To reduce right whale interactions with both the shipping and the fishing industry, better information on whale movements in "high-conflict" areas is needed. For all of these questions, the development of even a rudimentary capability to predict right whale distribution and movements is considered essential.

Habitat Use Hypothesis

The hypothesis of this Chapter is that right whale movement patterns are linked to measurable physical oceanographic cues, which may be correlated with appropriate feeding or breeding habitats. By using satellite-tracked movements of right whales, changes from long distance swimming to localized patterns of movement can be quantified. If changes in the whale's behavior can be linked with the oceanography, then habitat features critical to right whales may emerge. This Chapter is a feasibility study on the application of this approach to the satellite tracks of two right whales.

Methods

Tracking Known Right Whale Movements

Seven right whales were tracked by satellite telemetry during 1996 and 1997 in

98

the western North Atlantic between the coastal waters of Florida and the Nova Scotian Shelf. Tracking episodes lasted from 14 to 103 days, providing an average of two locations per whale per day (Slay et al. in prep.). Three of these tracks were from females migrating from the calving ground off of Florida and Georgia to the northern feeding grounds off of New England. Since they followed the coastline and did not represent foraging, these tracks were not included in the following analyses. Of the remaining four tracks, only two had a sufficient number of satellite fixes to statistically evaluate the relationship between their movements and the oceanographic and bathymetric features. The right whale movement tracks used in this study were both from mature females, one with a calf of the year (whale #1812), and the other a non-calving animal (whale #1125).

Photo-identification of Individual Right Whales. Both North Atlantic right whales were individually identified from photographs of the individually distinctive callosities, and both animals used in this study were matched to the catalog to determine age and sex (Kraus et al. 1986; Hamilton and Martin 1999).

Tags and Location Accuracy. Satellite tag electronics were provided by Telonics, and the tags were cylindrical, approximately 15 centimeters (cm) long by 2.5 cm in diameter. The tags were deployed by compound bow into the blubber layer on the whale's back with the antenna protruding above the skin (Slay and Kraus 1999). Location information was provided on a daily basis through the Argos satellite system (ARGOS 1996). Transmissions from the tags provided an estimated position, based upon two or more passes by a polar orbiting satellite. Argos provides estimates of position accuracy called location class (3-0, A, B, and Z in descending order of accuracy), which

99

are dependent on the number of transmissions received from the tag during each satellite pass, transmitter power, orientation of the antenna, and the track of the satellite pass relative to the tag location.

In this analysis, all location classes (LC) were used with a filtering approach that removed positions that required biologically unfeasible rates of travel. In this case, the top sustained swimming speed of a right whale was estimated to be less than five knots (Mate et al. 1997). Argos provides accuracy of location estimates for LC's 1, 2, and 3, predicting that 68% of LC 1 locations will be within 1 km of the true position, 68% of the LC 2 locations will be within 350 m of the true position, and that 68% of the LC 3 locations will be within 150 m of the true position. Recent studies showed less accuracy in longitude data and more in latitude, and suggest that LC's A and B provide better locations than expected (Hays et al. 2001; Vincent et al. 2002). Hays et al. (2001) reported that LC 0's were the least accurate of their locations, with a standard deviation from all true longitude positions of 15.02 km. In the same study, LC B positions had a standard deviation of 7.79 km from true longitude locations. Vincent et al. (2002) give 68% and 95% percentile errors for every LC, and for filtered class B locations, the 95th percentile encompassed all positions within 15.417 km of the true longitude position. In the Vincent et al. (2002) study, the 95th percentile included all filtered longitude positions within 3.866 km of LC A locations, and within 10.393 km of all LC 0 locations. Argos latitude locations were more accurate than longitude in all of the LC categories.

Our own calibrations, done at two different latitudes (45 degrees north and 28 degrees north) indicate that the Hays et al. (2001) and Vincent et al. (2002) results for LC's A and B are comparable to the data collected in this study. Because the location

100

point density analysis (see below) included all satellite-derived positions within 10 km, most of the filtered locations reported here were within the 95% accuracy ranges reported above. Therefore all LC classes (except Z) were used in these analyses.

Oceanographic Data

Sea-Surface Temperature and Frontal Data. For these analyses, absolute values of sea- surface temperature, indices of frontal density (temperature gradients derived from AVHRR data), and measurements of "distance to front" were used. Advanced Very High Resolution Radiometer (AVHRR) imagery was obtained from the University of Rhode Island's Distributed Oceanographic Data System (DODS). This dataset consists of geo-referenced, calibrated, sea-surface temperature imagery for the Western North Atlantic with a resolution of 1.1 km (Fig. 4.1).

Figure 4.1. Gulf of Maine with sample sea-surface temperature and bathymetry

Legend
Value

■	0.625 - 5.800000191
■	5.800000192 - 10.0625
▨	10.06250001 - 11.8125
▨	11.81250001 - 13
▨	13.00000001 - 14.10000038
☐	14.10000039 - 15.125
☐	15.12500001 - 16.15625
☐	16.15625001 - 17.375
☐	17.37500001 - 19.1875
▨	19.18750001 - 21.35000038
■	21.35000039 - 23.10416803
■	23.10416804 - 25.25
■	

101
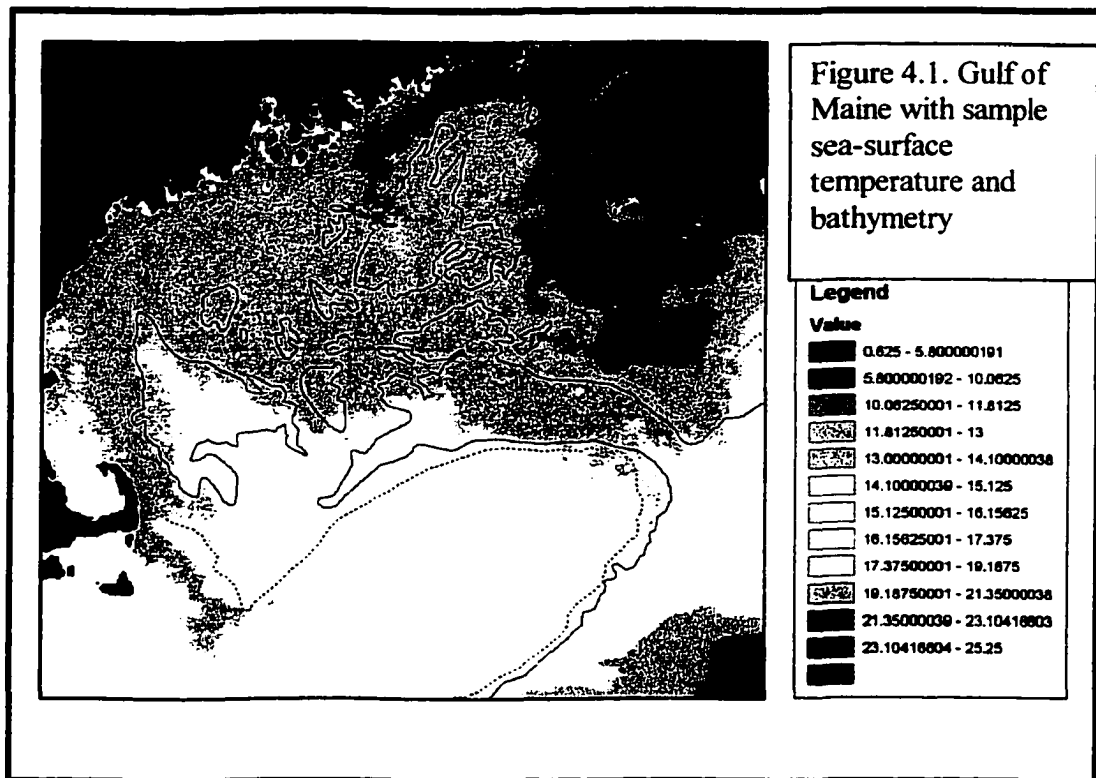
Frontal information from temperature gradients was obtained through the DODS program using methods described by Ullman and Cornillon (1999), which incorporate cloud detection and removal, and multi-image edge detection algorithms (Cayula and Cornillon 1995).

Sea-surface temperature fronts were parsed into two separate data layers with different temporal resolution, daily and semi-monthly. First, all fronts seen (after cloud masking) on a daily basis were incorporated into a daily data layer within ArcInfo (ESRI, etc.). Each data layer included information on front location, mean temperature, temperature gradient, and direction to warm water. From this layer, a distance to front grid was created in ArcInfo using a euclidean distance function (Fig. 4.2). This layer provided the distance from the nearest SST front for each satellite-derived location of a whale. To explore whether areas with frontal persistence were favorable foraging areas under the assumption that planktonic prey would be aggregated in areas of high frontal density, all fronts seen in the two weeks prior to a satellite location and created density layers were grouped together. This provided an index of frontal density for the previous two weeks at any location along the track.

Bathymetry and slope. Both absolute depth and an index of slope (the maximum difference in depth between a cell and its neighbors) were used in this analysis. Submarine topography data sets were acquired through the U.S. Geological Survey's (USGS) Woods Hole Field Center's bathymetric database. These data have an approximate spatial resolution of 0.5 km. Slope was calculated by using ArcInfo's slope function on the depth database.

102
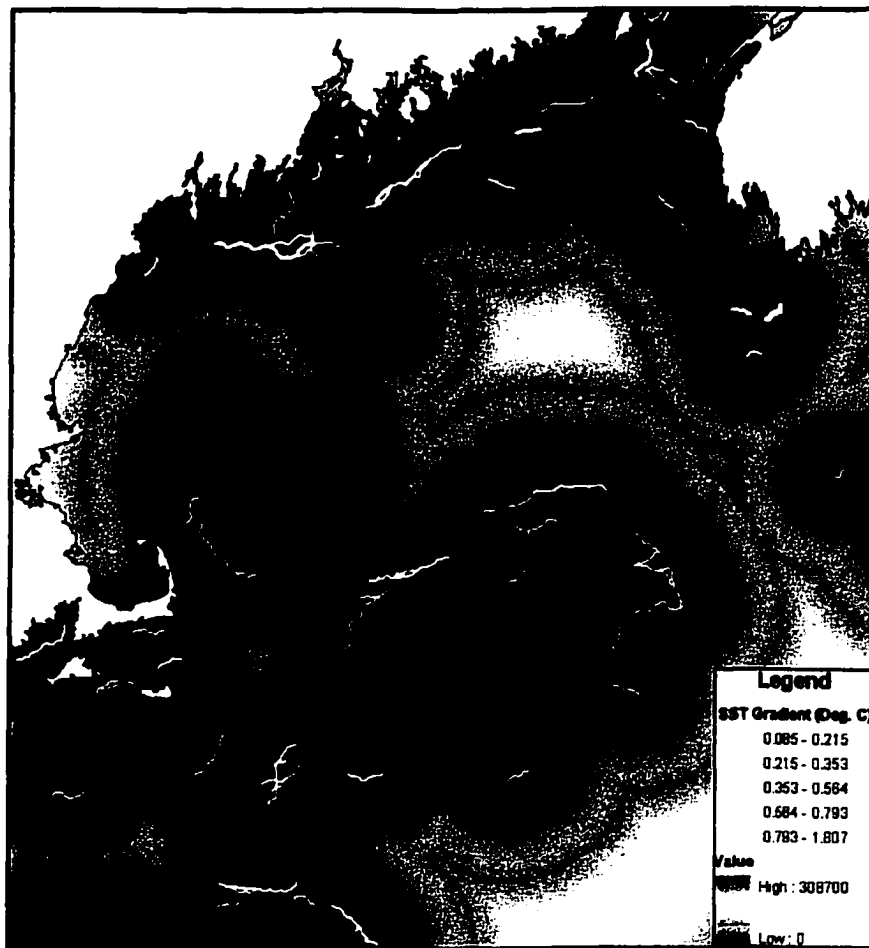
Figure 4.2. Fronts derived from SST data, layered on a "distance to front" grid in ArcInfo. Source: Univ. Rhode Island, DODS Program and NESDIS

• Front intensity (severity of temperature gradient) is shown by white line thickness.

• " Distance to front" values are in meters.

Analytical Methods

All data were entered into a geographic information system using ArcInfo. To

test the relationship between movement patterns and oceanography in each whale's track,

each satellite-derived location was transformed into an index of neighbor density, where

103

each neighbor is another location fix along the whale's track. Whale movements between fixes are unknown, but satellite transmissions were received regularly throughout the period, so this method works for larger scales. Location density was calculated using a 10 km window. The density of satellite locations from each whale were on a continuum from having no points nearby (i.e., rapid traveling through an area), to having multiple location points nearby (when a whale resided in an area for an extended period). All data layers were co-registered in a Lambert-Conic projection of the Gulf of Maine. Two different analytical methods, Classification and Regression Tree Analysis (CART: Breimann et al., 1984) and partial Mantel tests (Mantel 1967; Legendre and Fortin 1989; Leduc et al. 1992; 1998), were used to quantitatively assess the relationship between whale movement and the five environmental variables.

CART analysis was used to look for relationships between whale movements and sea-surface temperature, distance to front, frontal density, depth, and bottom slope. CART analyses are data partitioning algorithms that split the data into subsets based upon the best predictor variable, and sequentially do the same with each subset with the remaining variables. The splits are classified by the variable that explains most of the variance in the response variable. CART's are useful in analyses that are non-additive, where some predictor variables may be related to other predictors (e.g., slope and fronts), because they subset the data without specifying the interaction terms in advance of the analysis. Further, variables that operate at large scales appear early in the sub-setting tree process, and smaller scale or local variables will appear further down the tree. Regression trees were used to test point density against all environmental variables. The null

hypothesis was that points are not likely to differ in their correlation to environmental variables whether they are clumped or not.

Because all of the variables exhibit some degree of spatial autocorrelation, Mantel tests were used to test for the contributions of the five predictor variables to whale location (movement) patterns. Distance matrices were constructed to test if locations that were similar in one variable (point density) were also similar in another variable (frontal density, distance to front, SST, depth, slope, or space). Euclidean distance measures were used to compute similarity matrices to compare the predictor variable variation at each point location against the density of points at each location. Partial Mantel tests (Smouse et al. 1986) were used to test the correlation between whale density and each environmental variable. The advantage of this approach was that it removed the confounding effects of spatial autocorrelation in both the response and predictor variables. The effects of multiple comparisons on the p values were removed using the Hochberg method (Hochberg 1988; Legendre and Legendre 1998). When the CART and Mantel analyses were complete, plots of point density data against each of the significant explanatory variables were also created to identify detailed features of the relationships.

Results

Right whale #1812's movements were analyzed during the period she traveled in the Gulf of Maine from 11 April 1996 to 2 June 1996 (Fig. 4.3). Right whale #1125 movements were tracked from 15 August 1997 to 15 October 1997 (Fig. 4.4). The Gulf of Maine track of whale #1812 was comprised of 76 locations over 2692.3 km and 53 days. The track of whale #1125 was comprised of 80 locations over 2390.9 km and 60 days (Slay et al. in prep.).

105
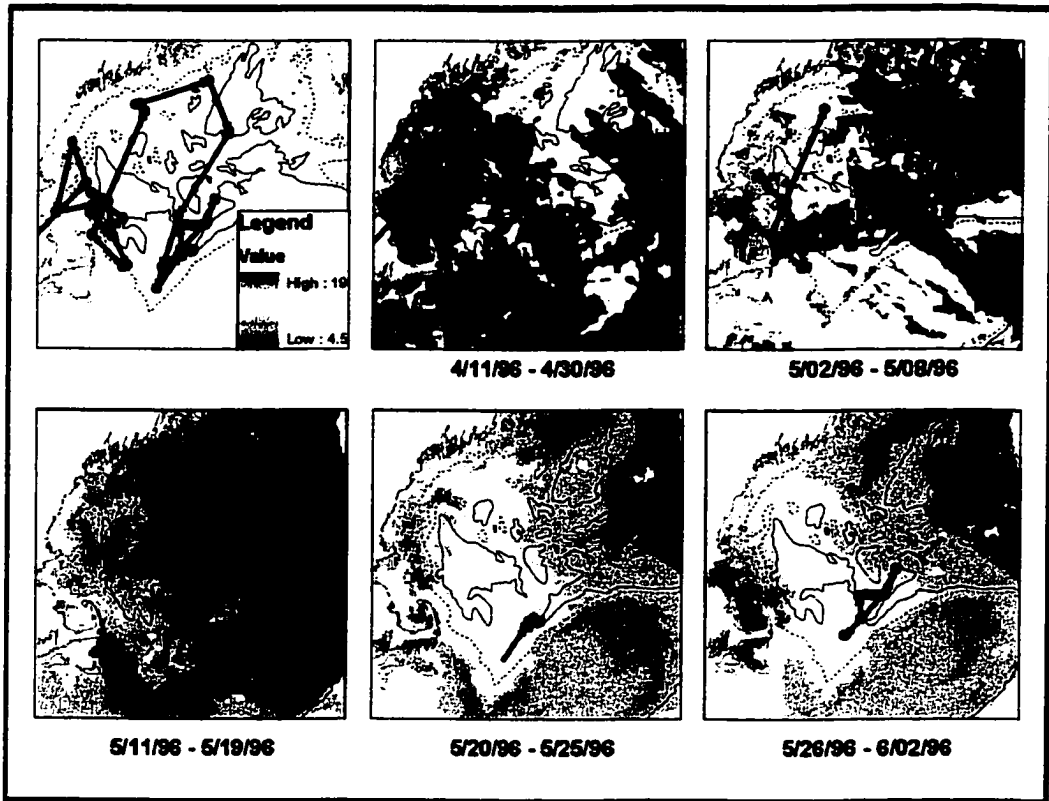
Figure 4.3. Right whale #1812's movements in the Gulf of Maine, 4/11 – 6/2, 1996.
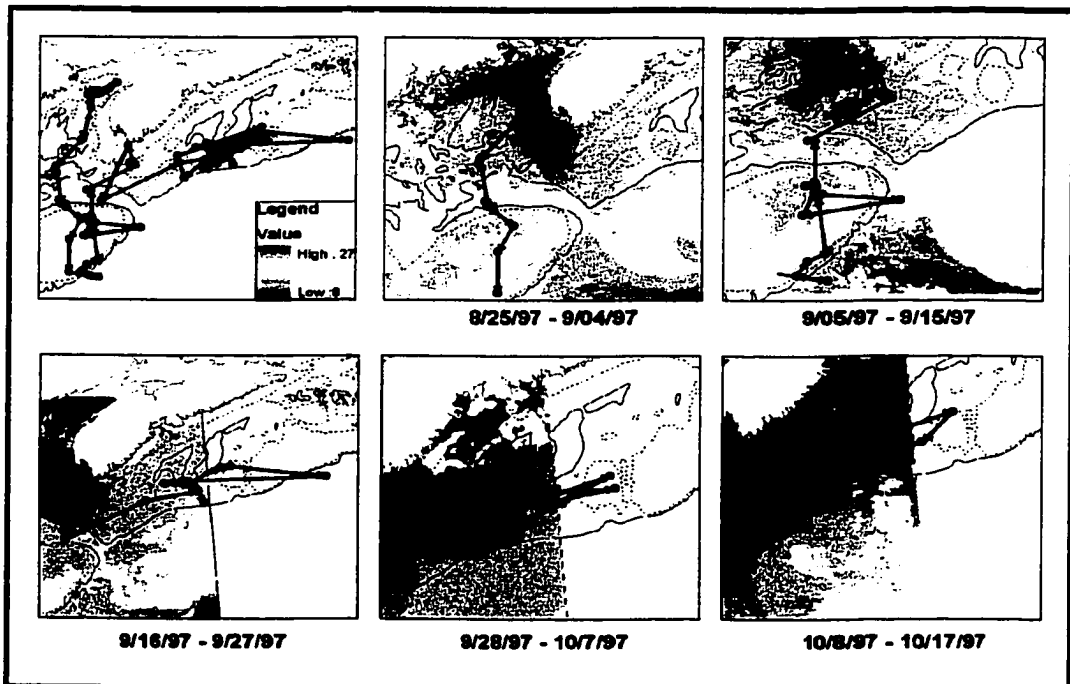
Figure 4.4. Right whale # 1125's movements, 8/25 – 10/17, 1997.

106

Because the two whales were tracked across the Gulf of Maine at different

seasons, the sea surface temperatures within the region were very different. Spring

temperatures within the Gulf of Maine ranged from 4°C to 11°C, and autumn

temperatures ranged from 11°C to 17°C (the higher temperatures encountered by #1125

occurred south of the Georges Bank).

Nevertheless, CART analysis of whale #1812's track showed that her clustering

of satellite fixes (point density) were primarily influenced by sea-surface temperature

(Fig. 4.5). An uncorrected Mantel test of the same whales' track weakly confirms this,

by showing that areas where the animal spent more time (i.e., high point density) were

most similar in temperature as opposed to the other variables tested (r = 0.1118, p =

0.0439)(Table 4.1). However, with the Hochberg (1988) correction for multiple

comparisons, this relationship becomes insignificant (Table 4.2 and Fig. 4.6).

Figure 4.5. CART
diagram from whale
#1812 in relation to
oceanographic and
bathymetric variables.

temp≤10.0833

slope≤0.686018

depth≤-185.025

front.dens≤0.00142446

0.009514   0.011560   0.020060

0.017790   0.036660

Note: Numbers at each split represent the value of the variable at which the
split in the tree was made (i.e. the temp. value is in degrees Celsius).

107
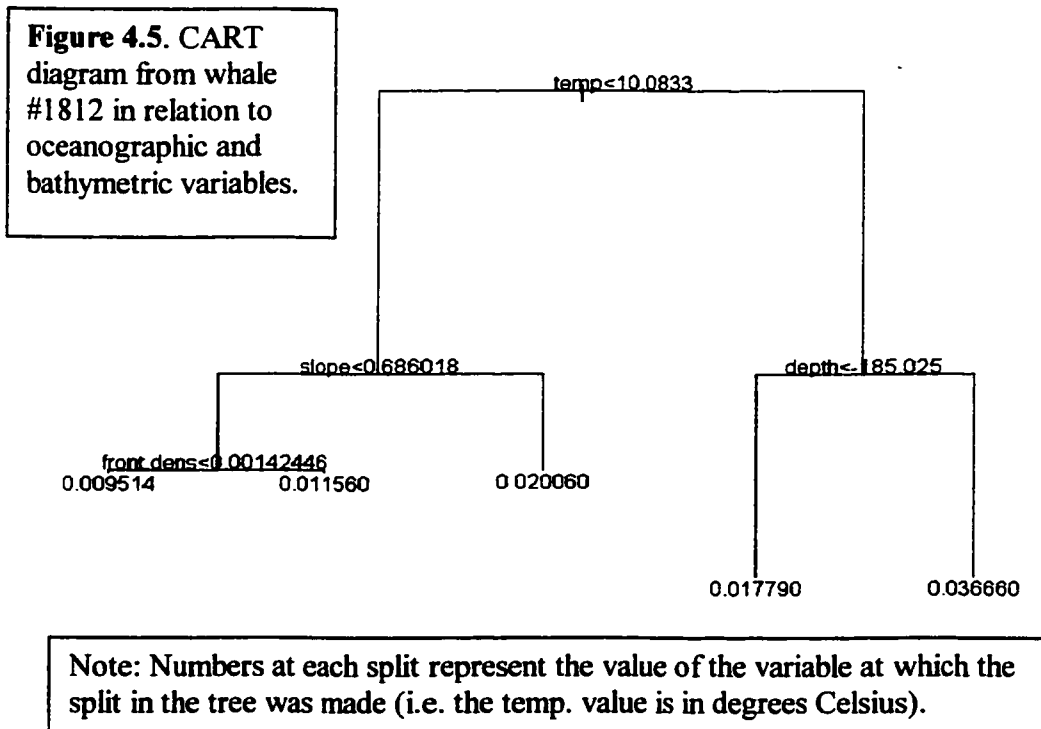
Table 4.1. Mantel results (r value with raw p-values in parentheses) for the Gulf of Maine portion of whale #1812's track.

	r_{we}[a]	$r_{(w\,or\,e)s}$	$r_{we \cdot s}$	$r_{we \cdot se}$[b]
Whales	-	Ns	-	Ns
Distance to Front	Ns	Ns	Ns	Ns
Frontal Density	Ns	0.351 ($p < 0.0051$)	Ns	Ns
Depth	Ns	0.1774 ($p < 0.0399$)	Ns	Ns
Slope	Ns	Ns	Ns	Ns
Temperature	Ns	0.5854 ($p < 0.0001$)	0.1273 ($p < 0.0361$)	0.1118 ($p < .0439$)

Table 4.2. Significant results with Mantel r values with adjusted p values (Hochberg method) for whale #1812.

	r_{we}[a]	$R_{(w\,or\,e)s}$		$r_{we \cdot s}$	$r_{we \cdot se}$[b]
Whales	-	-		-	-
Dist.front	-	-		-	-
Front.dens	-	0.351	**(0.08)**	-	-
Depth	-	-		-	-
Slope	-	-		-	-
Temp	-	0.5854	**(0.0006)**	-	-

[a]The notation in these tables represent a regression of an environmental variable (e), e.g., distance to front, frontal density, depth, slope, and temperature, on whale point density (w). The third column represents a regression of an environmental variable on whale point density controlling for spatial autocorrelation (s). The fourth column extends the regression to control for both spatial autocorrelation (s) and the correlation with other environmental variables (e).

[b]The first entry in this column is the effect of space on whale distribution controlling for all environmental variables.

Figure 4.6. Mantel test path diagram for whale # 1812.

CART analysis of whale #1125's track showed her movements were correlated with the "distance to front" variable (Fig. 4.7). The Mantel test of this whale's track confirms this result as well, with "distance to front" showing the strongest Mantel correlation of all variables tested (r = 0.334, Hochberg corrected p = 0.03) (Tables 4.3 and 4.4, Figure 4.8). Locations with low point density (i.e., the whale was traveling and did not stay in the area any length of time) were seen closer to fronts, while locations with higher point densities were seen further away from fronts (see also Figure 4.12).

Figure 4.7. CART diagram from whale #1125 in relation to oceanographic and bathymetric variables.

dfront<82308.1

slope<0.223311

0.025530

temp<16.4375

front.dens<7.20851

dfront<28734

0.013160 0.009619 0.011490 0.009909 0.012070

0.016800

0.010490 0.013960

Note: Numbers at each split represent the value of the variable at which the split in the tree was made (i.e., the value dfront is in meters).

Table 4.3. Mantel results (r value with raw p-values in parentheses) for whale #1125.

	r_{we}^a	$r_{(w \text{ or } e)s}$	$r_{we \cdot s}$	$r_{we \cdot se}^b$
Whales	-	ns	-	Ns
Dis.front	Ns	ns	0.334 (0.0089)	0.3301 (0.0083)
Front.dens	Ns	0.1690 (0.0001)	Ns	Ns
Depth	Ns	0.1401 (0.0002)	Ns	Ns
Slope	Ns	0.1464 (0.0022)	Ns	Ns
Temp	Ns	0.3996 (0.0001)	Ns	Ns

Table 4.4. Mantel r values with adjusted p-values (Hochberg method) for whale #1125

	r_{we}^a	$r_{(w \text{ or } e)s}$	$r_{we \cdot s}$	$r_{we \cdot se}^b$
Whales	-	-	-	-
Dis.front	-	-	0.334 (0.0332)	0.3301 (0.0332)
Front.dens	-	0.1690 (0.0016)	-	-
Depth	-	0.1401 (0.003)	-	-
Slope	-	0.1464 (0.0308)	-	-
Temp	-	0.3996 (0.0006)	-	-

[a]The notation in these tables represent a regression of an environmental variable (e), e.g., distance to front, frontal density, depth, slope, and temperature, on whale point density (w). The third column represents a regression of an environmental variable on whale point density controlling for spatial autocorrelation (s). The fourth column extends the regression to control for both spatial autocorrelation (s) and the correlation with other environmental variables (e).

[b]The first entry in this column is the effect of space on whale distribution controlling for all environmental variables.

Figure 4.8. Mantel Diagram of Whale #1125.

110

The satellite-tracked movements of whales #1812 and #1125 are superimposed over AVHRR imagery in Figs. 4.3 and 4.4. Histograms of the sea-surface temperature distributions for each whale's track are given in Fig. 4.9. An examination of the whale's tracks on the AVHRR imagery shows that whale #1812 spent the first 10 days in the southwestern Gulf of Maine, then moved northwards until water temperatures dropped to near 4.5 degrees centrigrade (°C), at which point she turned southward, spending the last two weeks of the tag's life in temperatures around 10 °C. In contrast, whale #1125 traveled south in three weeks from 11 °C water to 23 °C water, then turned north to return to water with temperature ranging from 10 to 14 °C for the last month of tag life. The temperature histograms show that whale #1812's temperature distribution was limited to a relatively narrow range (5 to 11 °C), and whale #1125's range spread from 11 to 23 °C. The histograms also show that for whale #1812, only three locations occurred in temperatures less than 6.4 °C, and that most were recorded in 9 to 11 °C water. For whale #1125, only five records occurred in temperatures above 18 °C, with most locations occurring in waters of 12-17 °C. Although the temperature data was not a significant predictor of whale #1125's movement patterns, it may be because SST data for whale #1125's track ended at 63° W longitude, so the analyses of both temperature and the distance to fronts for the eastern portion of this track were limited.

As pointed out earlier, there were significant seasonal differences in the Gulf of Maine temperatures observed during these two whale movement periods. The histograms shown in Figure 4.9 may reflect upper and lower temperature "preferences for right

111

whales with #1812 tending to spend more time in waters greater than 10°C, and #1125

moving to waters less than 18°C during their respective tracks. Further right whale

satellite tracking data will be needed to confirm this.
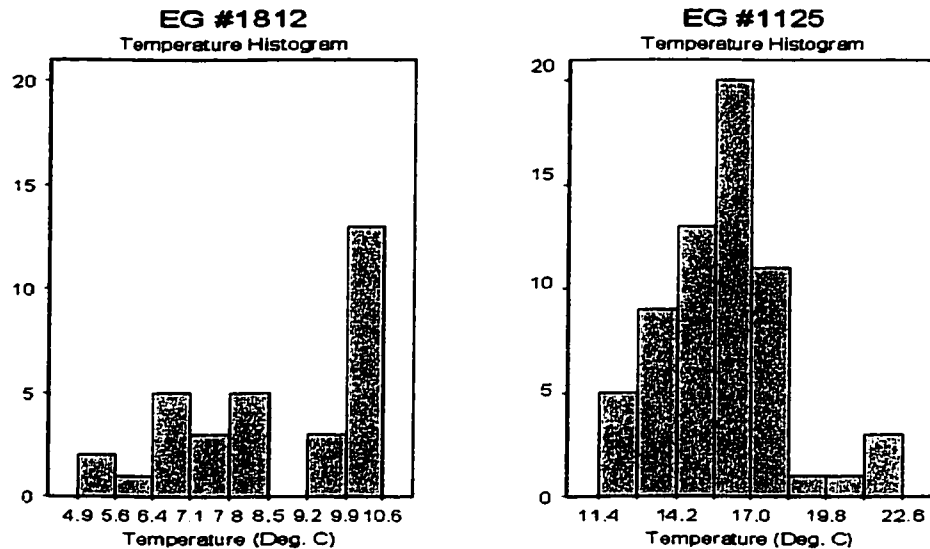
Figure 4.9. Temperature distributions for whales # 1812 (April-May) and #1125 (August-October)in the Gulf of Maine.

The satellite-tracked whale movements superimposed over the frontal density

maps are shown in Figs. 4.10 and 4.11, respectively. The track of whale #1812 does not

appear to show any pattern of movements with regard to frontal density, as her satellite

fixes appear on, near, and away from the high density frontal zones during the period she

was tracked. The track of whale #1125 is more linked to frontal zones while traveling,

as she appears to make course changes at fronts. However, her high point density periods

(little or no traveling) appear to be away from most frontal zones in the Bay of Fundy and

on the Nova Scotian Shelf.

112
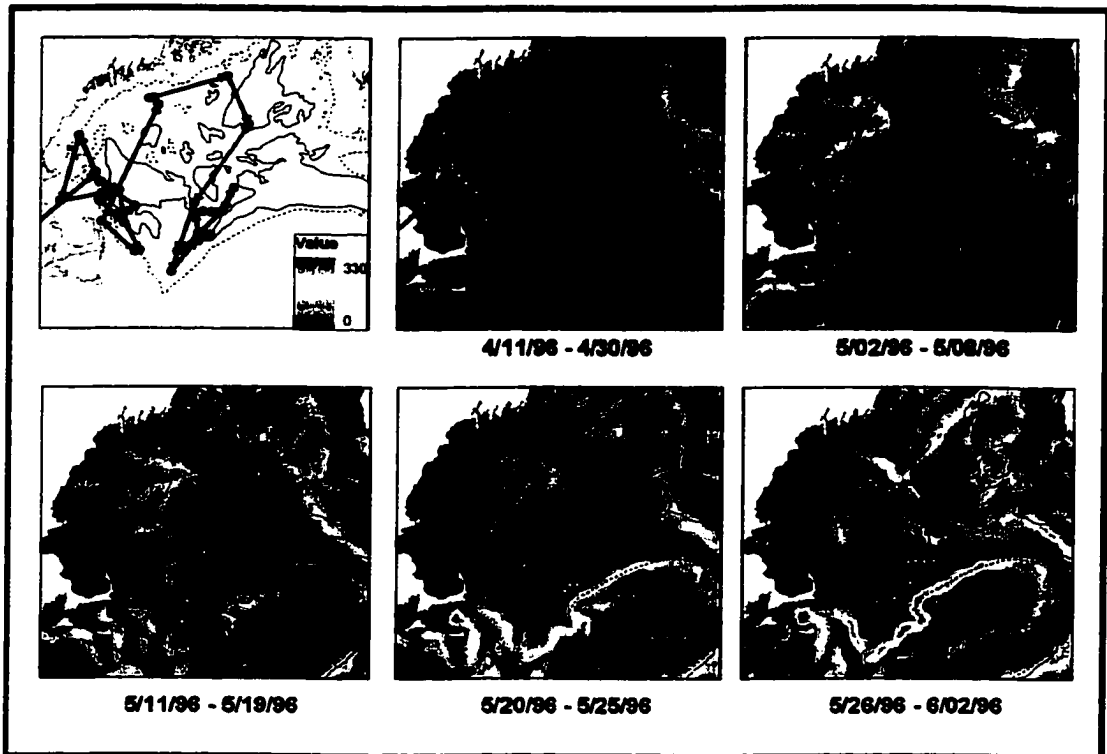
Figure 4.10. Track of right whale #1812 over frontal density patterns.
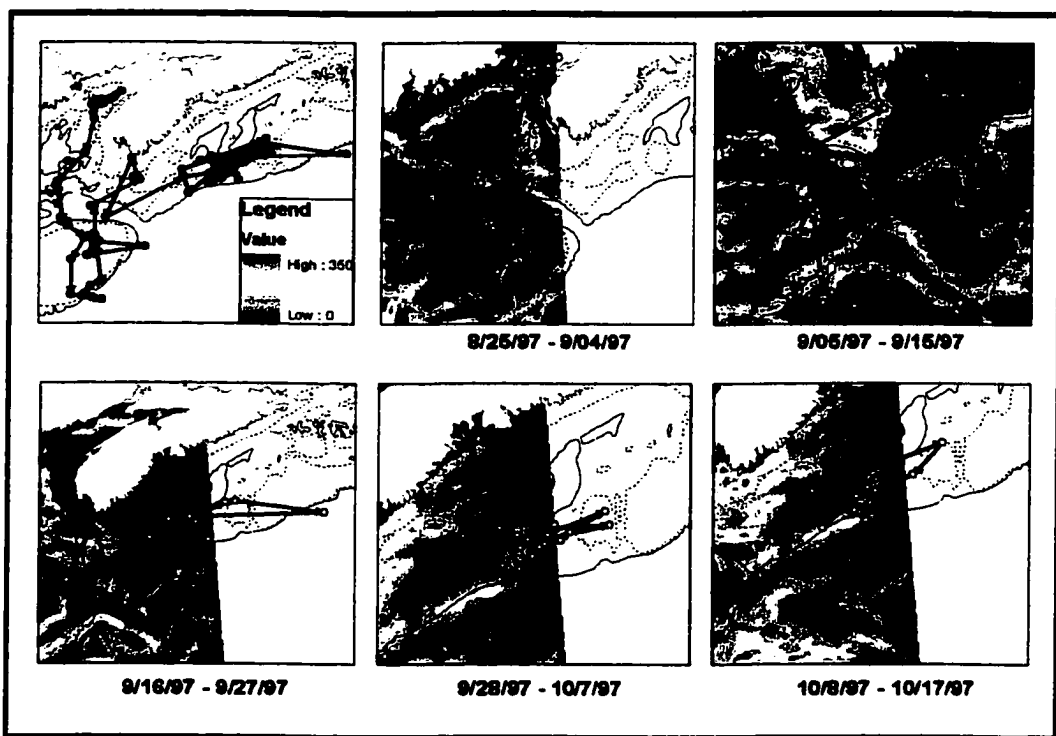
Figure 4.11. Track of right whale #1125 over frontal density patterns.

113

The movements of both animals in relation to temperature and frontal zones can more easily be seen in the graphs given in Figure 4.12. The highest point density of satellite locations for whale # 1125 with regard to temperature occurred between 14°C and 18°C. Also there was an increase in "distance to front" with an increase in point density. For whale # 1812, point density increases with increasing temperature, and the highest point densities were found 20 to 50 km from fronts (Fig 4.12).
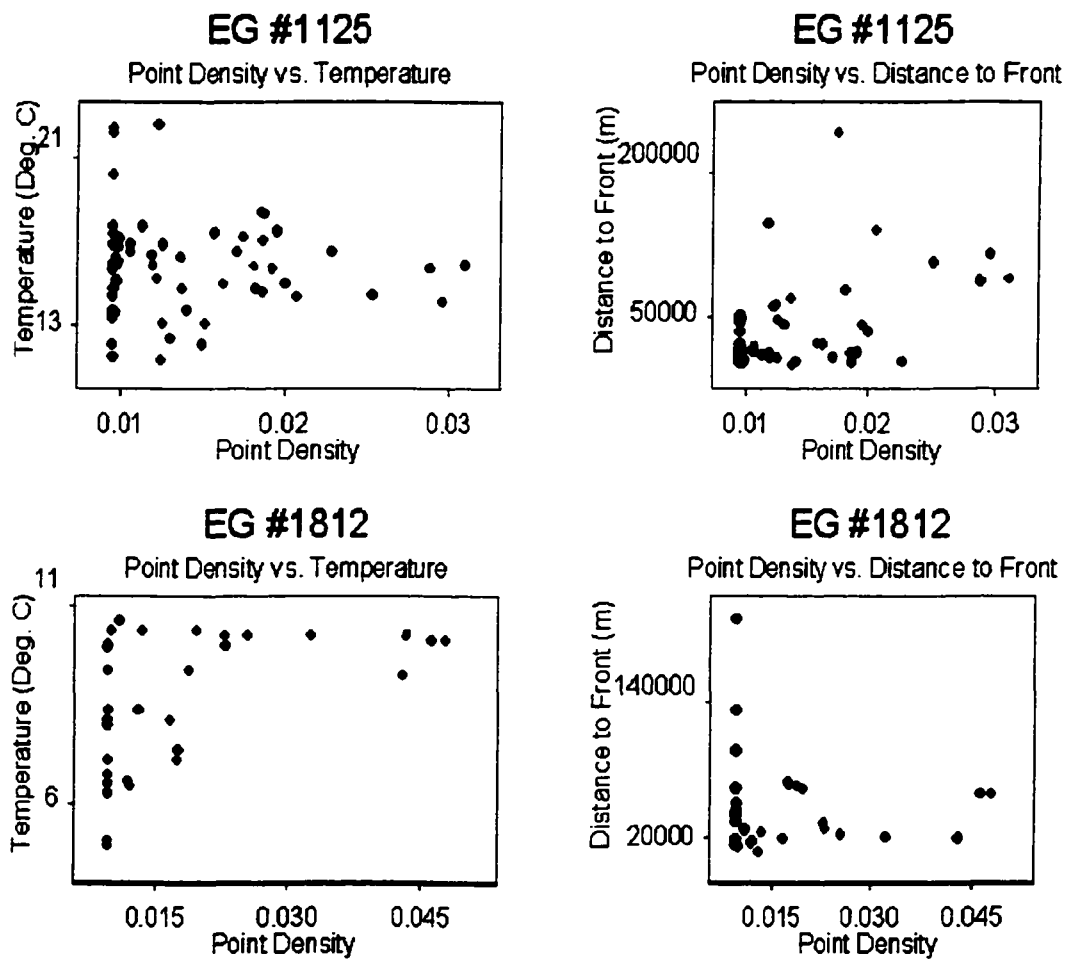
Figure 4.12. The relationships between point density, sea-surface temperature, and distance to front, for right whales # 1812 and #1125.

114

Discussion

The distribution and movement patterns of right whales are dictated by their search for food, members of the opposite sex, suitable habitat, and possibly by predator avoidance. With the exception of the thermal qualities of habitats, none of these things could be measured directly in this study. However, oceanographic factors influencing the whale's movement patterns probably work indirectly, either through hydrographic events that concentrate copepods, temperature regimes that reduce thermal stress, or poor visibility conditions that reduce the probability of predation (particularly on calves). Since some of these oceanographic conditions are detectable remotely (e.g., temperatures and fronts from SST satellite data and ocean color from SEAWIFS satellite data), this inferential approach to linking oceanographic features to habitat use patterns is promising. However, the difficulty of identifying which factors are most important to right whales remains before us.

In this study, the addition of other variables such as ocean color and copepod densities, were considered, but the spatial and temporal periods for both data sets did not overlap the satellite-tracked whales in this study. Synoptic copepod data, available through the Marine Resource Monitoring Assessment and Prediction (MARMAP) program of the National Marine Fisheries Service (NMFS) have been collected twice a year at stations that are approximately twenty- five km apart throughout the Gulf of Maine. Ocean color data for the region from the SEAWIFS satellite are only available after September 1997. Neither dataset provided information for equivalent time periods or locations of the tracks tested here. Nevertheless, the addition of this type of data (if collected concurrently with satellite tracking of an animal) would be an appropriate

115

extension of this approach.

There were also limitations to the statistical approaches described here. CART analyses tend to "overpredict" the data, identifying "exact" conditions in which one might expect to find the response variable (point density). For this reason, analyses of multiple whale tracks will be needed to provide robust information on oceanographic features governing movement patterns of right whales, and to eliminate idiosyncrasies of individuals. Mantel tests provide strong tests of correlations, but they are averaged over all distance classes, so do not provide much information on the spatial scales of the correlations. With a larger dataset, a Mantel correlogram might be applicable, and could offer a more refined view of how the traveling right whales use the Gulf of Maine. For both analytical techniques, normalizing data may offer some advantages.

Researchers have assessed the relationships between right whales and copepods in the Great South Channel (Wishner et al. 1988; Winn et al. 1995), the Bay of Fundy (Murison and Gaskin 1989) and Cape Cod Bay (Mayo and Marx 1990), and temperature-derived frontal features and depth in the Great South Channel (Brown and Winn 1989). The Wishner et al. (1988), Murison and Gaskin (1989), and Brown and Winn (1989) studies were based upon the distribution of multiple sightings of right whales in an area. The Mayo and Marx (1990) study was based upon close follows of individual right whales feeding at the surface, and the Winn et al. (1995) work was based upon dive patterns of animals radio-tagged with depth sensors. Mate et al. (1997) reported on satellite-tagged right whale movements throughout the Gulf of Maine, and referenced sea-surface temperature data as a potential factor in determining right whale movements. However, no multivariate studies have been done to simultaneously evaluate the effects

116

of all of these factors on right whales.

The two right whales sampled here showed significant differences in their movements in relation to the tested variables. The movements of a cow (whale #1812) with a calf were primarily dependent upon sea-surface temperature. This may reflect the immature thermoregulatory requirements of the calf, which will have a thinner blubber layer than the mother at this age. It is also possible the cow was seeking the optimum temperature range for finding appropriate prey sizes. Cold temperatures are known to inhibit copepod development, and right whales appear to preferentially target stage V *Calanus*. Thus the early spring foraging strategy of a right whale may focus on finding relatively warmer waters where zooplankton will mature more quickly.

In contrast, the movements of the adult female without a calf (whale #1125) were significantly associated with the distance to fronts. The curious thing about this association is that whale #1125 appeared to use fronts during her traveling mode as signposts, moving along some, and making sharp turns when reaching others. However, when point densities increased as she moved into what appears to be a foraging mode, she was farther away from the fronts than when traveling. This may be consistent with the potential use of fronts by other pelagic animals for navigation and feeding (Olson et al. 1994). However, #1125 also spent considerable time near and over deep ocean basins, in particular the Emerald Basin on the Nova Scotian shelf. These basins are known to be concentrating areas for deep-dwelling diapausing copepods, and this whale may have been feeding at depth in the area.

Right whales feed primarily on copepods, and copepods are associated with frontal boundaries (Wishner et al. 1988; Kenney et al. 2001). Therefore, high-density

117

food patches are likely to be associated with fronts, and one might expect feeding right whales to be strongly linked in space to the locations of fronts. However, the location data from whale #1125 shows that her point density was highest at ranges of 20-40 km from intense fronts. One possible explanation for this is that the oceanographic features responsible for creating aggregations of copepods are not always visible in satellite imagery. In the well-known feeding grounds (Bay of Fundy, Roseway Basin, Great South Channel), there is a fair amount of temporal variability in the intensity and location of consistent frontal features as viewed by satellite SST sensors (see Figure 4.10 for the Great South Channel, and Figure 4.11 for the Bay of Fundy and Roseway Basin). Thus, features that aggregate copepods may be occurring at depth, and may attract right whales, but will be invisible to available sensors. Thus, the high point densities of whale #1125 away from the frontal zones might occur if copepod densities are highest in the zones where the turbulence associated with fronts is minimized, such as the deep basins (Emerald, Roseway, and Georges) where copepods are known to occur. At this time, such aggregations are not predictable from the data used in this study

Adult right whales are well insulated by a thick blubber layer, and therefore are probably less sensitive to absolute temperatures than other factors. Nevertheless, both whales may have been using temperature and frontal events as navigation tools, either to find traditional feeding locations, or to find ephemeral concentrations of copepods on the basis of appropriate conditions (Olson et al. 1994). At these stages, both females are likely to have food as the main motivation in their movements, although whale #1812's movements may have be additionally mediated by the swimming speed of the calf, the calf's thermoregulatory limitations, and the potential for predation on the calf.

118

Appropriate analyses of satellite-tracked right whales may help identify the oceanographic characteristics correlated with their habitat use patterns. This would provide a supplement to the current practice of inferring habitat requirements from large-scale correlations between animal distributions and oceanographic or trophic features in the oceans. There is always the danger of extrapolating too much on the basis of limited sampling, although the two whale tracks analyzed here show significant differences. The differences may be differences in life stage (lactating versus non-lactating females), or they may simply be individual variations in preference. However, the use of satellite ocean imagery, GIS, and the application of these statistical methods to satellite tracking data suggest new opportunities for study. Such analyses might eventually predict potential movement and distribution patterns of different species, assisting managers in identifying areas where there are high levels of conflict with human activities. As the development of new satellite tracking technology provides better accuracy in locations, and as better satellite imagery with additional sensors becomes available, the definition of habitat use patterns will be improved, possibly leading to predictive models of right whale movements.

119

CHAPTER V

OPTIONS FOR RIGHT WHALE SURVIVAL

Introduction

The future of the North Atlantic right whale (*Eubalaena glacialis*, Borowski,

1781) remains uncertain. Recently published models indicate this species is on the path to

extinction (Caswell et al. 1999, Fujiwara and Caswell 2001), although the analyses

conducted in Chapter III suggest that those models may be flawed. Nevertheless, the

complexity of right whale biology, the coastal nature of the species, and the unknown

links between reproduction and right whale habitat are challenging for any management

strategy. In this Chapter, the science behind the threats to right whales is summarized,

and options for managing both the threats and the population are presented.

One of the general features of mortality demographics in right whales is that

anthropogenic mortalities affect juveniles and adults more frequently than natural sources

of mortality, which predominate in calves and two year olds (Chapter III). Those animals

considered presumed dead by extended absences from the sightings record display

demographic characteristics of the anthropogenic mortalities, and not those of natural

mortality. Although not proof of the cause of any given whale's disappearance, these

data indicate that most of the missing animals are probably dead due to human activities.

The documented cases of anthropogenic mortalities should therefore be considered minimum estimates of human effects on this population.

Right Whales Versus Shipping

Since 1970, there are 30 documented records of right whales being struck by ships along the east coast of the U.S. and Canada (Table 5.1). At least 18 have died from these collisions, and an additional 5 are presumed dead due to the injuries sustained, and the fact that they were never seen after the injured sighting. A review of the right whale mortalities from ship strikes shows that they have occurred in nearly every portion of their range from Florida to Nova Scotia. Shipping ports are present throughout the range of right whale habitats, and at least three of them (Fundy, Great South Channel, and the southeastern U.S.) have shipping lanes running through critical right whale habitat.

Policy work with the shipping industry and federal managers has led to some progress in reducing the probability of ships hitting whales. A mandatory ships reporting system was implemented in 1999, which requires commercial ships entering ports along the east coast of the U.S. to check in well offshore, at which time they are supplied with information on right whale distribution and behavior, and how ships can avoid them. The Navy, Army Corps, and Coast Guard vessels have now implemented operating procedures and training to reduce the possibility of hitting a whale with their ships.

In the southeastern U.S., NMFS, the Navy, the Army Corps, and Coast Guard, jointly fund and support an aerial surveillance "early warning system" for right whales, which provides near-real time information on the locations and trajectories for every right whale present in the area to all shipping traffic. Based upon records of interactions

121

between the survey crews and the ships, this system can be credited with saving several right whales per year.

Table 5.1. Documented right whale/ship collisions, 1972-2001. Data source: New England Aquarium

Year	Month	Day	Status	Ident.	Sex	Age	Location
1972	1	30	D	Unid72	U	C	TX
1976	4	15	D	Unid76	M	C	MA
1976	11	5	D	Unid76	U	U	ME
1979	3	5	D	Unid79	M	J	NY
1980	8	13	A	1019	M	U	BOF
1980	5	28	PD	1401	M	U	GSC
1983	2	21	D	1128	M	2	NJ
1984	8	5	PD	1432	U	U	SS
1986	8	7	D	1504	F	1	MB
1986	8	14	PD	1006	F	7	BOF
1987	2	14	A	1704	F	C	GA,FL
1987	8	28	A	1716	U	U	SS
1987	7	9	D	Unid87	M	J	NS
1991	2	11	A	2143	F	C	GA,FL
1991	3	12	D	1907	F	2	FL
1992	9	5	D	1223	F	A	BOF
1993	1	5	D	Unid93	M	C	FL
1993	12	6	D	Unid93	F	U	VA
1994	2	22	PD	2404	U	C	FL
1995	10	19	D	2250	M	U	BOF
1995	8	13	PD	1045	F	A	GOM
1996	1	30	D	1623	M	A	GA
1996	3	9	D	2220	M	U	MA
1997	8	19	D	2450	F	U	BOF
1998	1	3	A	2705	U	1	GA
1999	4	20	D	1014	F	U	MA
2000	7		A	2820	M	U	GOM
2001	1	1	A	1160	F	U	FL
2001	3	17	D	Unid 01	M	C	VA
2001	6	19	D	Unid 01	F	C	NY

122

Future Management Options for Shipping

Beyond these current activities, the options for managing shipping/whale conflicts are limited. Russell and Knowlton (2001), and Knowlton and Kraus (2001) identified three alternative strategies for reducing right whale mortalities from shipping, including routing ships to minimize travel times through high density right whale zones, slowing ships to "whale-safe" speeds (believed to be somewhere between ten and 13 knots), and technical solutions that would either allow whales to avoid ships or ships to avoid whales.

The first alternative of ship's routing, is being implemented in the Bay of Fundy, where the Canadian government, conservation groups, commercial shipping interests, and fishermen have all agreed to move shipping lanes to the east of the right whale habitat. A Canadian proposal to the International Maritime Organization to move the lanes was submitted in April 2002. The only other location where ships routing might be effective would be in the Great South Channel, where adequate room exists to move shipping lanes. However, oceanographic patterns vary from year to year, with right whales using the western side in warmer years and the eastern side of the channel in colder years. Until this alternating pattern of distribution is understood, moving shipping lanes is problematic – managers might mistakenly move them into a critical whale habitat that occurs only under oceanographic conditions that were not present in previous surveys.

The second alternative, of slowing ships to a "whale safe" speed within right whale areas, is perhaps most favored by the conservation community. This option has the advantage of affecting all ship/whale encounters favorably for the whales, and eliminates the dependence of whale survival on human detection abilities. However, it could be expensive for the shipping companies, which schedule their port arrival times and all

123

logistical factors to within 30 minutes. Delays in some areas (e.g., 40 miles or 10 knots in the lanes through the Great South Channel) could amount to delays of up to four hours. Further, port authorities don't like it because they are competitive with one another for shipping traffic, so ports with whales in their coastal waters suffer a significant disadvantage if they have a site-specific delay. These problems might be alleviated by rolling seasonal slow-downs that affect all east coast ports equally, and for short periods of time (< four months per year), but there has been little interest from either the shipping companies or the port authorities to pursue this option.

One problem with this idea is that the actual speed at which ships become safe to whales is not known with certainty. Laist et al. (2001) present very limited data on ship collisions with whales that suggest that most mortality occurs when collisions occur at speeds of 13 knots or greater, and that none has occurred with vessels going less than 10 knots. Intuitively this makes sense, as biologists have been using the "squirrel in the road" model, in which a car going 50 mph will probably kill it, but one going 20 mph probably won't. Still, there is little observational data to support any particular speed as "safe" for whales, and models of avoidance speed, reaction time, acoustic cues, and ship speeds are needed to evaluate the risks to whales of different vessel speeds. Issues of habituation (these whales live in a noisy ship-filled ocean), acoustic cues at the ocean's surface (ship noise is affected by wave height, Lloyd's mirror effects, thermoclines), and whale's behavioral responses to close approaches, will also need to be included. Nevertheless, slowing vessels is one way to reduce the mortality risk to right whales, even if the actual "whale safe" speed is unknown. The probability of killing a whale in a ships path at 30 knots is close to 1, and at 1 knot it is close to zero. The lethality of

124

collision is a function with multiple variables, but it is certainly a continuum, and as ships reduce speeds, there will be associated reductions in the probability of killing whales.

The third alternative of technological innovation involves proposed methods that are still in development and have not yet been adequately tested. These include the possibility of detecting whales acoustically (using either forward-looking sonar, or listening for whales tagged with acoustic tags), or by using satellites, radar, infra-red or heat sensors. The other technological approach has been to develop an acoustic or illumination device that would alert and move whales out of the path of a traveling vessel. Computer modeling has been used to investigate how hydrodynamic forces produced by moving ships might suck right whales toward the ship or push them away (Knowlton et al. 1995). Such insights could be used in designing new ships or new propulsion systems, such as enclosed turbo-jet hydraulic drives or magneto-hydrodynamic drives, actions that could eliminate the kind of injury responsible for most right whale deaths.

Some of these proposals probably have merit, and involve technology that has been proven in terrestrial or military circumstances. However, none of these ideas would be easy to implement, since thousands of ships are involved in eastern North American commerce from all over the world. Requiring successful devices (if one could be found) on these ships, and enforcing their maintenance and appropriate use seems improbable. Further, for active acoustic devices, there is concern in high-use vessel traffic areas that these would raise the ambient noise levels in the ocean, and possibly drive whales out of essential habitats. There are passive acoustic devices that are currently being tested to detect the natural sounds that right whales make, but unfortunately, these will never tell

125

us much about those animals that don't make sounds (and there may be significant numbers of them).

Some combination of these alternatives will probably be needed reduce ship kills of right whales to inconsequential levels. The change in routing in the Bay of Fundy will make a significant difference in that area. Studies are needed to determine if comparable changes will work in the Great South Channel, and possibly in the Roseway Basin area south of Nova Scotia. For Cape Cod Bay, shipping does not pass through the critical habitat, but shipping lanes do surround access to the Bay on the north and west. Routing is unlikely to work in Cape Cod Bay, but slowing vessels might be effective.

In the southeastern U.S. re-routing ships is unlikely to help much, as all of the shipping lanes into ports there must cross the calving ground of right whales. Here, slowing ships would be the most effective alternative. In the future, the nearshore and fixed nature of the shipping lanes suggest that some technological solutions might be effective in this habitat, because it is well-defined, limited in scope, and close to potential traffic control centers (Jacksonville, Savannah). If suitable whale detection systems could be found, this area might benefit from them, as they theoretically could be attached to existing navigation or military markers on or near shipping lanes in the region.

Because alterations in maritime navigation procedures requires approval of the International Maritime Organization, and such proposals can take years to be approved, efforts to reduce ship kills of right whales in all areas are unlikely to be effective for some time. Given the current state of technology, slowing vessels is the best option for mitigating ship/whale collisions in most areas, and ships routing has significant potential in Canadian waters and the Great South Channel.

126

Right Whales Versus Fishing

Because right whales spend a lot of their lives within 50 miles of the coastline of the U.S. and Canada, they become entangled in fixed fishing gear with some regularity. The lobster industry uses most of the Gulf of Maine and the continental shelf south of Nantucket to Long Island, the crab industry has pot fisheries across the shelf from New York to Cape Hatteras, and gillnets are used in a variety of fisheries from Georgia to Nova Scotia. There are additional fixed gear fisheries in these areas, and new emerging ones that are not yet regulated (e.g., hagfish traps).

Fixed gear fisheries are everywhere that right whales occur, but there are poor estimates of the quantities of various gear types by season and area. Part of this is due to the opportunistic nature of commercial fishing—most fishermen in this highly regulated environment work several different fisheries within a year, moving between them as seasons and closures allow. Also, many fishermen maintain permits for more gear than they currently fish, hedging bets against a future opportunities. This makes an assessment of the actual numbers of traps or gillnets in the water extremely difficult.

A summary of all well-documented right whale entanglements since 1980 is given in Table 5.2. This information comes from photographic data in the right whale catalog, disentanglement records at the Center for Coastal Studies, and NMFS researchers (Kenney and Hartley, 2001). A total of 39 individual right whales have been reported entangled 41 times, leading to five known deaths (in red). These numbers underestimate the impact of fishing gear on right whales (Kraus and Knowlton, 2001). Table 5.2 includes a group of animals (in yellow) that were never seen again after the entangling

127

Table 5.2. Right whale entanglements in fishing gear, 1981-2001. Sources: New England Aquarium, Center for Coastal Studies, National Marine Fisheries Service.

Year	Mo	Day	Stat	ID#	Sex	Age	Area	Type	DisET	Last sight
1981	8	27	A	1152	M	U	BOF	U	N	26-Sep-97
1983	5	15	A	1306	M	U	MA	LI	N	6-Sep-97
1984	9	6	A	1308	F	1	BOF	GN	N	12-Sep-97
1984	8	26	PD	U 84	M?	U	NFLD	CT	A	N/A
1985	5	2	A	1406	F	1	ME	LI	Y	4-Sep-97
1986	5	15	A	1411	M	2	GSC	U	N	28 Sept. 97
1986	8	29	PD	1163	F	5	MB	U	N	12-Feb-92
1987	7	10	A	1004	F	A	MB	U	N	25-Aug-97
1987	9	25	A	1113	M	U	SS	U	N	16-Mar-95
1988	11	9	D	U 88	U	U	BOF	LO	N	N/A
1992	1	11	PD	U 92	U	C	GA,FL	U	N	--
1993	7	9	PD	2233	F	1	GOM	LI,DN	P	22-Aug-93
1994	9	9	A	2320	F	U	BOF	GN	N	25-Aug-97
1994	1	7	A	1621	U	U	GA	U	N	4-Oct-97
1994	11	17	PD	2151	U	3	JL	U	A	--
1994	9	21	PD	1247	M	12	BOF	U	N	17-Aug-95
1995	9	16	A	2110	M	4	BOF	GN	P	1997
1995	7	17	D	2366	M	2	RI	LO	N	N/A
1996	1	6	A	1707	F	9	FL	U	A	25-Aug-97
1997	7	15	A	1705	F	10	BOF	S?	N	6-Sep-97
1997	4	12	A	1505	M	12	MB	U	N	26-Aug-97
1997	9	12	A	2027	M	7	BOF	U	P	5-Mar-98
1997	6	24	A	1971	M	8	GSC	LO	Y	11-Sep-97
1997	8	29	PD	2557	F	2	BOF	U	N+	19-Sep-97
1997	8	23		2212	M	5	BOF	U	N	14-Sep-98
1998	9	12		2212	M	6	CCB	LI	Y	14-Sep-98
1998	9	14	PD	2212	M	6	CCB	LO	Y	14-Sep-98
1998	7	24		2212	M	6	CCB	U	Y	14-Sep-98
1999	7	21	A	2710	F	2	BOF	PG	N	29-Mar-01
1999	5	19	A	1158	F	18	GSC	LO	P	7-Jan-01
1999	6	5	A	2753	F	2	BOF	U	Y	14-Sep-00
1999	5	10	D	2030	F	11	GOM	GN	A	
2000	2	8	A	2920	U	U	CCB	U	N	28-May-00
2000	3	23	A	1301	F	17	CCB	U	N	3-May-00
2000	5	31	A	1720	U	14+	GOM	U	N	31-May-00
2000	3	27	A	1167	M	19+	GSC	U	N	1-Aug-00
2000	7	9	A	2746	U	3	BOF	U	P	25-Aug-00
2000	8	18	A	2223	F	8	BOF	U	P	18-Aug-00
2000	3	1	PD	1130	M	21+	CCB	U	N	
2001	10	25	D	1238	M	?	GSL	S?	N	
2001	6	8	D	110?	M	21	GOM	U	A	
2001	7	20	PD	2427	M	7	GOM	LO	Y	

128

Gear Codes for Table 5.2:

CT	Codtrap	LO	Offshore type lobster gear
GN	Gillnet	PG	Pot Gear (unidentified target species)
DN	Driftnet	SE	Seine
LI	Inshore Lobster gear	UNK	Unknown gear (rope/line)

event, probably due to trauma sustained from the entanglement. These 10 animals are presumed to be dead, either by a complete disappearance from the sightings database for six years or more, and/or in some cases because the injuries sustained and the appearance of the animal indicated the survival was unlikely. When the known entanglement deaths and the presumed dead are combined, the total of 15 deaths attributable to encounters with fixed fishing gear is nearly equivalent to the number of right whale kills from shipping.

It is surprising how few records of entanglements there are in this dataset. Starting as early as 1990, there was strong evidence that nearly 60% of all right whales had been entangled in fishing gear at some time in their lives (Kraus 1990; Kraus and Knowlton 2001). This percentage has increased only slightly in the last ten years, but it suggests that at least 250 right whales were entangled at some time in their lives, and were able to free themselves. Many rope-scarred animals migrate, feed, engage in courtship and have babies. Thus a large number of entanglements may occur with no long-term effects. However, scarring from entanglements is still occurring at a rate of 10 to 20 animals per year, indicating that most entanglements of right whales are undetected.

A review of the data in Table 5.2 by area shows that right whales have been entangled in fishing gear in all areas along the eastern seaboard (Table 5.3). This is consistent with the fishery information given above–any co-occurrence of whales and

129

fixed gear will lead to encounters between them. In addition, entanglements affect males and females approximately equally, with 15 females, 19 males, and 8 of unknown sex being documented since 1980. There has been a significant increase (p = 0.0062) in the documented entanglements over the 22-year period (Figure 5.1), but this is almost certainly due to increased reporting and better awareness in the fishing community. The same thing can be said for the spatial information in Table 5.3 — high rates of reporting are present in the Bay of Fundy because of regular surveys have been conducted on right whales there every year since 1980. Rates of scarring from line entanglements in the photographic catalog have remained relatively consistent at about 15 events per year for the last ten years (Knowlton pers comm.).

Table 5.3. Right whale entanglement in fixed fishing gear by area

Area	Alive	Dead and PD	Total
Nova Scotia to Newfoundland	1	3	4
Bay of Fundy	10	3	13
Coastal Maine, Jeffreys Ledge (New Hampshire)	1	1	2
Massachusetts Coastal Waters, Stellwagen Bank	5	3	8
Offshore, Gulf of Maine	1	3	4
Great South Channel	4	0	4
Rhode Island, New York, and Mid Atlantic waters	0	1	1
Coastal Waters of Georgia and Eastern Florida	2	1	3
Totals	24	15	39

130

Figure 5.1. Reported right whale entanglements, 1980-2001[21]

Number of Whales per Year

- ◆ Whales
- —— Trend (regression)

Year
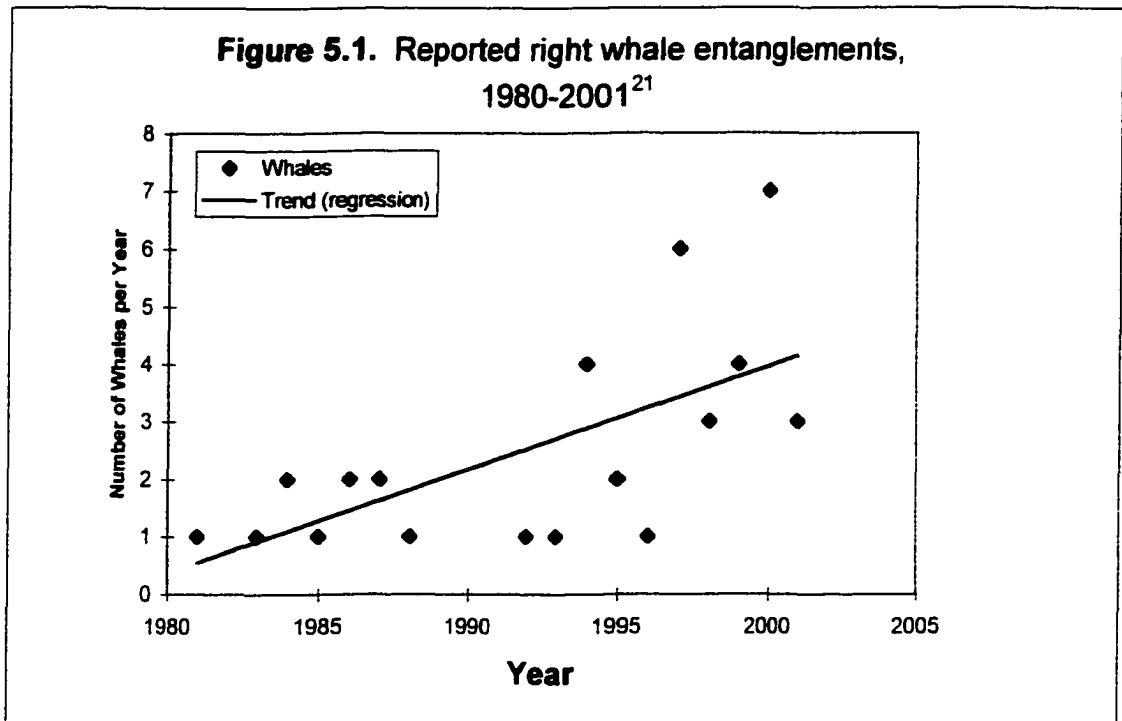
To identify seasons and gear types that presented the highest risk to right whales, analyses were conducted to evaluate the rates of entanglement by month and fishing gear. The probability of entanglement (P_{ent}) was calculated as a percentage of all entanglements. The probability of mortality (P_{mort}) was calculated as the percentage of mortalities that occurred in that category, month or gear. The risk to right whales for a particular month or gear type was evaluating by multiplying the probability of entanglement with the probability of mortality. Strictly speaking, these are not the true risks of entanglement, since such estimates would require knowledge of the distribution and abundance of entangling fishing gear, the movements of right whales through these areas with some precision, and better knowledge about how right whales get entangled if

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[21] Sources: Center for Coastal Studies, National Marine Fisheries Service, New England Aquarium

131

they encounter a line. These are unlikely to be developed for a variety of logistical reasons, so this method provides a rough estimate of the lethality of entanglements. The results are given by month in Table 5.4 and by gear type in Table 5.5. The small sample sizes in all categories render these data statistically non-significant, but the approach provides a method for evaluating those times and gear types that are the greatest problem for right whales.

The analysis of entanglements by month shows that entanglements occur most frequently in May, July, and September. These months approximate the timing of right whale movement between areas, or periods in which the distribution is unknown (Kenney et al. 2001). During May, animals are leaving the Great South Channel, to areas that are not well defined, but include places like Cashes Ledge, Platts Bank, Wildcat Knoll, and the Northeast Peak. During the July period, right whales are moving into summering habitats, including the Bay of Fundy, the Nova Scotian Shelf, and the Gulf of St. Lawrence. In September, right whales are beginning to leave the summering habitats for areas that are still unknown. During all of these times, right whales may be vulnerable because while moving between areas, the chances of encountering fishing gear will be elevated.

The entanglement rates combined with mortality rates suggest that risk to right whales is relatively constant for all of the May through November period. These numbers may reflect the peak fishing seasons within the Gulf of Maine and Mid Atlantic, and probably represent the time period that right whales are significantly at risk. The numbers of these entanglements and mortalities are not large enough to provide statistical significance.

132

Table 5.4. Right whale entanglements by month

Month	Alive	Dead & PD	Total	P_{ent}	P_{mort}	Risk = (P_e x P_m)
Jan	2	1	3	0.076	0.33	0.025
Feb	1	0	1	0.026	0	0
Mar	2	1	3	0.076	0.33	0.025
Apr	1	0	1	0.026	0	0
May	5	1	6	0.154	0.20	0.031
Jun	2	1	3	0.076	0.33	0.025
Jul	4	3	7	0.179	0.43	0.077
Aug	2	3	5	0.128	0.60	0.077
Sep	5	2	7	0.179	0.29	0.052
Oct	0	1	1	0.026	1.00	0.026
Nov	0	2	2	0.051	1.00	0.051
Dec	0	0	0	0	0	0
Totals	24	15	39			

The analysis of entanglement rates by gear type show that more than half (24/42) of all documented entanglements were not attributable to any particular gear type. This is because these entanglements were only ropes, most of which might have been used in a variety of fixed gear fisheries, but had no distinguishing characteristics. The remaining identified gear is distributed widely across gear type. Although the numbers are too low to be statistically meaningful, there is a trend of increasing mortality with increasing gear size, from inshore lobster gear, to gillnets, to offshore lobster gear, and finally to codtraps and seines. Regardless of the statistical validity of these data, they do indicate that right whales get entangled in all fixed gear types.

The analysis in Table 5.5 is useful in identifying that gear which would most benefit from research to reduce its risk to large whales. For example, codtraps and seines appear to be 100% fatal, but they are rarely encountered by right whales, so there would

133

be a low benefit to trying to alter these gear types. On the other hand, offshore lobster gear has the second highest encounter rate, and a relatively high mortality rate, and therefore seems a worthwhile target for mitigation work. The highest level of risk to right whales comes from unknown gear types. These are ropes and line unidentified with regard to a fishery. This means that right whales are at risk from any lines or ropes in the water column (i.e., all fisheries with vertical lines, and/or floating lines between traps or pots), and that this area should be the subject of research across all fishery gear types.

Table 5.5. Right whale entanglements by gear type

	CT	GN	DN	LI	LO	PG	SE	UNK	Total
Alive		3		2	2	1	1	15	24
Dead		1			2		1	1	5
Pres. Dead	1		1		2			6	10
Repeat				1				2	3
Totals	**1**	**4**	**1**	**3**	**6**	**1**	**2**	**24**	**42**
Ent. Rate	0.02	0.10	0.02	0.07	0.14	0.02	0.05	0.57	1.00
Mort. Rate	1.00	0.25	1.00	0	0.67	0	0.50	0.46	
Risk	0.02	0.025	0.02	0	0.0938	0	0.025	0.2622	

Gear Codes:
CT   Codtrap   LO   Offshore type lobster gear
GN   Gillnet   PG   Pot Gear (unidentified target species)
DN   Driftnet   SE   Seine
LI   Inshore Lobster gear   UNK   Unknown gear (rope/line)

Fishery Options

Closures. The NMFS has, in response to a lawsuit, developed a plan that creates fixed gear closures to protect right whales in the Gulf of Maine on a seasonal basis (Seasonal Area Management, or SAM closures) and on a dynamic basis in response to

134

temporary sightings of three or more right whales in an area (Dynamic Area Management or DAM closures). It is already widely thought in the fishing community that the DAM closures are flawed in concept, unenforceable, and probably ineffective. These two concepts will be addressed separately.

The DAM idea might have merit — if one could identify where all right whales were on a regular basis, and if one could predict whether they were passing through or staying for a while, and if fishermen could respond instantaneously to a dynamic closure, and finally, if the weather were good all the time so that all of these things could happen. Both lobstermen and gillnetters usually fish more gear than can be retrieved in a single day, so it is impossible for most fishermen to pick up and move out of an area immediately.

The weather requirements for aerial surveys to detect whales are much more stringent than the minimum weather conditions needed to go fishing. Further, weather conditions in some parts of the year could be sub-par for aerial surveys for months. This is, therefore, a poor mitigation strategy, because fishermen can continue to fish in areas where whales may be undetected because of poor sighting conditions. On the other hand, if a survey sights a group of whales that leads to a DAM closure, it is potentially bad for fishermen, because the closure remains in effect for two weeks or until a survey declares it clear. If weather prevents that survey for extended periods, it keeps fishermen out, whether the whales have moved on or not. In the end, both whales and fishermen are vulnerable to poor management because the contemporary survey and whale detection methods are weather dependent.

135

The SAM closure strategy also has merit, if right whales had predictable habitat use patterns that could inform closure area size and timing. However, with the exception of the critical habitats already identified in the U.S. and Canada, such areas do not exist, except in a broad-brush analysis that will close large sections of the Gulf of Maine. Also, there is some concern about the potential for a corralling effect, i.e., that fishermen will set gear in higher densities just around the borders of a closure, thus creating a higher risk entanglement zone for whale crossing into or out of a closed area. Also, 50% of the documented entanglements in the U.S. reported in Table 5.3 occurred outside of the identified critical habitats. Further, four of the five confirmed right whale deaths from entanglements in the U.S. appear to have occurred outside of any of the identified seasonal habitats. Since critical habitats are the best surveyed of all right whale habitats, this indicates that many more entanglements are occurring elsewhere, but are not reported. This premise is supported by the scarring data, which suggests much higher entanglement rates than are documented by the presence of gear on an animal (Knowlton pers comm.). Unless SAM closures were large enough to include vast areas of the Gulf of Maine, they would be unlikely to eliminate fatal entanglements, and they would probably reduce all entanglements by less than half.

Gear Modifications.

A variety of modifications to make fishing gear "whale-safe" have been proposed and some have been implemented over the last ten years. One category includes a number of "breakaway" links, designed to break at a pre-selected strength below the strength of the entangling line when a whale gets caught, and hopefully releasing the whale before it dies. The second major category was the modification of inter-trap lines

136

from float rope to sinking or neutral rope, to eliminate large loops of rope from the water column on strings of traps. The third category of proposals have included new technologies to eliminate vertical lines from the water (acoustic, electric, and galvanic releases), develop weak tag lines that would release the hauling line, degradable lines that would degrade if embedded in a whale, and other alternative modifications to line that would reduce the possibility of entanglements (illumination, colors, stiffness). However, most of the work on gear modifications has focused on the first two categories.

Weak Links/Breakaways. Weak links or breakaways are popular with the fishermen because they require minor or no changes in fishing practices. Weak links were based upon the idea that whales could free themselves if they could break away from the entangling gear in some way. Many whales were observed with lines running through the mouth, and if the lines could slide through the baleen without the impediment of a buoy at the end of the line, it seemed likely the whale could free itself. Also, some proponents of breakaways suggested that breakaway links could also be relied upon to reduce the probability that a flipper or fluke wrap would last long. This assumed that as a line slid across the flipper or fluke, that a breakaway would release as the buoy hit the appendage. Further, weak link technology has been applied to gillnet headropes. Since the top of a groundfish gillnet can float three to seven meters off the bottom, whales swimming near the bottom were vulnerable to capture. The observations of whales entangled in gillnets confirmed that this was a problem. The recent development of a breakaway headrope float that is similar in appearance and functionality to regular headrope floats could significantly reduce the danger that gillnets pose to right whales.

137

NMFS and fishermen have done some excellent work using load cells to identify the safest low breaking strength for weak links, a tricky matter dependent upon weather, tide, fishery, and hauling methods. Due to this testing over the last few years, weak link breaking strength requirements issued by NMFS have gradually been reduced in all fisheries.

Unfortunately, there is little evidence that breakaways will work for whales with regard to vertical lines or ground lines. A review of the five whales that died from entanglements with documentation shows that the two Canadian mortalities were probably due to drowning, one in a heavy seine, and one in heavy offshore lobster gear. It is possible that the lobster gear death could have been avoided if the gear had been equipped with breakaways, but it is unlike any modification could have helped the whale killed in the seine. The three U.S. mortalities were more clearcut, as they were killed by long-term wraps of unidentified line (one around the rostrum, one around a flipper, and one around the body between the flippers). All three entanglements occurred in the middle of the line, and no breakaways have yet been devised for mid-line whale releases.

In gillnets, headrope breakaways will probably be highly effective, because gillnets are heavily anchored at both ends, and NMFS requires 1 breakaway every 33 m of line. Theoretically, if a whale hits a gillnet, the anchors will provide the force against which the whale swims. Assuming the weak links work as expected, the whale could only acquire 33 m of line from an encounter with a gillnet headrope.

Weak links are one tool that should be used in the fixed gear fishery, but they are unlikely to mitigate many of the whale/gear conflicts as currently understood. They appear to have the greatest utility in the gillnet fishery, and may occasionally reduce risk

138

to a whale that gets entangled at or near the end of a vertical line with a breakaway. If they are easy for fishermen to use, and do not cost significantly more than the conventional gear, then they should continue to be used fishery-wide as a means for slightly reducing the risk to whales.

Sinking/Neutral Lines Between Traps. Lines that connect traps in strings of lobster gear are usually polypropylene with varying degrees of flotation. The natural flotation of the plastic creates large loops (up to 30 m long and up to 10 m off the bottom) in the water column between traps. On rocky bottoms, these floating lines have the advantage of staying out of the rocks, easing retrieval when hauled. However, given the large numbers of lobster strings present in the Gulf of Maine, it is believed that these floating loops between traps constitute a significant portion of the entanglement risk for all whales in the area.

One proposed gear modification is to eliminate floating lines between traps and replace them with sinking or neutral lines. Sinking line has actually been in use in some areas with sandy bottom for some time. The State of Massachusetts is in the process of implementing regulations that will only allow the use of sinking or neutral line in their lobster fishery. Tests are also underway in eastern Maine to determine whether neutrally bouyant line can be used in their hard bottom fishery. This gear modification appears to have the advantage of being useable by fishermen in most areas, and will provide a sizeable reduction in risk of entanglement to whales.

New Technology Options. The proposed new technologies for creating "whale safe" fishing gear have focused in two general areas, eliminating vertical lines in the water, and making gear more visible or less dangerous. To eliminate vertical lines from

139

the water column, several researchers have designed devices to hold the haul lines and buoys on the bottom until the vessel wants to pull the gear. To release the buoys from the bottom, they have developed and tested a variety of galvanic timed-release links, as well as acoustic releases triggered by a signal from the boat. This technology appears to be available and workable, but it has significant other problems. Fishermen don't like it because it leads to gear conflicts when trap strings are set across one another, or when draggers tow through an area without any visible gear at the surface. NMFS does not like this option because it is fraught with enforcement problems and the high potential for trap limit abuses. There are technological solutions to these problems using acoustic detection methods, but it would require an industry-wide change in fishing practices, including ocean zoning for particular gear types. This option is therefore unlikely to move quickly forward at this time.

Another proposed mitigation strategy, which has not received a lot of attention, is the idea that simple gear modifications might prevent entanglements from occurring in the first place. Whale vision is only moderately well understood, but there is some evidence that entanglements occur at night or depth, where darkness makes visibility poor. Further, most fishing line is black or green, colors that do not stand out underwater. Research is planned to test the effects of illuminated or fluorescent ropes on whales, but an industry shift from black to bright yellow lines might also reduce entanglement probabilities. Other proposals for entanglement prevention include exploring the potential for creating stiff or slick lines that would resist entanglement wrapping, or would slide off the animal quickly. Both of these options may have significant safety and

140

handling issues on the deck of fishing boats, but no research is currently underway to determine the merit of these proposals.

Finally, there are several "star wars" proposals to develop lines that would be unable to kill whales if they became entangled. One idea was lipid-soluble rope that would dissolve if it came into contact with whale skin or blubber. Another involved line that included dissolving catalysts that responded to frequencies of light not found in daylight, allowing for tuned remote laser disentanglement approaches. A third also involved dissolving catalysts embedded in traditional polyproplyene, but these would respond to bio-compatible chemical solutions deployed with paintball guns. None of these are currently under development, but one could imagine that the discovery of any methods like these could significantly reduce, if not eliminate, the likelihood that whales would die from entanglements.

Declining Reproduction

The decline in right whale reproductive rates since 1990 is significant, and if not reversed, does not bode well for this population. Managers in the U.S. and Canada have not approached the reproductive problems as a management issue, perhaps assuming that there is nothing that can be done. Unfortunately, the lack of information about why right whales are reproducing more slowly make this attitude self-fulfilling — the absence of studies on this will provide an absence of evidence of human impacts.

There are currently five hypotheses that might account for reduced reproduction in right whales. These include the effects of genetics, food limitation, infectious disease,

141

contaminants, and marine biotoxins. Of these five possible causes, there is probably little

humans can do with regard to genetic problems or ocean-wide food limitation (if either of

these prove to be a factor). However, the other potential problems may be either directly

or indirectly related to human activities and therefore should be subject to management

actions.

Contaminant studies have been limited to DDT and PCB congeners, a limited

number of other organochlorine pesticides and PAHs (Woodley at al. 1991; Weisbrod et

al. 1999), and some scientists have suggested that declining reproduction in right whales

may be linked to these chemicals (Colborn and Smolen 1996). O' Shea and Brownell

(1994) suggested (in a review of the concentrations of DDT and PCB congeners) that

levels in baleen whales are too low to have any biological impact. However, no work has

been done on a suite of chemicals that are known to have caused reproductive problems

in a number of other terrestrial and marine species through endocrine disruption (e.g.,

tributyltins, phthalates, and alkylphenols) (DeBoer et al. 1998; Lindstrom et al. 1999).

Given the potential for exposure of right whales to these chemicals (and others), studies

are warranted, particularly in light of the significant and continuing decline in right whale

reproductive rates over the last decade (Chapter II).

The sharp periodic declines in reproduction are consistent with epidemics that

might sweep through a population, affecting either food assimilation, hormone function,

or reproduction directly. Infectious disease studies in right whales are non-existent.

When reproductive rates declined markedly in the late 1990s, Marx et al. (1999)

conducted a preliminary study of skin lesions in North Atlantic right whales, finding a

significant increase during this period. Subsequently, the New England Aquarium team

has initiated a study on the potential to assess right whale health from external appearance. Still, no health studies have been conducted with any samples from ill and/or healthy right whales. Necropsies have proven of little use because carcasses have been too decomposed to yield bacterial or viral organisms not related to decomposition. Sampling options for diagnosing diseases in right whales include biopsy samples, fecal samples, and respiratory fluid. Blood collection is currently not an option in the field, although it may be in the future. Clinical trials on captive cetaceans have yielded a variety of tests that may be applicable to the samples researchers can obtain from free-swimming right whales, and the efficacy of these should be tested on wild populations. Recent successful attempts to develop a sedative drug delivery strategy for disentanglement efforts in large whales, suggests that if disease turned out to be a factor, it might be treatable with current technology.

Biotoxins from red tide organisms (also known as "Harmful Algal Blooms" or HABs) are known to be increasing in the Atlantic Ocean over the last several decades (Hallegraeff 1993; Epstein, 1998). While biotoxin effects on mammalian physiology are usually neurological, there is some evidence that chronic exposure may contribute to immuno-suppression (Landsberg and Shumway 1998), which could increase the impact of infectious diseases in wild populations. Also, there is strong evidence that some HABs are related to human effects on marine ecosystems, including both sewage effluent and agricultural or silvacultural runoff (Epstein 1998). Given these factors, it appears that the potential for biotoxins to reduce right whale reproduction warrants serious study, both to assess the potential for exposure and to evaluate potential health and reproductive

effects. Further, it seems very likely that HABs will turn out to have a human related

etiology, in which case, all downstream impacts are definitely a concern for management.

It is most likely that some combination of these hypotheses is working against

right whales in the North Atlantic. The declining reproductive rates of whales that use

coastal habitats suggest that the nearshore effects of contaminants or infectious diseases

related to human activities cannot be ruled out. Global warming, or North Atlantic

Oscillation effects may both be playing a role in diminishing prey production, which

could reduce reproduction by reducing general health. The small genetic window

through which right whales passed may have left them vulnerable to disease, or other

combinations of the above factors. Infectious disease and biotoxins could cause

reproductive failure directly, or might work indirectly to reduce caloric assimilation

efficiency, or impair behavioral responses in courtship activities. If some combination of

factors is responsible for low reproduction in right whales, it will be difficult to tease out

the important ones, but that does not mean it shouldn't be attempted. Emerging

technologies will soon be available to test for wild animal sensitivities to contaminants

and biotoxins, and infectious diseases — and these should be employed as soon as

feasible.

It is also possible that right whales have a significantly different life history than

previously suspected. The recent work on bowheads by George et al., (1999) showed that

bowheads live well over 100 years, and some may reach 200 years of age. The closely

related right whales may have comparable life-spans, which would necessitate a re-

thinking of the demography of this species. A long-lived right whale scenario would

probably include older mean ages of sexual maturity, lower juvenile/adult ratios than most large baleen whales, longer reproductive life-spans, and more flexibility in reproductive strategies for both females and males. The age of first parturition has been steadily climbing upwards since the first estimates in the early 1990's, and now is estimated at 11 years (Chapter II). This is lower than the Bowhead estimate of 15+ years (George et al. 1999), but as the study period increases, it is likely that the mean age of first parturition will continue to climb. Hamilton et al (1998) reported lower juvenile/adult ratios for right whales than other baleen whales, which is consistent with a longer-lived life history pattern. In the north Atlantic right whale population, several females have been identified with reproductive life spans well over 30 years, which is also consistent with long-lived animals.

The selective pressure for the development of long life spans may be the high variability in reproductive success relative to ecological conditions. Right whales live in a patchy environment, and the shifts in distribution within the last twenty years suggest that right whales have been adjusting to spatial and temporal shifts in prey distribution within the study area during that time. If right whales have a reproductive life span of 50 years or more, decadal periods of poor or unpredictably distributed prey may not matter. Such times would certainly contribute to a short-term (ca. 10 – 20 year) decline in reproductive success, but the overall lifetime reproductive success of individuals might not be significantly affected. It is possible that the 1980's were a "good" period for reproductive success in right whales, and the 1990's represents one of those periods of "poor" reproduction for which a long-lived animal has evolved. A long lived evolutionary strategy would be to survive the lean years and reproduce in the good ones.

145

One consequence of this scenario is that managers of right whale/human conflicts may have more time to deal with the potential effects of humans on reproduction. The first goal must be to keep those animals alive that will subsequently reproduce in the long-term. This means reducing human sources of mortality permanently. It does not mean managers can ignore potential effects on reproduction, since some of the potential causes may be cumulative (contaminants), or may leave permanent sterility (disease or bio-toxins). However, the management and protection of whales that may live over 100 years will require a somewhat different approach than the traditional fisheries management strategies.

Conclusions

Despite the doom and gloom prognostications about the survival of this species, proactive and well-measured management and research actions can probably resolve a lot of the difficulties this species faces within ten to twenty years. The long life and reproductive spans of this species gives it some breathing room to account for our mistakes. Still, the U.S. and Canadian governments must take a series of specific and forward thinking actions for this species to recover.

As a start, governments with a popular mandate to recover endangered species must balance the usual standards of statistical proof against an alternative "weight of evidence" approach (Ross 2000). As demonstrated here in Chapter III, even the most statistically robust models can be fooled when sample sizes are small, and individual variation is high. In severely endangered species, sample sizes will always be small, and waiting for statistical certainty in population analyses may lead to extinction before mitigating actions are implemented. Therefore, managers must act cautiously on the

basis of the accumulated evidence in favor of the species. In this particular case, there are several actions that, if implemented today, would start to make a significant difference in the recovery of right whales in the North Atlantic.

To alleviate the impact of shipping on right whales, several actions should be taken. Ships should be slowed to 10 knots from mid-December to mid March between Brunswick Georgia and Cape Canaveral Florida out to 30 miles. The Cape Cod Bay and Great South Channel shipping lanes should also be slowed to this speed for the period from March 15th to June 15th. However, additional research work on the Great South Channel should be conducted to determine if it might be possible to route ships at full speeds away from whales, perhaps dependent upon oceanographic conditions. The Roseway Basin habitat should be declared an area to be avoided by the IMO for all Canadian-U.S. and transatlantic shipping traversing that area. With changes in the shipping lanes in the Fundy habitat, that area appears to be safe, due to the remarkable cooperative efforts of private, commercial and federal interests in Canada. Recognizing the high costs of these measures, a simultaneous research program on technological solutions should be undertaken, in hopes that better detection, tracking, and/or distribution prediction methods for right whales can be developed in order to limit the slow speed measures only to periods when right whales are present.

To mitigate the conflict between fishing and whales, several innovative measures have been taken, but much work needs to be done. Critical habitats should remain closed to fixed fishing gear. Large-scale closures should be eliminated in favor of industry-wide gear modifications as follows. All gillnets should have weak links in the center and at the end of every net panel, and those weak links should be designed to break at or below 900

147

lbs. All trap gear should have neutral or sinking groundlines between traps. All fixed gear should have breakaways at the surface buoys of 600 lb or less breaking strength. NMFS is implementing many of these measures, although the breaking strengths proposed here are somewhat lower. In particular, offshore lobster fishermen must develop methods to fish with buoy breakaways of less than 600 lbs in strength, as the current limits of 2000 lbs and 1500 lbs are meaningless mitigation measures — at least two of the dead whales were killed by line with lower breaking strengths than this. Finally, there must be an aggressive and broad-based research program to find a solution to the problem of vertical lines in the water. Priorities should be to prevent entanglements if possible, and if not, develop gear that cannot kill whales even if entangled. Given adequate funds and the appropriate chemical and fishing gear engineers, the development of lines that would dissolve if wrapped around a whale seems possible, and would eliminate most, if not all of the mortalities in large whales from fishing gear. Alternatively, there may be mid-line breakaways that would prevent lethal entanglements without negatively impacting fishing operations.

To identify the causes, and if possible, reverse the decline in right whale reproduction, all of the needed work at this point is research and development. Studies on right whale health, disease, biotoxins, and contaminants are needed to determine if human activities may be responsible for the current reproductive decline in right whales. Also, efforts should be made to determine the full life history of right whales in the North Atlantic. Supplementary studies on feeding, habitat use, and genetics are also needed to determine if and to what extent these are co-factors in the decline. Research to develop

148

new benign sampling methods is also needed. The sedation deployment work, which may have the unexpected potential to deliver medicine or vaccines, should continue. Right whales should be viewed as black-footed ferrets, or California Condors, just bigger.

Right whales thrived in a period before humanity turned to the sea to make its fortune, and then were brought closer to extinction than any other whale species that still survives. A moratorium on their killing, even though in place for over 65 years, has not led to the recovery of this species. The "enlightenment" of humanity with regard to whaling and endangered species, has not helped, since these whales live in one of the most heavily urbanized pieces of ocean in the world. The irony of the right whale's situation is that the responsibility for their decline has shifted from directed killing by hunters, to all of us who drive cars, eat fish, buy imported goods, or rely upon a Coast Guard or Navy to protect us. This species may have habituated to our noisy presence in their habitat, but they cannot apparently adapt to avoid the lethal dangers our activities create. The survival of right whales depends upon our ability to develop a strategy of co-existence in the ocean, allowing both commerce and wildlife to flourish.

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150

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154

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Appendix 1. North Atlantic Right Whale Consortium Data Use Approval
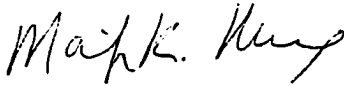
February 21, 2002

Mr. Scott Kraus
New England Aquarium
Central Wharf
Boston, MA 02110

Dear Scott,

Your proposal to the North Atlantic Right Whale Consortium for access to their database has been approved. You hereby have full access to the sighting records from the entire Catalog for your analysis of mortalities and reproduction rates in North Atlantic right whales. The reviewers of your proposal were Dr. Phillip Clapham, National Marine Fisheries Service, Dr. Robert Kenney, University of Rhode Island, and Amy Knowlton, New England Aquarium. All three reviewers gave your request full approval with no restrictions.

Should you have any questions please do not hesitate to contact me.

Best Regards,

Marilyn K. Marx
Consortium Secretary

Appendix 2. N.E.Aquarium.

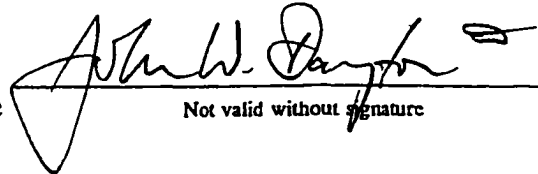# ANIMAL CARE AND USE COMMITTEE
PROTOCOL REVIEW

PROJECT/EXHIBIT TITLE: Right Whales in the Northern Atlantic

PRINCIPAL INVESTIGATOR(S): Scott D. Kraus

DATE RECEIVED: 6/17/97   PROTOCOL #: 97-2

TO   :   Scott D. Kraus, Research Department

FROM   :   John Dayton
Animal Care & Use Committee

Not valid without signature

The above referenced project/exhibit has been reviewed by the New England Aquarium's Animal Care and Use Committee (ACUC). The project has been:

☒ APPROVED UNCONDITIONALLY

☐ APPROVED CONDITIONALLY. The project may proceed at this time but the Principal Investigators MUST respond to the following ACUC concerns before_____.

_____

_____

_____

☐ REJECTED. The project may NOT proceed until the protocol is re-submitted, addressing the following concerns of ACUC.

_____

_____

_____

ACUC PROTOCOL RESPONSE   FORM ACUC-1 REVISED 1/94