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Increase rates in severely depleted stocks of baleen whales

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The status of all known stocks of baleen whales that were severely depleted (to an estimated less than 10% of their original abundance) is reviewed. Of 44 such stocks, 18 are classified as not feasible to monitor. Of the remaining 26 stocks, 12 have been or are being monitored, and significant rates of increase have been demonstrated for 10 of them. At least 10 of the 16 monitorable stocks, for which a significant rate of increase has not been demonstrated, are believed to be increasing. The reasons for a lack of monitoring in most of these 16 stocks do not seem to be related to population size, and may reflect practical difficulties in obtaining representative samples due to temporal or spatial segregation of the animals in relation to the study areas. In total, at least 77% of monitorable stocks are either believed or demonstrated to be increasing.

Rates of increase measured in one bowhead, four right, one gray, one blue, and three humpback whale stocks range from 0.031 to 0.144. Estimates of stock depletion associated with these increase rates are only available for six stocks; the more depleted stocks show higher rates of increase than the less depleted. Under the "strong convexity" hypothesis for the relationship between sustainable yield rate and population size, the maximum sustainable yield rate (MSYR) is more than half the *per capita* increase rate at very low population sizes; this translates into MSYR values of 0.026 to 0.049 (mean 0.039) in seven of these severely depleted stocks. The remaining two stocks are believed to be at or slightly above 50% of their initial size, and thus in the vicinity of the maximum sustainable yield level for baleen whales as conventionally adopted by the International Whaling Commission; their increase rates (adjusted for hunting mortality) are 0.034 and 0.045. These data tend to support MSYR values (for these stocks) at the higher end of the range 0.01–0.04 (of total population size) as sometimes used in baleen whale assessments.

Key words: baleen whales, stocks, monitoring.

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Introduction

Most species of baleen whales (bowhead, right, gray, humpback, blue, fin, sei, Bryde's and minke whale) have been exploited commercially by man, beginning in some instances as long as 900 years ago. This exploitation has in most cases led to depletion well below levels at which maximum net productivity might be expected, although the ultimate degrees of depletion have varied from stock to stock. Legal protection has been afforded to these species at different times and not always simultaneously in different areas, and the application or enforcement of such protection has not always been universal.

Nevertheless, if whale populations respond to a reduction in population size as might be expected by standard population dynamics theory, then effective legal protection should be followed by recovery. For many years this recovery was documented for only one stock, the American stock of gray whales, and this led to speculation that *inter alia* there was a lack of a density-dependent response in greatly reduced baleen whale stocks (Holt, 1985), particularly in the case of right whales (Allen, 1974), and that some stocks might have been reduced to levels below which they could not survive (McVay, 1966; Small, 1971).

This paper reviews recent data on trends in population size of protected species, and discusses these data in light of their importance for an understanding of baleen whale population dynamics in general. Because they represent an extreme case, only those species and stocks listed by Allen (1980) as severely depleted (i.e. estimated to be reduced at one time to less than 10% of their original stock size) have been considered, with one exception, the American stock of gray whales, which Allen listed as moderately exploited (depleted to 20–70% of original stock size). More recent analyses suggest that this population at its lowest point (ca. 1900) was probably less than 23% of its original population size, if historical catches are adjusted for possible underestimation (Butterworth

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et al., in press b, who require the extent of this underestimation to be at least sufficient for a simple population model to provide a growth rate of 2% per annum over the period for which the point estimate of growth rate from censuses is 3.2%). If the degree of adjustment for catch underestimation is made sufficient to produce a rate of increase close to that observed, then the population at its lowest could have been as little as 13% of initial (Butterworth *et al.*, in press b, table 15), so the stock has been included in this paper as at one time being severely depleted.

A preliminary examination of recovery rates in whale stocks that had been protected for at least 20 years (Best, 1990a) was criticized on the grounds that the analysis was self-selecting: only those stocks that had increased significantly would be monitored because only they were large enough (IWC, 1990). In this paper, therefore, the status of all known stocks of severely depleted baleen whales is examined, in order to establish their size and whether those in which there is an apparent lack of a recovery are being or could potentially be monitored.

Materials and methods

The stock definitions adopted have generally followed those used for the most recent assessments by the Scientific Committee of the International Whaling Commission, or the most recently published review, as follows.

1. Bowhead whale – IWC (1992) with the exception that the Hudson's Bay stock has been combined with the Davis Strait stock, the distinction between the two being not well established.
2. Right whale – IWC (1986a) with the exception that the area 60–62°N, 33–35°W has not been considered separately (this corresponded to the nineteenth-century "Cape Farewell" whaling ground, and was recognized simply because allocation to eastern or western Atlantic "stocks" was controversial).
3. Gray whale – IWC (in press).
4. Humpback whale – Winn and Reichley (1985), with the exception that the north Pacific is divided into three stocks (north-west Pacific, central, and north-east Pacific) instead of two. Humpback whales off Iceland are referred to the north-west Atlantic stock (Katona and Beard, 1990).
5. Blue (excluding pygmy blue) whale – Gambell (1979).

It must be stressed that these stock divisions are based on data of very varied nature and quality. Some, such as the bowhead and gray, are fairly non-controversial and based on good biological information, others, such as the blue whale, are extremely tentative, and mostly based on analogy with other species because (*inter alia*) breeding grounds have never been identified for this species in most oceans.

In Table 1 the history of legal protection for each species is listed by ocean region. Two points to be borne in mind are that, first, not all active whaling nations in a region immediately acceded to these international conventions, and some members "opted out" of protection by objecting to the provision, as they were entitled to do in terms of the Convention. For example, Japan and the USSR did not accede to the 1931 Convention for the Regulation of Whaling (CRW) or the 1937 Agreement for the Regulation of Whaling (ARW), and continued to take gray and right whales in the north Pacific and humpback whales in the Antarctic (during periods of protection in 1938/1939–1939/1940) until both nations joined the International Whaling Commission (IWC) in 1946; Iceland and Denmark objected to the 1955 IWC provision protecting blue whales in the north Atlantic, and Iceland continued taking blue whales until 1959. Second, some signatories to the Conventions were amiss in extending provisions to their local regulations (South Africa, for instance, only protected right whales in 1940), while others were less than scrupulous in their observance of the legal provisions for protection (the taking of right whales by a Soviet factory ship at Tristan da Cunha in the 1960s – Best (1988) – is perhaps the best known example). Hence the dates of legal protection frequently do not coincide with the actual cessation of catching.

In addition, both the CRW and IWC contained provisions which permitted the taking of right (including bowhead) whales by aboriginal peoples, and the IWC a provision allowing the taking of gray (and later humpback whales) by or on behalf of aboriginal peoples, despite legal protection from other forms of whaling.

Status of stocks

The aspects of each putative stock reviewed below include not only estimates of current population size, and determination of whether it has been or is currently being monitored for trends in abundance, but also an assessment of whether, given the distribution and habitat of the whale, it is feasible to expect monitoring to take place. In addition, an indication is given where there is circumstantial evidence (such as from incidental sightings) that a recovery might be taking place even if no systematic monitoring has been undertaken. Although this latter inference is inevitably somewhat subjective, it is just such evidence that frequently leads to the initiation of a monitoring programme, so that it is important in evaluating the degree of self-selection.

Bowhead whales

Of the four putative stocks of bowhead whales, only one, the Bering/Chukchi/Beaufort Sea stock, has been systematically monitored and a statistically significant rate of

Table 1. Dates and instruments of legal protection by ocean region for severely depleted stocks of baleen whales (note: in the southern hemisphere, "1919" refers to the 1918/1919 pelagic season, etc.). [CRW = Convention for the Regulation of Whaling, Geneva; ARW = International Agreement for the Regulation of Whaling, London; IWC = International Convention for the Regulation of Whaling, Washington; PCSP = Permanent Commission of the Conference on the Use and Conservation of the Marine Resources of the South Pacific, Santiago].

	Ocean region								
	North Atlantic			North Pacific			Southern hemisphere		
Species	Date	Instrument	Area	Date	Instrument	Area	Date	Instrument	Area
Bowhead	1935	CRW 1931*	Entire	1935	CRW 1931*	Entire	–		–
	1938	ARW 1937	Entire	1938	ARW 1937	Entire	–		–
	1948	IWC 1946*	Entire	1948	IWC 1946*	Entire	–		–
Right	1935	CRW 1931*	Entire	1935	CRW 1931*	Entire	ca. 1922	(Local)	Falkland Islands
	1938	ARW 1937	Entire	1938	ARW 1937	Entire	1935	CRW 1931*	Entire
	1948	IWC 1946*	Entire	1948	IWC 1946*	Entire	1938	ARW 1937	Entire
							1948	IWC 1946*	Entire
							1952	PCSP 1952*	Chile, Peru, Ecuador
Gray	–	–	–	1938	ARW 1937	Entire	–	–	–
				1948	IWC 1946*	Entire			
Humpback	1955	IWC 1946*	Entire	1966	IWC 1946	Entire	1919	(Local)	South Georgia (limited)
							1922–1926	(Local)	South Georgia (total)
							1939–1955	ARW 1937, IWC 1946	S of 40° S, 70–160° W
							1939–1940	ARW 1937	S of 40° S
							1942–1949	ARW 1937	S of 40° S
							1955–1963	IWC 1946	S of 40° S, 0–70°(60°) W
							1964	IWC 1946	Entire
Blue	1955	IWC 1946	Entire	1966	IWC 1946	Entire	1939–1955	ARW 1937, IWC 1946	S of 40° S, 70–160° W
							1964	IWC 1946	S of 40° S except N of 55° S, 0–80° E
							1966	IWC 1946	S of 40° S
							1968	IWC 1946	Entire

*Exemption provided for taking by, or on behalf of, aboriginal peoples.

increase demonstrated (Zeh *et al.*, 1991). The most reliable estimate of recent stock size is 7500 in 1988 (Raftery and Zeh, 1991).

The remaining three bowhead whale stocks are classified as essentially impractical to monitor, given the harsh and relatively inaccessible nature of their habitat; the census series for the Bering/Chukchi/Beaufort Sea stock has only been possible because of the expenditure of "millions of dollars" (Broadhead, 1990), something which is highly unlikely to occur in the other stock areas of the species. The dramatic effect that systematic surveys can have on perceptions about the status of such stocks is shown in Figure 1. In 1978, at the initiation of the census series, the perception of the Bering/Chukchi/Beaufort Sea stock of bowheads was that it was of the order of 600–2000 animals, with a best estimate of 1300 whales (Tillman, 1980); 10 years later the most reliable estimate is 7500 whales (Raftery and Zeh, 1991). Extrapolating backwards given the observed rate of increase over that time period suggests that the 1978 population was probably of the order of 5500 whales – or more than four times the best estimate of perceived abundance at that time.

The status of the Davis Strait/Hudson Bay population is controversial. Although Davis and Koski (1980) estimated that the population was in the low hundreds at most, more recent data indicate that the population is larger than was previously believed, in the low hundreds "at least" rather than "at most" (Zeh *et al.*, in press). An increase in sightings during the 1970s was attributed largely to increased searching effort (Davis and Koski, 1980), but the recent appearance of numbers of bowheads in areas (such as south-western Hudson Bay) where they have not been seen since the end of commercial whaling is a cause for cautious optimism; Zeh *et al.* (in press) agree with Davis and Koski (1980) that the recovery "has been at best, exceedingly slow". As regards the Hudson Bay "component" of the stock, Reeves and Mitchell (1990) conclude that while much of the former range is still occupied by at least a few tens of whales, without focused surveys at appropriate seasons and places it is impossible to evaluate current total abundance. These authors also point out that continued low-level hunting by Inuit in eastern Canada since the cessation of commercial whaling in 1915 (and which lasted until at least 1976 – Mitchell

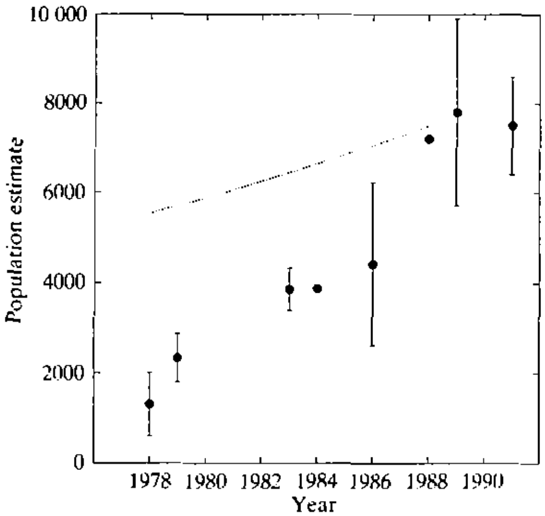

Figure 1. Estimates of population size for the Bering/Chukchi/Beaufort Sea stock of bowhead whales, plotted against the year of assessment. Dotted line indicates the likely trend in actual population size over the same period.

and Reeves, 1982) has probably inhibited the population's recovery.

The Okhotsk Sea stock has been estimated to number 150–200 animals (Berzin *et al.*, 1986), although Zeh *et al.* (in press) consider this likely to be an underestimate. There was no apparent increase in numbers between 1967 and 1984.

Sightings of bowhead whales in the Spitsbergen stock area still occur, and although these have been attributed to strays from other stocks (Jonsgard, 1981), Zeh *et al.* (in press) agree with Christensen *et al.* (1992) that there is still a small remnant population. Wiig (1991) notes that if all the observations of bowheads reported by Belikov *et al.* (1989) in the vicinity of Franz Josef Land are correct (including about 100 in autumn 1981 and 1983), the status of this stock seems to be better than earlier believed.

Right whales

As no winter calving grounds close to shore have been identified for right whales in either the north-west or north-east Pacific (Scarff, 1986), and the summer feeding areas seem remote from the shore, I have not considered either stock as feasible to monitor. In the north-west Atlantic the situation is different in that at least some of the summer feeding area is close to the eastern seaboard of the USA and Canada, and some winter nursery areas in coastal waters of the south-eastern USA have been discovered. On the assumption that a similar pattern might exist for the north-east Atlantic, I have included both stocks as potentially feasible to monitor.

In practice, only one northern right whale stock (that in the north-west Atlantic) has been extensively investigated recently. Estimates of population size range from a minimum count of 240 to a sighting estimate of 493, with very wide confidence intervals (Kraus *et al.*, 1988). Kraus *et al.* attribute the apparent increase in right whale sightings over the past 20 years to increased observer effort. Although they suggest that the population may be displaying a slow rate of growth, their conclusion is that all the survey data collected to date are too imprecise to identify any increase or decrease in this population, although the number of "recruits" to the population of identified animals each year (excluding calves) is very low. Kraus (1990) considered that mortality from anthropogenic sources (ship strikes, entanglement in fishing gear) might be an important factor inhibiting population growth. However, Kenney (1991) has found a statistically significant increase in the sighting rates of right whales in aerial surveys of the Great South Channel region carried out between 1979 and 1989, although correction factors for possible increased survey effectiveness mean that the actual rate of increase is uncertain. The few recent sightings in the north-east Atlantic suggest that there are very few whales present in that population, although possible wintering grounds on the north-west African coast need to be investigated (Brown, 1986).

The population of north Pacific right whales is believed to be very small, Berzin and Yablokov (1978) estimating that there might be 300–500 whales in the entire north Pacific, of which more must occur on the western than eastern side (Scarff, 1986). According to the latter author, there is no persuasive evidence of an increase in the population(s) in the last 100 years, the increase in sightings during the last 30 years compared to the preceding 60 years being probably the result of greatly increased searching effort and reporting efficiency.

Of the 13 putative stocks of southern right whales, four (western Australia, Argentina, east Africa and west Africa) are being monitored and all have revealed statistically significant rates of increase (Bannister, 1991MS; Payne, Rowntree *et al.*, 1990; Best, 1990b). In practice, the surveys of the South African coastline have crossed the "boundary" between east and west African "stocks" (at 20°E, or Cape Agulhas), so the results of the surveys have been applied to both. Totals of 293 adults and 146 calves have been individually identified off western Australia between 1976 and 1987, although there is no actual estimate of population size (Bannister, 1990). Payne, Rowntree *et al.* (1990) estimated that 99 females (S.E. 18) calved on the Argentine coast in 1986, equivalent to a total population of about 1190 animals. Using a purpose-built mark-recapture model, Best and Underhill (1990) estimated that there were 286 adult females (95% CL 265, 310) in the population supplying the South African coast in 1987; estimates of total population size are not available.

Of the nine remaining stocks, five are considered impossible to monitor systematically, as they are centred round remote islands or oceanic areas where the logistics of such surveys would be very difficult to arrange; these are Campbell Island, Crozet, Kerguelen, central Indian Ocean, and Tristan da Cunha. It is interesting to note that incidental sightings at Campbell Island have been indicative of an increasing trend from 1910–1913 to 1978–1982 (Cawthorn, 1983MS), and circumstantial evidence suggests that right whales increased at Tristan da Cunha from the late nineteenth century to the 1950s, before illegal exploitation in the 1960s substantially depleted the population (Best, 1988). There is very little information about the status of the "stocks" round Crozet, Kerguelen, and the central Indian Ocean, although Robineau (1984) reported that three sightings near the Kerguelen Islands from 1979 to 1982 were the first in the region since 1909, and he considered that these sightings plus the observations in the coastal waters of Crozet reported by Stahl (1982) created the suspicion that the population in this part of the Indian Ocean might be increasing.

The remaining four stocks of southern right whales (Chile, Brazil, New Zealand, and east Australia) all visit the coastline of major continents or islands at some stage in their migratory cycle, and are therefore considered available to be monitored. Sightings of right whales along the Chilean coast led to the view that the species, although considerably reduced in numbers, never completely disappeared from these waters (Aguayo and Torres, 1986). According to Cardenas *et al.* (1987), the population is making a slow recovery (and may be expanding its distribution on the Chilean coast—Yanez *et al.*, 1990); one of the causes of the slow recovery may be the catching of right whales, which continued as late as 1968 [13 being reported as landed between 1952 and that date (Aguayo and Torres, 1986)]. Similarly, sightings of right whales are frequently made on the Brazilian coast (Castello and Pinedo, 1979; Pinedo, 1985; Camara and Palazzo, 1985), from which it has been concluded that a probable recovery might be taking place (Camara and Palazzo, 1985), together with reoccupation of parts of the former range (Pinedo, 1985). This is despite an illegal take of right whales in Brazilian waters from about 1952 till as late as 1973 (Castello and Pinedo, 1979; Palazzo and Carter, 1983MS), in which as many as 20 whales may have been taken in a year (Palazzo and Carter, 1983MS). In New Zealand waters, incidental sightings of right whales between 1915 and 1982 show an increasing trend since 11963, but in the absence of true measures of effort and more rigorous survey methods, it is impossible to state unequivocally that the population has increased (Cawthorn, 1983MS). A similar situation exists in east Australia, where Bannister (1986) has analysed incidental sightings from 1900 to 1982. Before 1960 there were very few sightings recorded, but from 1970 (and particularly since 1975) there has been a marked increase. While reporting effort cannot be quantified, but has presumably increased recently, these data cannot give unequivocal evidence of an increase in the population, although it seems likely that such an increase has occurred.

Gray whales

Both stocks of gray whales are considered feasible to monitor, as they may travel along heavily populated coastlines during some stage of their annual migration. The American stock has been systematically monitored through a series of shore-based surveys on the Californian coast, and a statistically significant rate of increase has been detected (Buckland, in press). The current (1987/1988) stock size is estimated as 21 113 (S.E. 688) animals (IWC, in press). The Asian stock has not been systematically monitored, but there have been no obvious signs of recovery comparable to those for the American stock. A recent review of the catch history of this stock, however, has shown that after a rapid decline in catches from about 100–200 a year in the 1910s to 10–20 a year in the late 1920s (indicating stock depletion), catching in Korean waters did not cease for another 40 years, during which time an average of perhaps 10–20 whales a year were taken (Kato and Kasuya, in press). As these authors conclude, this last phase of catching could have been responsible for suppressing any recovery equivalent to that of the American stock. There have only been five records of gray whales on the Pacific coast of Japan between 1968 and 1990, indicating little if any recovery of this population (Kato and Kasuya, in press). However, Berzin (in press) has documented several sightings of gray whales since 1983 on the assumed summering ground for this stock off north-east Sakhalin Island and in the Tartar Strait between Sakhalin Island and the mainland. These include 34 whales off north-east Sakhalin Island in September 1989, and 17 gray whales in the Tartar Strait in the same year. Berzin (in press) concludes that "we can positively state that there is a gradual increase of abundance and summer area of the Okhotsk-Korean population . . .", for which he estimates the current population as 200 individuals.

Humpback whales

Of the 11 putative stocks of humpback whales worldwide, four are being systematically monitored; those in the north-west Atlantic, Area III (on the east coast of South Africa), Area IV (on the west coast of Australia), and Area V (on the east coast of Australia). Statistically significant rates of increase have been detected in three of them (Katona and Beard, 1990; Sigurjonsson and Gunnlaugsson, 1990; Bannister *et al.*, 1991; Bryden *et al.*, 1990; Paterson and Paterson, 1989), the exception being the east coast of South Africa, where the time series so far consists of only 3 years. In Area V there is an apparent contrast between the eastern and western migratory components of the stock; although there has been no systematic monitoring of humpback whales migrating past New Zealand, incidental sighting data so far fail to suggest an increase such as that seen in eastern Australia, and a limited boat survey of Tongan waters in 1991 failed to reveal a significant increase in density compared to a similar survey in 1979 (Abernethy *et al.*, 1992MS). A small-scale fishery for humpback whales persisted at Tonga after legal protection in 1963, and lasted until 1978. Catch figures for 1973–1978 totalled 35 animals (IWC, 1980), but the struck and lost rate could have been three (or more) whales for each one landed (Anon., 1981). The sex ratio in a sample of the catch was also heavily biassed towards females (25/27 or 92.6%; IWC, 1980), and it is possible that this fishery could have affected the recovery rate of the eastern component of the Area V stock, at least until 1979. In the north-west Atlantic, Katona and Beard (1990) have estimated the population size from a series of annual mark-recapture estimates between 1979 and 1986 as 5505 (95% CL 2888, 8122). On the east coast of South Africa, shore-based surveys in 1990 at Cape Vidal produced provisional estimates of 1802 humpback whales migrating northwards and 1773 southwards (Findlay *et al.*, 1991MS). These figures assume equal day–night migration speeds and include estimates of the proportion missed. Although the time series is too short to detect a trend as yet, it is concluded from a comparison of these numbers with catches at the Durban whaling station immediately prior to protection that this population must have increased since protection (Findlay *et al.*, 1991MS). An independent estimate of 1954 (CV 0.38) from a sighting survey off Mozambique in 1991 presumably refers to the same stock (Findlay *et al.*, 1992MS). On the west coast of Australia a comparison of the sighting rate in 1991 with that in 1963 from commercial spotter aircraft suggests a population size of 3302 animals (Bannister, in press). On the east coast of Australia, Paterson and Paterson (1989) have estimated from the numbers seen (and assuming equal day–night migration speeds) that 1107 whales passed on the northward migration in 1987.

Of the seven remaining stocks, one (Arabian Sea) is considered impossible to monitor at this stage, as very little is known of its distribution or patterns of migration (Reeves *et al.*, 1991).

The remaining six stocks (north-east Atlantic, north-west Pacific, central-north Pacific, north-east Pacific, Area I and Area II) are considered available for monitoring, in that they are known or believed to occur close to major continental masses or islands during at least some stage of their annual migrations. There is no certain evidence of the location of the breeding areas of the north-east Atlantic stock (or the migration routes to and from them); it is possible that they breed in the vicinity of the Cape Verde Islands, and humpback whale song has been recorded there (Katona and Beard, 1990), or they may in fact form a feeding aggregation of the north-west Atlantic stock (Christensen *et al.*, 1992). Sighting surveys in the Norwegian and Barents Seas produced estimates of 1025 (CV 0.31) in 1988 and 700 (CV 0.59) in 1989; Christensen *et al.* (1992) conclude that there are "approximately 1000 individuals" in this population. In the north-west Pacific (the population wintering south of Japan), humpback whales were greatly reduced by commercial whaling, but recent sightings indicate that the species is returning to the Bonin and Ryukyuan winter grounds (Uchida, 1991; Helweg *et al.*, 1990). Darling (1991) estimates that there may be 500–1000 animals in the region. Estimates of population size for the central-north Pacific stock wintering round Hawaii (and generally considered to be the biggest in this ocean) are highly variable and not always comparable; this has complicated any analysis of trend. Baker and Herman (1987) consider their most reliable estimate to be 1407 (95% confidence limits 1113, 1701) animals over the period 1980–1983. This compares with an earlier estimate of 895 (95% confidence limits 592, 1837) calculated by Darling *et al.* (1983) for the years 1977–1979. For the north-east Pacific stock, wintering off Mexico, Urban *et al.* (1989) have identified 588 individuals, giving a population estimate of "around 1000 whales". Forney and Barlow (in press) have made a provisional estimate from aerial surveys of 402 (CV = 0.42) humpback whales on the Californian coast in winter; this is almost certainly an underestimate because it makes no allowance for whales submerged during the overpass by the aircraft. Baker *et al.* (1992) estimated the number of humpback whales on the summer feeding grounds in south-eastern Alaska in 1986 as 547 (95% confidence limits 504, 590), but these are presumably included in the estimates of the Hawaiian or Mexican breeding populations given above. Although the total north Pacific population of humpback whales is estimated to have been "no more than 1000 animals" at the time it received international protection, which would therefore indicate that some overall recovery must be taking place, Perry *et al.* (1990) conclude that the extent to which it has recovered over the last 20 years "is a controversial question at present". Baker *et al.* (1992), however, conclude that the south-eastern Alaska feeding aggregation increased between 1979 and 1986 at a rate of between 3.4 and 10.4%; as whales from this feeding ground migrate to both Hawaii and Mexico (Baker *et al.*, 1986), it is possible that both the eastern and central-north Pacific stocks are increasing.

In the southern hemisphere, humpback whales in Area I (60–120°W) of the Antarctic are generally assumed to overwinter off the western seaboard of South America, a conclusion supported by a recent record of an individual migrating from the Antarctic Peninsula (64°20'S 62°27'W) to the coast of Colombia (2°57'N 78°12'W) (Stone *et al.*, 1990). Protection to the species was finally afforded in this region later (1967 in Peru, 1970 in Chile) than elsewhere in the southern hemisphere. Between 1986 and 1988 a total of 108 individuals has been identified off equatorial Colombia, the seasonality of which suggests a southern hemisphere population. Mark-recapture estimates indicate a population size of 107–450 individuals (Florez-Gonzalez, 1991). There is also the possibility (as discussed by Stone *et al.*, 1990) that some whales from this feeding ground move to the eastern seaboard of South America, but it is generally assumed (e.g. Mackintosh, 1942) that this wintering ground is supplied by whales from Area II (0–60°W). Humpback whales in the south Atlantic as a whole were very heavily depleted early in the history of the Antarctic fishery, so that there is little information available on stock identity. It has in fact been suggested that whales feeding in Area II could also migrate to the west coast of Africa (Mackintosh, 1942). Humpback whales are currently found overwintering in the Abrolhos Bank area off Brazil, where Siciliano and Lodi (1989) record sightings of 127 whales; no population estimates are available, and although whaling for the species in Brazil continued until at least 1967, Siciliano and Lodi conclude that the recent increase in records of humpback whales along the Brazilian coast probably reflects a population increase, and a possible recovery of its geographic distribution. On the west coast of South Africa, where catches at the Donkergat whaling station in the 7 years prior to protection averaged only five animals per season (Best, 1974), the current level of incidental sightings is such that the population must clearly have recovered to some extent (pers. obs.). There are no estimates of population size, however, and it is unclear whether these animals are spending the summer in Antarctic Areas II or III.

From sighting surveys between 1978/1979 and 1990/1991 in the high latitudes of the Antarctic in summer, Butterworth *et al.* (in press a) estimate that there are 20 000 humpback whales south of 30°S, but the coefficient of variation for this estimate is quite large (0.38).

Blue whales

Of the 10 putative stocks of blue whales, only one, the north-east Atlantic stock, has been monitored through sightings made from whaling boats on the Icelandic whaling grounds, using indices of relative rather than absolute abundance (Sigurjonsson and Gunnlaugsson, 1990). Although Gunnlaugsson and Sigurjonsson (1990) considered that an upper bound to the population size in this region was 442 animals, Christensen *et al.*, (1992) state that a more recent survey indicates a higher number, possibly in excess of 1000 whales. This is considered a relatively discrete feeding population; large areas of major prior exploitation of blue whales in the north-east Atlantic still hold few whales of this species (Sigurjonsson and Gunnlaugsson, 1990).

Of the remaining nine stocks, seven (the north-west Pacific, central-north Pacific, and Areas I, II, III, IV, and V in the Antarctic) are considered not feasible to monitor, as they are too remote from inhabited continents throughout their migratory range to be readily accessible for surveys. An estimate of abundance for the total Antarctic, based on sighting surveys from 1978/1979 to 1990/1991, is 710 (CV 0.64) (Butterworth *et al.*, in press a).

Blue whales are being studied in both of the remaining stock areas. In the north-west Atlantic, Sears *et al.* (1990) have individually identified 203 blue whales in the Gulf of St Lawrence, Canada, between 1979 and 1988, but the data do not lend themselves to estimation of population size or trend (Hammond *et al.*, 1990). In the north-east Pacific, Calambokidis *et al.* (1990b) have individually identified 179 blue whales in the Gulf of Farallones region of central California between 1986 and 1988. Blue whale numbers increased in the study area during the 3 years of research, continuing an increase that began in the late 1970s or early 1980s; the reason for this increase is not clear but could be a response to protection and/or a shift in distribution (Calambokidis *et al.*, 1990b). Reilly and Thayer (1990) reported on 211 sightings of 355 blue whales made in the eastern tropical Pacific from 1975 to 1988; over 90% of the sightings were made in two areas, along Baja California (presumably a segment of the population that migrates seasonally into central Californian waters) and in the vicinity of the Costa Rica Dome near 9°N, 89°W. The latter area was occupied year-round, and its links with other populations (if any) remain obscure (Reilly and Thayer, 1990). Wade and Gerrodette (in press) have estimated the size of the population of blue whales in the eastern tropical Pacific as 1415 (95% confidence interval 1078, 2501), and quote Barlow (pers. comm.) as giving an estimate from shipboard surveys off the coast of California of 2364 whales. As the two surveys took place at the same time of year, a combined estimate for the north-east Pacific might be 3779.

Rates of increase

In Table 2 the rates of increase observed in monitored stocks are presented for one stock of bowhead whales, three stocks of right whales, one stock of gray whales, three stocks of humpback whales, and one stock of blue whales. Although a statistically significant rate of increase has been detected for the north-west Atlantic stock of right whales, this has not been included here because a correction factor for increased search effectiveness has only been incorporated in a preliminary manner (Kenney, 1991). Where there are independent estimates of the increase rate (from entirely different data sets, for instance, or for different components of the population), these have been included. Also listed are the "depletion levels" (the current stock size expressed as a percentage of the initial, unexploited population), where these have been estimated.

Table 2. Increase rates in severely depleted stocks of baleen whales (values in brackets refer to rates including an allowance for hunting mortality).

Species	Stock	Method	Period of monitoring	Increase rate	95% CL	Propn of initial	Source
Bowhead	Bering/C/B	Shore counts	1978–1988	0.031 (0.034)	0.01, 0.062		Zeh *et al.* (1991)
						0.44–0.65	IWC (1992)
Right	West African/ east African	Aerial counts (cows and calves)	1971–1987	0.068	0.046, 0.09		Best (1990b)
						ca. 0.03	Butterworth and Best (1990)
		(other adults)	1971–1987	0.067	0.048, 0.086		Best (1990b)
						ca. 0.03	Butterworth and Best (1990)
	Argentine	No. of calvings	1974–1986	0.073	0.039, 0.108		Payne *et al.* (1990)
	W Australia	Aerial counts (cows and calves)	1977–1988, 1990	0.127	0.076, 0.178		Bannister (1991MS)
		(other adults)	1977–1988, 1990	0.127	0.053, 0.201		Bannister (1991MS)
Gray	American	Shore counts	1967/1968–1987/1988	0.034 (0.045)	0.024, 0.044		Buckland (in press)
						0.70–0.88	Butterworth *et al.* (in press)*
Humpback	NW Atlantic	Mark/recapture	1979–1986	0.094	−0.12, 0.30		Katona and Beard (1990)
	NW Atlantic	Shipboard counts	1979–1988	0.138	0.114, 0.162		Sigurjonsson and Gunnlaugsson (1990)
	W Australia	Aerial counts	1977–1988	0.088	0.030, 0.146	0.16–0.21	Bannister *et al.* (1991)†
	E Australia	Shore counts	1981–1987	0.144	?	0.11	Bryden *et al.* (1990)‡
	E Australia	Shore counts	1981–1987	0.097	0.06, 0.13	0.11	Paterson and Paterson (1989)‡
Blue	NE Atlantic	Shipboard counts	1979–1988	0.051	0.026, 0.076		Sigurjonsson and Gunnlaugsson (1990)

*Corresponds to multiples of historical catches by a factor of 1.5 to 2.5, which in turn provides an estimated recent population growth rate from a simple model ranging from 0.013 to 0.030.
†Based on estimated original population size for Area IV of 12 000–16 000 (Chittleborough, 1965), population estimate for 1991 of 3302 (Bannister, in press), and assuming population growth rate 1977–1991 of 0.088.
‡Based on estimated original population size for Area V of 10 000 (Chittleborough, 1965) and a 1987 estimate of 1100 (Paterson and Paterson, 1989).

Not shown are other estimates of increase rate derived for the same stocks from either different methods of analysing the same data sets, or from somewhat different (but not totally independent) data sets to those in Table 2. These have usually been considered by the authors as not as reliable as the estimates shown in Table 2 (for the reasons listed under Remarks), but have been included here in Table 3 for the sake of completeness, and to avoid suggestions that the increase rates in Table 2 are a biased selection.

The time series over which these estimates were made varied from 7 (east Australian humpback) to 21 years (American gray whale). Average increase rates calculated over longer time series might be expected to be somewhat less than those calculated over shorter periods, given that longer time series are more likely to include a period of a reduction in growth rate. However, analysis of the longest time series in Table 2 (that for American gray whales) has indicated that the census data are inadequate to detect a curvature in the population trajectory (IWC, in press), so that this is not considered likely to be a significant source of bias.

The two lowest rates of increase in Table 2 are for stocks that were subjected to an "aboriginal" take during the period of monitoring, namely the Bering/Chukchi/Beaufort Sea stock of bowhead whales and the American stock of gray whales. Consequently, the observed rates of increase for these stocks should be adjusted upwards to account for the excess mortality. This has been done by taking the average catch over the period of monitoring and expressing it as a proportion of the population size estimate nearest to the middle of the monitoring period; this proportion is then added to the observed average rate of increase. This procedure assumes that the age and

Table 3. Alternative estimates of increase rate in severely depleted stocks of baleen whales.

Species	Stock	Method	Remarks	Years of surveys	Increase rate	95% CL	Source
Bowhead	Bering/C/B	Shore counts	Omitting one year at a time	1978–1988	0.015–0.042		Zeh *et al.* (1991)
			Smaller probability of missing whales	1978–1988	0.027	−0.002, 0.057	Zeh *et al.* (1991)
Right	West African/ east African	Aerial counts (cows and calves)	Expressed as whales per survey hour	1971–1987	0.069	0.045, 0.092	Best (1990b)
		(other adults)	Expressed as whales per survey hour	1971–1987	0.086	0.070, 0.102	Best (1990b)
	W Australia	Aerial counts (cows and calves)	Smaller survey area	1977–1988, 1990	0.139	0.068, 0.21	Bannister (1991MS)
		(other whales)	Smaller survey area	1977–1988, 1990	0.099	0.011, 0.187	Bannister (1991MS)
Humpback	NW Atlantic	Shipboard counts	Longer, cruder time series	1970–1988	0.115	0.073, 0.157	Sigurjonsson and Gunnlaugsson (1990)
	W Australia	Aerial counts	Different year combinations	1963–1988	0.063	0.033, 0.093	Bannister *et al.* (1991)
				1963–1988	0.050	0.024, 0.076	Bannister *et al.* (1991)
				1963–1988	0.060	0.032, 0.088	Bannister *et al.* (1991)
				1977–1988	0.095	0.037, 0.153	Bannister *et al.* (1991)
				1982–1988	0.067	−0.011, 0.145	Bannister *et al.* (1991)
Blue	NE Atlantic	Shipboard counts	Longer, cruder time series	1969–1988	0.048	0.019, 0.077	Sigurjonsson and Gunnlaugsson (1990)

sex composition of the kill is similar to that of the population being monitored, and that the entire hunting mortality is additive. As both populations were subject to an aboriginal hunt, where commercial incentives for selection of particular size classes are presumably non-existent, the first assumption would seem reasonable. Likely rates of natural mortality (5–10%) are also so low as to make a correction to the effective kill rate extremely small. The adjustments for hunting mortality therefore effectively increase the bowhead recovery rate by 0.03/0.31 or 10%, and the gray whale recovery rate by 0.011/0.034 or 32%. Holt (1992) has criticized the increase rate for blue whales in the north-east Atlantic on the grounds that it is internally inconsistent and confounded by changes in the location of whaling operations over time. Holt compares the increase rate for the period 1979–1988 calculated from a crude time series (0.028) with that calculated from a much more refined analysis (0.051, S.E. 0.011), and points out that because the former rate (which is not significantly different from zero) lies outside the confidence limits of the latter, that it is non-confirmatory evidence. However, the 95% confidence limits for the refined data (± 2.3 (0.011), d.f. = 8) actually include the increase rate from the cruder time series. Holt also draws attention to the wide variation in increase rates in different parts of the whaling ground, and speculates that this might be due to segregation by age or sex or both. However, similar differences in increase rates have been demonstrated for coastal right whales on a much finer geographical scale than this (Best, 1990b), and the critical issue is not the internal consistency but whether the overall increase rate is representative of the population. As Sigurjonsson and Gunnlaugsson (1990) have described the blue whales off Iceland as a relatively discrete feeding population, with very few sightings elsewhere in the north-east Atlantic, it seems reasonable to conclude that the observed rate is representative of the population.

In general, the observed rates of increase (ranging from 0.031 to 0.144) are much higher than the range of 0.01 to 0.04 often referred to in reports of the Scientific

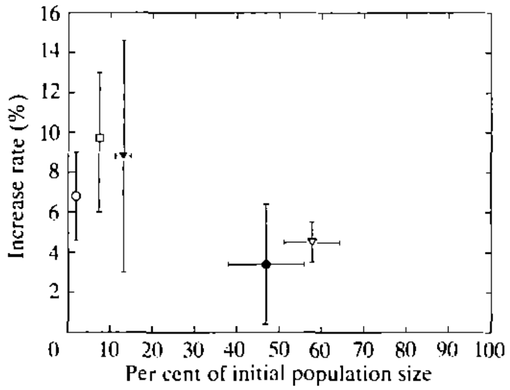

Figure 2. Increase rates recorded for five stocks of severely depleted baleen whales (open circle – east/west African right whales; open square – east Australian humpback whales; solid triangle – west Australian humpback whales; solid circle – Bering/Chukchi/Beaufort Sea bowhead whales; open triangle – American gray whales). These have been adjusted for fishing mortality where appropriate, and plotted against the estimated level of depletion of the population (from its initial level) at the midpoint of the time series of surveys from which increase rates were calculated.

Committee to the International Whaling Commission as the "possible" or "likely" range of maximum net recruitment rates for baleen whales (Butterworth and Punt, 1992). This is not surprising, as many of the stocks must be considered well below any reasonable estimate of the level giving maximum net productivity (conventionally referred to as the MSY level, or MSYL), and so can be expected to be exhibiting *per capita* growth rates near their maximum. Appropriate interpretation of the observed increase rates in fact requires some associated measure of stock depletion, and this is only available for five of the stocks in Table 2; the Bering/Chukchi/Beaufort Sea stock of bowhead whales, the west African/east African stock of right whales, the American stock of gray whales, and the Area IV and Area V stocks of humpback whales (Fig. 2). Clearly, as these increase rates involve four different species, and there are large (or sometimes unknown) errors associated with some of the estimates, it would be imprudent to draw any conclusion from these data over the shape of a general stock recruitment curve for baleen whales, except to say that, as expected, the more depleted stocks/species show greater rates of increase than those less depleted.

The magnitude of the increase rates estimated for some of the more depleted stocks raises the question of whether they are in fact biologically feasible. An upper limit to the maximum possible growth rate for a cetacean population is set by its gross recruitment rate, or the birth rate per head of population. If equal numbers of male and female calves are born, and on the assumption that they all survive to maturity, then the gross recruitment rate would be equivalent to half the pregnancy/birth rate of mature females times the proportion of mature animals in the population. Accurate estimates of pregnancy/birth rate and the proportion of mature animals in the population, however, are not easy to obtain. Pregnancy rate data from commercial whaling operations can be affected by selection against lactating females, differential migration of pregnant and non-pregnant females, and incomplete reporting of foetuses (where the data were not collected by a biologist). For these reasons data on calving intervals of known females could be considered as being more reliable, although based on much smaller sample sizes and (in some cases) subject to a potential negative bias where sighting histories between calves are incomplete (Table 4). Direct estimates of the proportion of mature animals in the population are even more intractable, given the segregation by size, sex, or reproductive status frequently seen, and (in the case of commercial whaling operations) the exclusion of smaller animals because of size selection. Indirect (i.e. model-derived) estimates are obviously dependent on the values used for age at maturity and survival rate, the value of the latter for juveniles in particular being very difficult to obtain. The most intensive attempt to measure this parameter directly has been made for the Bering/Chukchi/Beaufort Sea stock of bowhead whales, where photogrammetric surveys have enabled the size composition of the population to be examined. Zeh *et al.* (in press) conclude that the best available data strongly suggest a population in which half or fewer of the animals are sexually mature.

Estimates of gross recruitment rate, using a proportion mature in the population of 50% and an equal sex ratio of calves, are shown in Table 4. Those for bowhead and gray whales substantially exceed observed rates of increase, as might be expected given that the populations of these animals are well above levels at which maximum rates would be expected. Reilly (1984) earlier calculated a maximum rate of increase for gray whales of 0.067, but this assumed no density dependence in adult survival. For right whales off South Africa and Argentina, observed increase rates are virtually identical to maximum possible rates calculated in this way. This is consistent with independent analyses which showed that such increase rates were only possible if mortality rates and/or ages at maturity were less than normally assumed for large cetaceans (Best, 1990c; Payne *et al.*, 1990). On the other hand, right whale increase rates of the order of 0.13, as recorded for west Australia, would seem to be unlikely from this analysis, without proposing some degree of immigration; the survey flights in question did not cover the known distribution on the coast, and during the time series an increasing proportion of sightings was made in the easternmost blocks of the survey area (Bannister, 1990). Thus, although the wide confidence limits of the west Australian estimates do not exclude more "realistic" increase rates, they have not been considered further here. For humpback whales the increase rates reported range from 0.088 to 0.144, while

Table 4. Estimates of likely maximum gross recruitment rates for severely depleted stocks of baleen whales.

Species	Birth rate (= 1/calving interval)	Source	Gross recruitment rate
Bowhead	0.172–0.303	Miller *et al.* (1992)	0.043–0.076
Right	0.275–0.318	Bannister (1990), Payne *et al.* (1990)	0.069–0.080
Humpback	0.426–0.441	Clapham and Mayo (1990)*	0.106–0.110
Gray	0.444–0.474	Jones (1990)†	0.111–0.118

*Alternative calving intervals calculated with or without intervals with incomplete sighting histories.
†Alternative calving intervals calculated with or without four females with incomplete sighting histories.

calculated maximum gross recruitment rates are around 0.11. The value of 0.144 for east Australia thus seems somewhat high, and as there is no associated standard error, the alternative estimate for this stock of 0.097 (95% confidence limits 0.06, 0.13) is preferred. The value of 0.138 for the north-west Atlantic humpback whale is also high, although its lower confidence limit (0.114) is close to the likely maximum rate of gross recruitment given here. As an alternative rate for this stock (of 0.094, but with very wide confidence limits) is available, it is also preferred.

Discussion

The argument that those stocks for which an increase rate has been calculated are a self-selected sample is based on the hypothesis that, given heavily depleted stocks of a similar size at protection, those that grow faster will reach a population size large enough to be monitored before those that grow slower.

This review of the status of the stocks of severely depleted baleen whales shows that of the 44 putative stocks worldwide of five species, 18 (41%) are classified as not feasible to monitor (Table 5). Of the remaining 26 stocks, 12 (46%) have been or are being monitored since protection; statistically significant rates of increase have been demonstrated for 10 (83%) of them, and in both of the remaining two it is believed that an increase has occurred but either the time series is too short to measure its rate, or further analysis of changes in searching efficiency need to be made. This means that of the monitorable stocks, 12 (or 46%) are increasing or believed to be increasing. The critical question in regard to self-selection is whether the failure to document an increase (in effect, to initiate a monitoring programme) in the remaining 14 stocks is due to their small size and/or their failure to increase.

Unfortunately, estimates (or even indications) of stock size are available for only half these populations (Table 5). The Asian stock of gray whales is estimated as 200 individuals, the Area I humpback population as 107–450, the north-west Pacific humpback whale population as 500–1000, the north-east Atlantic and north-east Pacific stocks of humpback whales as approximately 1000, the central-north Pacific (Hawaiian) population of humpback whales as 1407, and the north-east Pacific stock of blue whales as 3779. Three of the last four are of the same order as estimates of population size for the Argentine right whales and humpback whales off the east coasts of South Africa and Australia, while the fourth (the north-east Pacific blue whale population) is of the same order as the Area IV stock of humpback whales, all of which are being monitored and for three of which at least rates of increase have been estimated. The north-west Pacific humpback whale population is of the same order as the estimated size of the north-east Atlantic blue whale population and larger than the number of adult female right whales in the east/west African populations, for all of which rates of increase have been measured. Furthermore, some of these stocks may initially have been rather small; the Korean stock of gray whales, for example, has been estimated to have been only some 1000 to 1500 whales in 1910 (Rice and Wolman, 1971). Hence, in at least some of the monitorable but unmonitored stocks, small present population size alone does not necessarily seem to have been responsible for the failure to begin monitoring, nor indeed does it necessarily imply a failure to recover. However, it is unlikely that any of these populations are as abundant as, for instance, the American stock of gray whales (21 000 animals), although it should be pointed out that at the inception of monitoring, the second biggest severely depleted stock (the Bering/Chukchi/Beaufort Sea bowhead whales) was believed to be only 600–2000 animals (within the range of some of the unmonitored stocks here).

Is there any evidence that the monitorable but unmonitored stocks have failed to show signs of a recovery? At least eight (or 57%) of the 14 such stocks are in fact suspected to be increasing. Hence, the failure to institute a monitoring programme also does not necessarily imply that these stocks are not increasing. It is as likely to reflect a lack of resources or a redirection of research priorities in those areas.

It is also possible, however, that such a failure reflects difficulties in obtaining representative and unbiased indices of population abundance. Of the 13 increase rates

Table 5. Summary of status of severely depleted stocks of baleen whales (see text for sources).

Species	Stock	Considered monitorable?	Being monitored?	Increase: Measured?	Increase: Suspected?	Current stock size
Bowhead	Bering/Chukchi/Beaufort	Yes	Yes	Yes		7500
	Davis St/Hudson Bay	No			No	"low 100s at least"
	Okhotsk Sea	No			No	150–200
	Spitsbergen	No			No	~ 100?
Right	NW Pacific	No			No	300–500 (NW and NE Pacific)
	NE Pacific	No			No	
	NW Atlantic	Yes	Yes	Yes?		240–493
	NE Atlantic	Yes	No		No	?
	New Zealand	Yes	No		?	?
	Campbell Island	No			Yes	?
	East Australia	Yes	No		?	?
	West Australia	Yes	Yes	Yes		?
	Central Indian	No			No	?
	Kerguelen	No			Yes?	?
	Crozet	No			Yes?	?
	East Africa	Yes	Yes	Yes		286 ad females (East and West Africa)
	West Africa	Yes	Yes	Yes		
	Tristan da Cunha	No			Yes	?
	Brazil	Yes	No		Yes	?
	Argentina	Yes	Yes	Yes		1190
	Chile	Yes	No		Yes	?
Gray	American	Yes	Yes	Yes		21 113
	Asian	Yes	No		Yes?	200
Humpback	NW Pacific	Yes	No		Yes?	500–1000
	Central N Pacific	Yes	No		Yes?	1407
	NE Pacific	Yes	No		Yes?	~ 1000
	NW Atlantic	Yes	Yes	Yes		5505
	NE Atlantic	Yes	No		No	~ 1000
	Antarctic Area I	Yes	No		No	107–450
	Antarctic Area II	Yes	No		Yes?	?
	Antarctic Area III	Yes	Yes	No	Yes	1954 (Areas I–V: 20 000)
	Antarctic Area IV	Yes	Yes	Yes		3302
	Antarctic Area V	Yes	Yes	Yes		1107
	Arabian Sea	No			No	?
Blue	NW Pacific	No			No	?
	Central N Pacific	No			No	?
	NE Pacific	Yes	No		Yes?	3779
	NW Atlantic	Yes	No		No	?
	NE Atlantic	Yes	Yes	Yes		442–1000
	Antarctic Area I	No			No	
	Antarctic Area II	No			No	
	Antarctic Area III	No			No	710 (Areas I–V)
	Antarctic Area IV	No			No	
	Antarctic Area V	No			No	

listed in Table 2, 10 (or 76.9%) were obtained from shore or aerial counts of migrating whales (bowhead, gray, and humpback), or from counts or mark/recapture estimates of resident components of the population (right whales). In the former, virtually the whole population is available to be counted as it moves past a vantage point, while in the latter, virtually the whole of one component of the population (adult females in a perinatal condition) remains in highly predictable locations for weeks to months of the year. In both cases either the whole population or a fixed component of it is fully represented in either one location over time, or at one time over several locations. This makes obtaining reliable annual indices of population size relatively simple. In the 14 monitorable but unmonitored stocks, however, 10 (or 71.4%) have been studied either on the feeding ground (north-west Atlantic right whales, Asian gray whales, north-east Atlantic humpback whales, north-west Atlantic blue whales, and north-east Pacific blue whales), or on the breeding ground, but not on a specific component of the population (north-west Pacific, Area I and Area II humpback whales), or on both feeding and breeding grounds (central Pacific and north-east

Pacific humpback whales). In none are studies being carried out on the migration route, or on a specific, resident component of the population on the breeding grounds. Localized surveys of abundance in feeding areas can be affected by major shifts in distribution from year to year due to changes in food availability (Payne, Wiley *et al.*, 1990) or oceanographic conditions (Tershy *et al.*, 1991), and by variations in arrival and departure times (Kenney, pers. comm.). On breeding grounds, biases in availability can be caused by temporal stratification of different age classes and sexes, lack of fidelity to (or absenteeism from) the breeding ground, and sex- or age-specific differences in behaviour (Perry *et al.*, 1990). It then becomes very difficult to sample representatively from year to year from such temporally or spatially stratified populations (Baker and Herman, 1987; Calambokidis *et al.*, 1990a; Hammond *et al.*, 1990).

Cato (1991) has pointed out that humpback whales in the north Atlantic and north Pacific are more readily accessible on breeding grounds than on migration paths, and Clapham and Mattila (1990) have shown that some north Atlantic humpback whales adopt oceanic rather than coastal migration routes. If in fact these stocks do not migrate coastally (as is claimed for humpback whales in the western north Atlantic and off the west coast of South America by Winn and Reichley, 1985), or if their breeding ground has not been properly identified (as for blue whales and Asian gray whales), then my definition of a monitorable stock may in fact be too generous, in the sense that for some of these stocks although minimum estimates of population size may be readily attainable, estimates of year-to-year trends in population size are not.

A case can therefore be made for including those unmonitored but monitorable stocks for which an increase is suspected with those for which an increase has been demonstrated, on the grounds that in the former an actual increase rate is likely to be more difficult to measure. If this is done, the ratio of monitorable stocks for which an increase is suspected or demonstrated to those in which no increase is demonstrated or suspected is at least 20:6, or 77%. The argument that the sample of 10 stocks for which rates of increase have been estimated is a self-selected sample thus does not seem very strongly supported by these data.

It is also perhaps pertinent that individuals are still being seen in all the putative stock areas, indicating that extinction of none of these assemblages has occurred.

Butterworth and Best (1990) have attempted to infer possible lower bounds to MSY rates for baleen whale stocks well below MSY level, under the assumption that the curve of *per capita* sustainable yield rate is convex (viewed from above) at all points in the range of population size from zero to the carrying capacity. This so-called "strong convexity" constraint is, according to Butterworth and Best (1990), implied from Fowler's (1981) analysis of demographic factors contributing to the *per capita* increase rate in 27 populations of large mammals; in 22 of these it is said that a convex relationship with population size is indicated, suggesting that MSY level must be above 50% of the initial population size. Under this strong convexity assumption, it can then be deduced that the MSY rate (in terms of total population size) must be more than half the *per capita* sustainable yield rate at very low population sizes.

Adopting this constraint, point estimates for the lower bounds to MSY rates for seven of the heavily depleted populations of baleen whales in Table 2 can be estimated as follows:

right whales –	
west African stock:	−0.034;
east African stock:	−0.034;
Argentine stock:	−0.037;
humpback whales –	
west Australian stock:	−0.044;
east Australian stock:	−0.049;
north-west Atlantic stock:	−0.047;
blue whales –	
north-east Atlantic stock:	−0.026;

These rates range from 0.026 to 0.049, with a mean of 0.039.

De la Mare (1990) has shown through simulation modelling that the effects of bias in absolute abundance estimates on estimates of MSY rate deduced from rates of recovery are least for stocks that are heavily depleted, but at the same time the bias arising from model mis-specification would be highest in such stocks. The effects of model mis-specification can be reduced by monitoring stocks near the MSY level, but here the effects of bias in abundance estimates are much higher, and there is the additional problem of expanding confidence limits of estimates of MSY and MSY rate at around 50–60% of initial population size (i.e. near a likely range for MSY level) – although these effects are much reduced when the real MSY rate is at the higher end of the range 1–4%.

The remaining two stocks, the Bering/Chukchi/Beaufort Sea stock of bowhead whales and the American stock of gray whales, are estimated to be at 0.44–0.65 and 0.70–0.88, respectively, of their original population sizes (Table 2 – see also the third footnote of that table). Butterworth *et al.* (in press b) have shown that, due to selective harvesting of adult females in the past, the current population of adult female gray whales may be somewhat more depleted (0.48–0.69 of initial) than indicated for the total population in Table 2. The population level at which MSY is achieved is unknown for whales. Although it has been considered likely on both evolutionary (Fowler, 1981; Holt, 1981) and systems-level grounds (Fowler, 1980; May *et al.*, 1979) that the MSY level is greater than half the initial population size, there is no basis on which to decide how much greater than half it might be, and the IWC's decision to adopt an MSY level of 0.60 for baleen whales was a somewhat arbitrary way of adopting a more cautious approach to management (Allen, 1981).

Although Gerrodette and DeMaster (1990) deduced from a dynamic response analysis that the gray whale population had actually passed through its maximum net productivity level between 1967 and 1980, or during the series of shore-based censuses, their methodology has been questioned (Butterworth, Borchers, and Punt, in press). Furthermore, if further data points are added to the series their conclusion is no longer so clear cut; Boveng (in press) suggests that the power of this type of analysis is unacceptably low for animal populations with maximum *per capita* growth rates of less than 10% a year and coefficients of variation for censuses of greater than 10%. However, the finding that two populations of baleen whales are exhibiting growth rates (allowing for hunting mortality) of 0.034 and 0.045 while at or just above half their original population sizes suggests that their maximum net productivity may be of a similar order, under the assumption that such a level occurs at about 60% of carrying capacity.

Butterworth and Best's (1990) approach has been criticized by Holt (1990), principally on the grounds that their definition of convexity is unnecessarily restrictive, and that there could still be an upward inflection of the *per capita* increase rate at very small population sizes without altering the "generally convex" nature of the relationship with population size; such an inflection would effectively negate the deduction that the MSY rate must be more than half the increase rate at very low population size.

In a review of animal population dynamics at extremely reduced population levels, Fowler and Baker (1991) dispute the likelihood of an upward inflection in *per capita* increase rates at very low population size, as proposed by Holt (1990). They conclude that the reverse effect, a depression of the capacity for increase (or "Allee effect"), is a general characteristic of the dynamics of animal populations at very low levels. Although the empirical data on population dynamics of large mammals at very low densities is not extensive, it could be expected from evolutionary arguments that most or all of their capacity for increase would be brought out at population levels close to the carrying capacity. The little empirical data available for large mammal populations also indicate that reproduction or survival rates are near their physiological maxima at intermediate population levels, making further increases in *per capita* growth rate at smaller populations very unlikely.

De la Mare and Cooke (1992) propose that whale yield curves could be related to the shape of the "habitat suitability profile", so that a hypothetical population occupying a "basin" of optimal habitat surrounded by suboptimal peripheral habitat would demonstrate a non-linear relationship between increase rate and stock depletion. In this way very high *per capita* rates of population increase at low population levels could still be compatible with low MSY rates for a stock. The fact that whales are highly mobile, wide-ranging animals would seem to suggest that such basin models are inappropriate, although there is evidence that some depleted whale stocks have apparently contracted their range (see below).

Irrespective of the validity of predicting maximum sustainable yield rates from observed rates of increase, the data in Tables 2 and 3 provide greater optimism for the future recovery of the severely depleted stocks of baleen whales than previously existed. The question remains why it has taken so long for such increases to become apparent. This is particularly relevant in the case of bowhead, right, and gray whale stocks, where legal protection has existed for over 50 years. In some of these instances (Asian gray whales, or bowhead whales in the eastern Canadian Arctic, for example), legal protection was not followed by an immediate cessation of all exploitation, so that protection was more apparent than real. In others (the Bering/Chukchi/Beaufort Sea stock of bowheads, for example), a recovery was probably taking place but was not apparent because of the practical difficulties of monitoring the population.

The possibility of this delayed recovery being due to a reduction in net recruitment rate at very low population sizes (an "Allee effect") has been mentioned by several authors, but there is virtually no data to support or deny it. The drop in pregnancy rates of southern blue and fin whales from 1934/1935 to 1945/1946 attributed by Watt (1968) to impaired fecundity resulting from "ruinously hard exploitation" would now be considered very suspect, given the inherent problems with biological data derived from the industry (Best, 1989). Bannister *et al.* (1991) provide some data for humpback whales off western Australia that raise the tantalising possibility that the recovery of this stock may have been somewhat delayed. The recent finding that in the bowhead whale, the age at first parturition may be as high as 20 years (Schell *et al.*, 1989), raises the possibility that in this species at least, long generation time could have created some initial lag in the response to protection.

An alternative hypothesis is that a recovery has been taking place, but that it has not been detected. One reason for this could be a suggested tendency for mysticete populations to condense their ranges to focal areas as numbers are reduced (IWC, 1986b). Such a contraction in present-day compared to historical distribution has been described for bowhead whales (Dahlheim *et al.*, 1980; Miller *et al.*, 1986), right whales (Best, 1981), and blue whales (Sigurjonsson and Gunnlaugsson, 1990). In such cases, monitoring trends in stock abundance is really only feasible in areas of present-day concentrations (or on migration routes thereto), and elsewhere in the historical range there may be little or no sign of recovery. Hence the apparent recovery in some stocks rather than others may to some extent reflect the chance discovery of concentration areas; the right whales of Peninsula Valdes, Argentina, and in the Bay of Fundy, for instance, remained "unknown to science" until 1969 and 1980, respectively (Gilmore, 1969; Reeves *et al.*, 1983).

A second reason for the possible failure to detect a recovery even though it was taking place has been proposed in the case of southern right whales. Best (1988) has suggested that the degree of historical depletion of the stocks may have been generally underestimated, and that the remnant population may have been so small that the initial recovery was virtually undetectable. In the case of the South African population, circumstantial evidence (extremely small catches despite great commercial interest) provides some indirect support for a very low abundance at protection. Although this hypothesis has been criticized as not necessarily being the most parsimonious explanation (Holt, 1990), it has received some support recently in the case of the north-west Atlantic right whale, where the possibility of the population being as low as about 40 animals when protected in 1935 would be the natural conclusion of assuming that the population has been increasing since protection at the best estimate of the current growth rate (Kenney, 1991). Preliminary analyses of genetic material from the present-day population is also consistent with a model that suggests the north Atlantic population was reduced to very few individuals by the early 1900s, and that only a few animals were responsible for the survival of the population for many generations (Brown, 1991).

Thus, for many of the stocks that have been protected for decades without any documented recovery, the hypothesis that a combination of range contraction and underestimation of the extent of depletion has hindered detection of a recovery would seem to be at least as valid a hypothesis as assuming that no recovery has taken place.

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