

Estimation of mortality coefficients and survivorship curves for minke whales (*Balaenoptera acutorostrata*) in Korean waters

Chang Ik Zhang^a, Kyung-Jun Song^{b*} and Jong-Hun Na^a

^aDivision of Marine Production System Management, Pukyong National University, Busan 608-737, Republic of Korea; ^bUniversity-Research Institute Interdisciplinary Program of Fisheries and Oceanography, Pukyong National University, Busan 608-737, Republic of Korea

(Received 22 April 2010; received in revised form 26 July 2010; accepted 27 July 2010)

Population ecological characteristics of growth and mortality play an important role in understanding the population dynamics of marine mammals. The instantaneous coefficients of natural and bycatch mortality were estimated for minke whales (*Balaenoptera acutorostrata*) in Korean waters using a population assessment model composed of bycatch and abundance data. The survivorship curve of this population was fitted to the data, and then the curve was revised using age-specific relative bycatchability coefficients (q_t). Instantaneous coefficients of natural and bycatch mortality of minke whales were estimated as 0.024/year and 0.076/year, respectively, and from this the survival rate was estimated as 0.905. This estimated survival rate was comparable to other cetaceans in other regions. The q_t for this population ranged from 0.020 to 0.193. The revised survival rates were higher when the q_t was taken into account. The mortality coefficient, survival rate, q_t and survivorship curves had not previously been determined for minke whale in this area. This estimate could serve as fundamental information to assess the status of this population and for conservation and rational management.

Keywords: mortality coefficient; survival rate; age-specific relative bycatchability coefficient; survivorship curve; minke whale

Introduction

Minke whales (*Balaenoptera acutorostrata*) are widely distributed in most oceans of the world including Korean waters (Jefferson et al. 1993). It is thought that there are two stocks of minke whales in the western North Pacific, the J stock (East Sea–Yellow Sea–East China Sea stock) and the O stock (Okhotsk Sea–West Pacific stock) (IWC 1983). According to a recent analysis, the abundance of the J stock was estimated at 7600 individuals (coefficient of variation; CV = 0.4) (IWC 1984), and is considered the most abundant baleen whale in Korean waters. Several studies were conducted on Korean minke whales, and included analysis of stock structure (Park et al. 2004), abundance (Gong 1988; Sohn et al. 2001; Park et al. 2009), bycatch (Kim et al. 2004; Kim 2008; Song et al. 2010), and age structure (Na 2005).

This stock was seriously damaged by intensive commercial whaling in the western North Pacific until the moratorium on commercial whaling was imposed in 1986. Unfortunately, since the moratorium, human-induced mortality of minke whales still continuously occurs in Korean waters (Kim 1999, 2008; Kim et al. 2004). According to reports, approximately 100 minke whales per year were bycaught on average (Kim et al.

2004; Kim 2008). Furthermore, based on simulations this stock is predicted to become extinct over the next few decades at this rate (100–150 individuals/year) (Baker et al. 2000).

Large quantities of accurate data on the population dynamics of marine mammals are needed for effective conservation and management. Population ecological characteristics such as the survival rate can play an important role in understanding the population dynamics of marine mammals (Barlow and Boveng 1991; Fujiwara and Caswell 2001). However, the mortality coefficient, survival rate, age-specific relative bycatchability coefficients and survivorship curves for minke whales in Korean waters have not been previously investigated.

The survival rate of marine mammals such as the minke whale can be estimated using age composition data of death individuals from catch and bycatch (Caughley 1966; Ohsumi 1979; Chapman 1983) or age composition data of living individuals based on photo-identification (Barlow and Boveng 1991; Barlow and Clapham 1997). For the minke whale, specifically in the southern hemisphere, several studies estimated instantaneous mortality ranging from 0.06 to 0.15/year (Ohsumi 1979; Chapman 1983). Although several

*Corresponding author. Email: kjsong329@hanmail.net

studies have reported the bycatch of minke whales in Korean waters (Kim 1999, 2008; Kim et al. 2004), there was little effort to investigate population ecological characteristics using these data. Only Na (2005) reported the age structure of minke whales using bycatch data obtained between 2002 and 2004 in Korean waters.

The objective of this study is to estimate the instantaneous coefficients of natural and bycatch mortality for minke whales in Korean waters, and to determine the survivorship curve of this population using age-specific relative bycatchability coefficients (q_t). This includes mechanisms of availability, encounterability, and selectivity for fishing gear.

Materials and methods

To estimate mortality coefficients for minke whales in Korean waters, we used data on bycatch and abundance of minke whales in this area from five years (2000, 2002, 2003, 2005 and 2006) (Figure 1) (Kim et al. 2004; Kim 2008; Park et al. 2009). Generally, the numbers of a cohort at time t are given by the following equation:

$$N_t = N_0 e^{-Zt} = N_0 e^{-(M+BF)t}$$

where N_t is the number at time t , N_0 is the number at time 0, Z is the instantaneous coefficient of total mortality, M is the instantaneous coefficient of natural mortality and it is assumed that M is constant for all ages over time and BF is the instantaneous coefficient of

bycatch mortality. Based on the assumption that the age structure of the bycaught population is representative of the natural or equilibrium state of population, assuming random distribution and random selectivity, we used bycatch data to estimate the mortality coefficient and survival rate of this population. The instantaneous coefficient of natural mortality (M) was estimated from the following equation (Zhang and Megrey 2006), based on the assumption that life history of early stage cetaceans is similar to that of fish:

$$M = \beta K / (e^{k(t_{mb}-t_0)} - 1)$$

where β is the power parameter of the length-weight relationship, K is the von Bertalanffy growth parameter and t_{mb} ($= C_i \cdot t_{max}$; C_i is the constant for each specific ecological group i and t_{max} is the maximum age) is the age at maximum biomass. The instantaneous coefficient of bycatch mortality (BF) was estimated from the following equation:

$$BF = BC/N$$

where BC is the number of bycatch at a given year and N is the abundance at a given year. The instantaneous coefficient of total mortality (Z) and survival rate (S) were estimated from the following equations:

$$Z = M + BF$$

$$S = e^{-Z}$$

The age-specific relative bycatchability coefficients (q_t) for minke whales in this area were estimated from the following equations:

$$BC_t = N_t BF_t (1 - e^{-(M+BF_t)}) / (M+BF_t) \quad (t = 0 \sim t)$$

$$BF_t = q_t BF$$

where BC_t is the number of bycatch at age t (individuals), N_t is the number at the beginning of age t (individuals), BF_t is the instantaneous coefficient of bycatch mortality at age t (/year), M is the instantaneous coefficient of natural mortality (/year), and BF is the instantaneous coefficient of bycatch mortality (/year). The q_t was estimated from the age structure in bycaught minke whales in Korean waters in 2006 ($n = 80$) (Figure 2). The q_t at age 1 (q_1) is assumed as 1.0.

We fitted survivorship curves considering only natural mortality ($N_t = N_0 e^{-Mt}$), or considering both natural and bycatch mortality ($N_t = N_0 e^{-(M+BF)t}$). We then revised the second curve using the q_t ($N_t = N_0 e^{-(M+q_t BF)t}$). We estimated a survivorship curve using the catch curve method based on the assumption that (1) the survival rate for all age classes is constant; (2) the bycatch for each age class is proportional to abundance for each age class; (3) the recruitment for

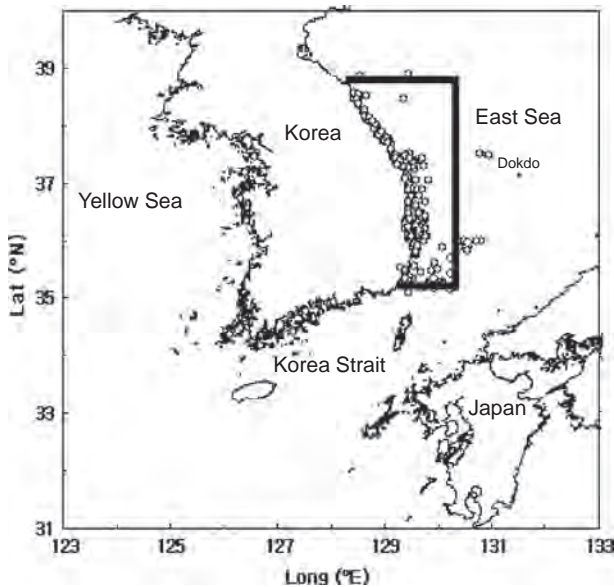


Figure 1. Bycaught sites (circles) of minke whales in Korean waters. The survey block (thick line) depicts the sighting and bycatch survey area.

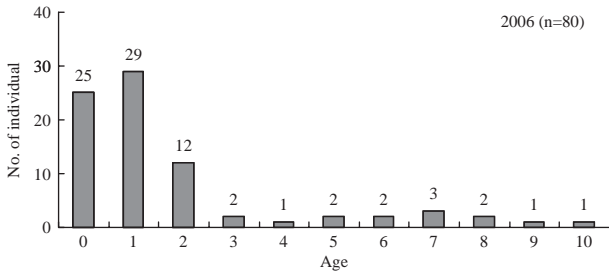


Figure 2. Age distribution of bycaught minke whales in Korean waters in 2006.

each age class is constant; (4) the estimation of age is accurate.

Results

Mortality coefficient and survival rate

The instantaneous coefficient of natural mortality (M) for minke whales in this area was estimated at 0.024/year using the value of β ($= 2.675$; Wang 1985), K ($= 0.167$; Na 2005), t_{mb} [$= C_i$ ($= 0.302$; Zhang and Megrey 2006) $\cdot t_{max}$ ($= 47$; Trites and Pauly 1998) $= 14.194$] and t_0 (t_0 is assumed as 0). The instantaneous coefficient of bycatch mortality (BF) was estimated at 0.076/year using the mean value of BC ($= 73$ individuals; Kim et al. 2004; Kim 2008) and N ($= 959$ individuals; An et al. 2009) during specific periods. As a result, the instantaneous total mortality coefficient (Z) was estimated at 0.100/year using the value of M ($= 0.024$ /year) and BF ($= 0.076$ /year). Also, the overall survival rate (S) was estimated as 0.905 using the value of Z ($= 0.100$ /year).

Survivorship curve

The overall survivorship curve for this population was similar to that of other marine mammals (Spinage 1972) (Figure 3). As expected, survival rates at all ages on the survivorship curve which considered both natural and bycatch mortality were lower than those

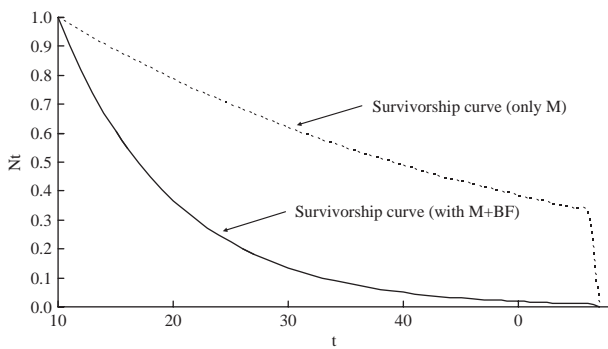


Figure 3. Survivorship curve for minke whales in Korean waters.

of the survivorship curve that considered only natural mortality. However, these survivorship curves have some limitations because of the assumption of a constant age-specific relative bycatchability coefficient.

Age-specific relative bycatchability coefficient (q_t)

The q_t for this population is shown in Figure 4. The q_t for this population ranged from 0.020 to 0.193. The coefficients at old ages were lower than those at young age. These results suggest the possibility that rates of bycatch in young individuals were higher than those of old individuals.

Revised survivorship curve using q_t

The revised survivorship curve for this population using the q_t is shown in Figure 5. Survival rates at all ages are higher on the revised survivorship curve for this population compared to rates using the original survivorship curve (Figure 5).

Discussion

The estimated survival rate (0.905) and instantaneous coefficient of total mortality (0.100/year) of minke whales in our study were similar to those of minke whale in other regions (Table 1). In the southern hemisphere, several studies have shown mortality estimates for minke whales that range from 0.060 to 0.150/year (Ohsumi 1979; Chapman 1983). The estimated survival rate was generally comparable to those of cetaceans in other regions (Table 1). Estimates for individuals younger than 1 year ranged from 0.759 to 0.867 (Wells and Scott 1990; Herzing 1997; Mann et al. 2000; Gabriele et al. 2001; Haase and Schneide 2001; Kogi et al. 2004), and estimates for adult individuals ranged from 0.850 to 0.976 (Ohsumi 1979; Chapman 1983; Buckland 1990; Hersh et al. 1990; Olesiuk et al. 1990; Wells and Scott 1990; Barlow and Clapham 1997;

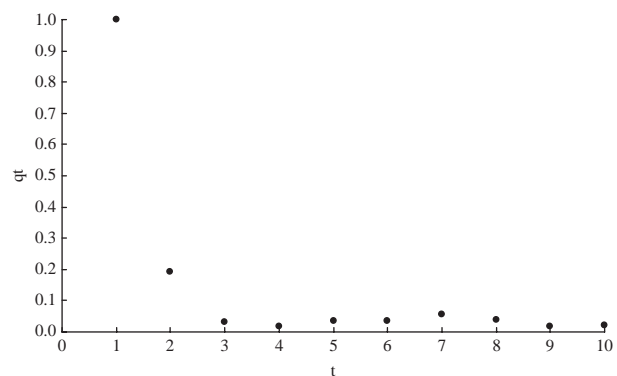


Figure 4. The q_t curve for minke whales in Korean waters.

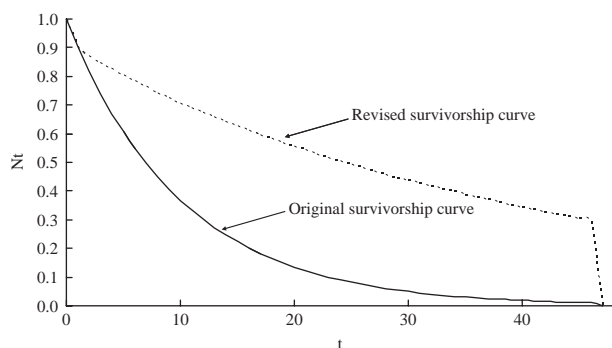


Figure 5. Original survivorship curve and revised survivorship curve using the q_t for minke whales in Korean waters.

Krahn et al. 2002; Calambokidis and Barlow 2004; Evans and Hindell 2004; Verborgh 2005). The estimated survival rate was higher than rates for the finless porpoise, which is frequently found in the Yellow Sea of Korea (Park 2006). According to a study by Park (2006), the estimated survival rate for finless porpoises in this area was calculated as 0.722. In addition, this estimate was considerably higher than that of fish in this area, such as the chub mackerel (0.275; Choi et al. 2004).

Survival rates and mortality coefficients for marine mammals can be estimated from the age distribution of dead individuals using catch or bycatch data (Caughley 1966; Ohsumi 1979; Chapman 1983),

the age distribution of living individuals using photo-identification data (Barlow and Boveng 1991; Barlow and Clapham 1997), or the population assessment model using abundance data (Horwood 1990). Methods using catch or bycatch data are very useful for fish. However, they have limitations for marine mammals because age distribution using these data may not be representative of the whole population, and it is difficult to obtain age structure data (Caughley 1966; Ohsumi 1979; Chapman 1983). Photo-identification is a valuable tool for obtaining this estimate over consecutive years. However, this estimate can be biased because of the instability of marks used to identify individuals (Barlow and Boveng 1991; Barlow and Clapham 1997). Finally, a population assessment model is not necessary to obtain age structure data (Horwood 1990). However, it also has assumptions that confound estimation, for example assuming a constant rate of pregnancy.

The age of minke whales bycaught in this area ranged from 0 to 10 years old (Figure 2). The majority of dead individuals were less than 2 years old, and old individuals over 10 years old were not bycaught in our study despite the longevity of the minke whale (over 45 years old; Trites and Pauly 1998). A possible reason for this characteristic has been reported (Song et al. 2010). According to their study (Song et al. 2010), it may be related to individuals' experience with fishing gear. It is also

Table 1. Estimated survival rates of several cetaceans.

Age class	Species	Survival rate	Method	Reference
Adult	Minke whale	0.865	Age data (catch)	Ohsumi (1979)
	Minke whale	0.878	Age data (catch)	Chapman (1983)
	Blue whale	0.850	Photo-identification data	Calambokidis and Barlow (2004)
	Humpback whale	0.951	Photo-identification data	Buckland (1990)
	Humpback whale	0.960	Photo-identification data	Calambokidis and Barlow (2004)
	Humpback whale	0.960	Photo-identification data	Barlow and Clapham (1997)
	Sperm whale	0.905	Age data (stranding)	Evans and Hindell (2004)
	Killer whale	0.961	Photo-identification data	Krahn et al. (2002)
	Killer whale	0.976	Photo-identification data	Olesiuk et al. (1990)
	Long-finned pilot whale	0.976	Photo-identification data	Verborgh (2005)
	Bottlenose dolphin	0.920	Photo-identification data	Hersh et al. (1990)
	Bottlenose dolphin	0.961	Photo-identification data	Wells and Scott (1990)
	1 year	Humpback whale	0.759	Photo-identification data
Bottlenose dolphin		0.800	Photo-identification data	Haase and Schneide (2001)
Bottlenose dolphin		0.830	Photo-identification data	Wells and Scott (1990)
Indo-Pacific bottlenose dolphin		0.770	Photo-identification data	Mann et al. (2000)
Indo-Pacific bottlenose dolphin		0.867	Photo-identification data	Kogi et al. (2004)
Atlantic spotted dolphin		0.760	Photo-identification data	Herzing (1997)
Juvenile	Minke whale	0.905	Age data (bycatch)	This study

possible that minke whales are spatially segregated according to age, which may increase the bycatchability of certain age classes. Segregation according to age has been reported (Wada 1989; Hatanaka and Miyashita 1997), and it was demonstrated that young minke whales tend to migrate along coastlines. Finally, this discrepancy might be due to the entrance size of fishing gear, such as set-nets. However, it is still unclear which of these factors are responsible for bias in the size of bycaught minke whales.

Generally, a relatively high mortality rate has been shown to occur at all ages (Caughley 1966). Therefore, the age structure derived from bycatch data in our study is not representative of the whole population when taking into account the longevity of the minke whale. Our survival estimate only covered 10 years, and this time scale may not be adequate for an analysis of the whole population. Further research is needed to estimate the survival rate of the minke whale in Korean waters more accurately, using high-quality data that can be regarded as representative of the whole population.

There are large differences in age- and sex-specific survival rates for marine mammals (Caughley 1966; Stolen and Barlow 2003). These differences can play an important role in determining the growth of the population (Gaillard et al. 1998). Unfortunately, our study did not provide sufficient data on the differences in age- and sex-specific survival rate. Other studies have also had difficulty in obtaining suitable data for estimating these parameters (Olesiuk et al. 1990; Barlow and Boveng 1991). Further investigation of differences in age- and sex-specific survival rates of the minke whale in this area is needed to assess the status of this population.

Mortality coefficient, survival rate, q_t and survivorship curves for minke whales in Korean waters have not been previously investigated, and this is the first attempt to estimate these parameters in this area. This estimate may be considered fundamental information for assessing the status of this population accurately, and for conserving and managing the population effectively.

Human-induced mortality of minke whales, including bycatch, continuously occurs in Korean waters (Kim 1999, 2008; Kim et al. 2004). Although the effect of bycatch on the survival of this population is currently unknown, it is considered a significant threat to minke whales in this area. Further studies should focus on investigating the impact of bycatch on this population, and should examine the effectiveness of mitigation measures to reduce the bycatch of minke whales in this area.

Acknowledgements

We wish to acknowledge the many volunteers who reported the bycatch of minke whales in Korean waters. This work was financially supported by the Cetacean Research Institute of National Fisheries Research and Development Institute, Republic of Korea.

References

- An YR, Kim ZG, Choi SG, Park KJ. 2009. Abundance estimation of common minke whales in the Yellow Sea and the East Sea using the Korean sighting data from 2000 to 2008 with $g(0) = 1$. Paper SC/61/NPM2 presented to the IWC Scientific Committee, May 2009, Madeira, Portugal. 4 pp.
- Baker CS, Lento GM, Cipriano F, Palumbi SR. 2000. Predicted decline of protected whales based on molecular genetic monitoring of Japanese and Korean markets. *Proc R Soc Lond B*. 767:1191–1199.
- Barlow J, Boveng P. 1991. Modelling age-specific mortality for marine mammal populations. *Mar Mamm Sci*. 7(1):50–65.
- Barlow J, Clapham PJ. 1997. A new birth-interval approach to estimating demographic parameters of humpback whales. *Ecol*. 78:535–546.
- Buckland ST. 1990. Estimation of survival rates from sightings of individually identifiable whales. *Rep Int Whaling Comm (special issue)*. 12:155–160.
- Calambokidis J, Barlow J. 2004. Abundance of blue and humpback whales in the eastern north Pacific estimated by capture-recapture and line-transect methods. *Mar Mamm Sci*. 20(1):63–85.
- Caughley G. 1966. Mortality patterns in mammals. *Ecol*. 47:906–918.
- Chapman DG. 1983. Some considerations on the status of stocks of southern hemisphere minke whales. *Rep Int Whaling Comm*. 33:311.
- Choi YM, Zhang CI, Kim YS, BAIK CI, Park YC. 2004. Ecological characteristics and biomass of chub mackerel, *Scomber japonicus* Houttuyn in Korean waters. *J Kor Soc Fish Res*. 6(2):79–89 [in Korean].
- Evans K, Hindell MA. 2004. The age structure and growth of female sperm whales (*Physeter macrocephalus*) in southern Australian waters. *J Zool Lond*. 263:237–250.
- Fujiwara M, Caswell H. 2001. Demography of the endangered North Atlantic right whale. *Nature*. 414:537–541.
- Gabriele CM, Straley JM, Mizroch SA, Baker CS, Craig AS, Herman LM, Glockner-Ferrari D, Ferrari MJ, Cerchio S, Ziegesar O, et al. 2001. Estimating the mortality rate of humpback whale calves in the central North Pacific Ocean. *Can J Zool*. 79:589–600.
- Gaillard JM, Festa-Bianchet M, Yoccoz NG. 1998. Population dynamics of large herbivores: Variable recruitment with constant adult survival. *Trends in Ecol Evol*. 13:58–63.
- Gong Y. 1988. Distribution and abundance of the Sea of Japan-Yellow Sea-East China Sea stock of minke whales. *Bull Nat Fish Res Dev Agen*. 41:35–54 [in Korean].
- Haase PA, Schneide K. 2001. Birth demographics of bottlenose dolphins, *Tursiops truncatus*, in Doubtful Sound, Fiordland, New Zealand—preliminary findings. *New Zealand J of Mar Freshwater Res*. 35:675–680.
- Hatanaka H, Miyashita T. 1997. On the feeding migration of the Okhotsk Sea-West Pacific stock of minke whales,

- estimates based on length composition data. Rep Int Whaling Comm. 47:557–567.
- Hersh SL, Odell DK, Asper ED. 1990. Bottlenose dolphin mortality patterns in the Indian/Banana River system of Florida. In: Leatherwood S, Reeves RR, editors. The bottlenose dolphin. London: Academic Press. p. 155–164.
- Herzing DL. 1997. The life history of free-ranging Atlantic spotted dolphins (*Stenella frontalis*): age classes, color phases, and female reproduction. Mar Mamm Sci. 13:576–595.
- Horwood J. 1990. Biology and exploitation of the minke whale. Baton Rouge (FL): CRC Press. 238 pp.
- International Whaling Commission. 1983. Report of the Subcommittee on minke whales. Rep Int Whaling Comm. 33:91–122.
- International Whaling Commission. 1984. Report of the Scientific Committee, Annex E2. Report of the subcommittee on Northern Hemisphere minke whales. Rep Int Whaling Comm. 34:102–111.
- Jefferson JA, Leatherwood S, Webber MA. 1993. FAO species identification guide. Marine mammals of the world. Rome: FAO. 320 pp.
- Kim YH. 2008. A study on the characteristics of minke whale (*Balaenoptera acutorostrata*) bycatch in Korean waters [MS thesis]. Busan, Korea: Pukyong National University. 52 pp [in Korean].
- Kim ZG. 1999. Bycatches of minke whales in Korean waters. J Cetacean Res Manage. 1 (Suppl):98–100.
- Kim ZG, An YR, Sohn H, Baik CI. 2004. Characteristics of minke whale (*Balaenoptera acutorostrata*) by-catch in Korean waters. J Korean Fish Soc. 6(2):173–182 [in Korean].
- Kogi K, Hishii T, Imamura A, Iwatani T, Dudzinski KM. 2004. Demographic parameters of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) around Mikura Island, Japan. Mar Mamm Sci. 20(3):510–526.
- Krahn MM, Wade PR, Kalinowski ST, Dahlheim ME, Taylor BL, Hanson MB, Ylitalo GM, Angliss RP, Stein JE, Waples RS. 2002. Status review of Southern Resident killer whales (*Orcinus orca*) under the Endangered Species Act. U.S. Dept. Commer., NOAA Tech. Memo. NMFS-NWFSC-54. 133 pp.
- Mann J, Connor RC, Barre LM, Heithaus MR. 2000. Female reproductive success in bottlenose dolphins (*Tursiops sp.*): life history, habitat, provisioning and group-size effects. Beh Ecol. 11:210–219.
- Na JH. 2005. Age and growth of minke whale, *Balaenoptera acutorostrata*, in Korean waters [M.S. thesis]. Busan, Korea: Pukyong National University. 52 pp [in Korean].
- Ohsumi S. 1979. Population assessment of the Antarctic minke whale. Rep Int Whaling Comm. 29:407.
- Olesiuk PF, BIGG MA, Ellis GM. 1990. Life history and population dynamics of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington state. In: Hammond PS, Mizroch SA, Donovan GP, editors. Individual recognition of cetaceans: use of photo-identification and other techniques to estimate population parameters. Cambridge: International Whaling Commission. p. 209–243.
- Park JY, Sohn H, Kim ZG, Kim WJ, Park DW, An YR. 2004. Genetic diversity of by-caught minke whales in Korea based on mitochondrial DNA control regions. J Korean Soc Fish Res. 6(2):163–172 [in Korean].
- Park KJ. 2006. Population ecological characteristic and stock assessment of finless porpoise, *Neophocaena phocaenoides*, in the western sea of Korea [Ph.D. dissertation]. Busan, Korea: Pukyong National University. 174pp [in Korean].
- Park KJ, An YR, Kim ZG, Choi SG, Moon DY, Park JE. 2009. Abundance estimates of the minke whale, *Balaenoptera acutorostrata*, in the East Sea, Korea. Korean J Fish Aqua Sci. 42(6):642–649. [in Korean]
- Sohn H, Kim ZG, Miyashita T. 2001. Abundance estimate of minke whale, *Balaenoptera acutorostrata*, by sighting survey in the Yellow Sea, spring 2001. J Korean Soc Fish Res. 4:51–63 [in Korean].
- Song KJ, Kim ZG, Zhang CI, Kim YH. 2010. Fishing gears involved in entanglements of minke whales (*Balaenoptera acutorostrata*) in the East Sea of Korea. Mar Mamm Sci. 26(2):282–295.
- Spinage CA. 1972. African ungulate life tables. Ecology. 53:645–652.
- Stolen MK, Barlow J. 2003. A model life table for bottlenose dolphins (*Tursiops truncatus*) from the Indian river lagoon system. Mar Mamm Sci. 19(4):630–649.
- Trites AW, Pauly D. 1998. Estimating mean body masses of marine mammals from maximum body lengths. Can J Zool. 76(5):886–896.
- Verborgh P. 2005. Population estimation and survival rate of long-finned pilot whales (*Globicephala melas*) in the Strait of Gibraltar [MS thesis]. University of Wales. 70 pp.
- Wada S. 1989. Latitudinal segregation of the Okhotsk Sea-West Pacific stock of minke whales. Rep Int Whaling Comm. 39:229–233.
- Wang P. 1985. Studies on the breeding habits of the minke whale (*Balaenoptera acutorostrata*) in the Yellow Sea. Chin J Oceanol Limnol. 3:37.
- Wells RS, Scott MD. 1990. Estimating bottlenose dolphin population parameters from individual identification and capture-release techniques. Rep Int Whaling Comm (special issue) 12:407–415.
- Zhang CI, Megrey BA. 2006. A revised Alverson and Carney model for estimating the instantaneous rate of natural mortality. Trans Am Fish Soc. 135(3):620–633.