KILLER WHALE (Orcinus orca): Eastern North Pacific Southern Resident Stock

STOCK DEFINITION AND GEOGRAPHIC RANGE

Killer whales have been observed in all oceans and seas of the world (Leatherwood and Dahlheim 1978). Although reported from tropical and offshore waters, killer whales prefer the colder waters of both hemispheres, with greatest abundances found within 800 km of major continents (Mitchell 1975). Along the west coast of North America, killer whales occur along the entire Alaskan coast (Braham and Dahlheim 1982), in British Columbia and Washington inland waterways (Bigg et al. 1990), and along the outer coasts of Washington, Oregon, and California (Green et al. 1992; Barlow 1995, 1997; Forney et al. 1995). Seasonal and vear-round occurrence has been noted for killer whales throughout Alaska (Braham and Dahlheim 1982) and in the intracoastal waterways of British Columbia and Washington State, where pods have been labeled as 'resident,' 'transient,' and 'offshore' (Bigg et al. 1990, Ford et al. 1994) based on aspects of morphology, ecology, genetics, and behavior (Ford and Fisher 1982, Baird and Stacey 1988, Baird et al. 1992, Hoelzel et al. 1998). Through examination of photographs of recognizable individuals and pods, movements of whales between geographical areas have been documented. For example, whales identified in Prince William Sound have been observed near Kodiak Island (Matkin et al. 1999) and whales identified in Southeast Alaska have been observed in Prince William Sound, British Columbia, and Puget Sound (Leatherwood et al. 1990, Dahlheim et al. 1997).

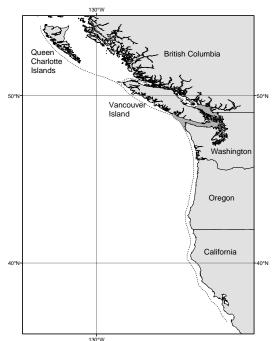


Figure 1. Approximate April-October distribution of the Eastern North Pacific Southern Resident killer whale stock (shaded area) and range of sightings (dotted line).

Studies on mtDNA restriction patterns provide evidence that the 'resident' and 'transient' types are genetically distinct (Stevens et al. 1989, Hoelzel 1991, Hoelzel and Dover 1991, Hoelzel et al. 1998). Analysis of 73 samples collected from eastern North Pacific killer whales from California to Alaska has demonstrated significant genetic differences among 'transient' whales from California through Alaska, 'resident' whales from the inland waters of Washington, and 'resident' whales ranging from British Columbia to the Aleutian Islands and Bering Sea (Hoelzel et al. 1998). However, low genetic diversity throughout this specie's world-wide distribution has hampered efforts to clarify its taxonomy. At an international symposium in cetacean systematics in May 2004, a workshop was held to review the taxonomy of killer whales. A majority of invited experts felt that the Resident-and Transient-type whales in the eastern North Pacific probably merited species or subspecies status (Reeves et al. 2004).

Most sightings of the Eastern North Pacific Southern Resident stock of killer whales have occurred in the summer in inland waters of Washington and southern British Columbia. However, pods belonging to this stock have also been sighted in coastal waters off southern Vancouver Island and Washington (Bigg et al. 1990, Ford et al. 2000, NWFSC unpubl. data). The complete winter range of this stock is uncertain. Of the three pods comprising this stock, one (J1) is commonly sighted in inshore waters in winter, while the other two (K1 and L1) apparently spend more time offshore (Ford et al. 2000). These latter two pods have been sighted as far south as Monterey Bay and central California in recent years (N. Black, pers. comm., K. Balcomb, pers. comm.) They sometimes have also been seen entering the inland waters of Vancouver Island from the north–through Johnstone Strait–in the spring (Ford et al. 2000), suggesting that they may spend time along the entire outer coast of Vancouver Island during the winter. In May 2003, these pods were sighted off the northern end of the Queen Charlotte Islands, the furthest north they had ever previously been documented (J. Ford, pers. comm.).

Based on data regarding association patterns, acoustics, movements, genetic differences and potential fishery interactions, five killer whale stocks are recognized within the Pacific U.S. EEZ: 1) the Eastern North Pacific Northern Resident stock - occurring from British Columbia through Alaska, 2) the Eastern North Pacific Southern

Resident stock - occurring mainly within the inland waters of Washington State and southern British Columbia (see Fig. 1), 3) the Eastern North Pacific Transient stock - occurring from Alaska through California, 4) the Eastern North Pacific Offshore stock - occurring from Southeast Alaska through California, and 5) the Hawaiian stock. The Stock Assessment Reports for the Alaska Region contain information concerning the Eastern North Pacific Northern Resident and Eastern North Pacific Transient stocks.

POPULATION SIZE

The Eastern North Pacific Southern Resident stock is a trans-boundary stock including killer whales in inland Washington and southern British Columbia waters. Photo-identification of individual whales through the years has resulted in a substantial understanding of this stock's structure, behaviors, and movements. In 1993, the three pods comprising this stock totaled 96 killer whales (Ford et al. 1994). The population increased to 99 whales in 1995, then declined to 79 whales in 2001, and most recently numbered 89 whales in 2006. (Fig. 2; Ford et al. 2000; Center for Whale Research, unpubl. data). The 2001-2005 counts included a whale born in 1999 (L-98) that was listed as missing during the annual census in May and June 2001 but was subsequently discovered alone in an inlet off the west coast of Vancouver Island (J. Ford, pers. comm.). L-98 remained separate from L pod until 10 March 2006 when he died due to injuries associated with a vessel interaction in Nootka Sound. L-98 has been subtracted from the official 2006 population census. In addition, four whales that have not been observed during the fall 2006 surveys will not be confirmed as missing from the population until the official census is completed in May/June 2007 (Center for Whale Research, unpubl. data).

Minimum Population Estimate

The abundance estimate for this stock of killer whales is a direct count of individually identifiable animals. It is thought that the entire population is censused every year. This estimate therefore serves as both a best estimate of abundance and a minimum estimate of abundance. Thus, the minimum population estimate (N_{MIN}) for the Eastern North Pacific Southern Resident stock of killer whales is 89 animals.

Current Population Trend

During the live-capture fishery that existed from 1967 to 1973, it is estimated that 47 killer whales, mostly immature, were taken out of this stock (Ford et al. 1994). The first complete census of this stock occurred in 1974. Between 1974 and 1993 the Southern Resident stock increased approximately 35%, from 71 to 96 individuals (Ford et al. 1994). This represents a net annual growth rate of 1.8% during those years. Since 1995, the population declined to 79 whales before increasing from 2002-2006 to a total of 89 whales (Ford et al. 2000; Center for Whale Research, unpubl. data).

CURRENT AND MAXIMUM NET PRODUCTIVITY RATES

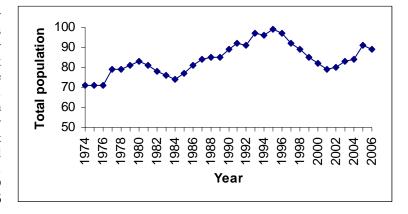


Figure 2. Population of Eastern North Pacific Southern Resident stock of killer whales, 1974-2006. Each year's count includes animals first seen and first missed; a whale is considered first missed the year after it was last seen alive (Ford et al. 2000; Center for Whale Research, unpubl. data).

A reliable estimate of the maximum net productivity rate is currently unavailable for this stock of killer whales. Studies of 'resident' killer whale pods in British Columbia and Washington waters resulted in estimated population growth rates of 2.92% and 2.54% over the period from 1973 to 1987 (Olesiuk et al. 1990, Brault and Caswell 1993). For southern resident killer whales, estimates of the population growth rate have been made during the three periods when the population has been documented increasing since monitoring began in 1974. From 1974 to 1980 the population increased at a rate of 2.6%/year, 2.3%/year from 1985 to 1996, and 2.5%/year from 2002 to 2003 (Krahn et al. 2004). However, a population increases at the maximum growth rate (R_{MAX}) only when the population is at extremely low levels; thus, any of these estimates may be an underestimate of R_{MAX} . Hence, until additional data become available, it is recommended that the cetacean maximum theoretical net productivity rate (R_{MAX}) of 4% be employed for this stock (Wade and Angliss 1997).

POTENTIAL BIOLOGICAL REMOVAL

The potential biological removal (PBR) level for this stock is calculated as the minimum population size (89) <u>times</u> one-half the default maximum net growth rate for cetaceans (½ of 4%) <u>times</u> a recovery factor of 0.1 (for an endangered stock, Wade and Angliss 1997), resulting in a PBR of 0.18 whales per year.

HUMAN-CAUSED MORTALITY AND SERIOUS INJURY

Fisheries Information

NMFS observers have monitored the northern Washington marine set gillnet fishery since 1988 (Gearin et al. 1994, 2000; P. Gearin, unpubl. data). Observer coverage ranged from approximately 40 to 83% in the entire fishery (coastal + inland waters) between 1998 and 2002. There was no observer coverage in this fishery from 1999-2003. However, the total fishing effort was 4, 46, 4.5 and 7 net days (respectively) in those years, it occurred only in inland waters, and no killer whale takes were reported. No killer whale mortalities have been recorded in this fishery since the inception of the observer program.

In 1993, as a pilot for future observer programs, NMFS in conjunction with the Washington Department of Fish and Wildlife (WDFW) monitored all non-treaty components of the Washington Puget Sound Region salmon gillnet fishery (Pierce et al. 1994). Observer coverage was 1.3% overall, ranging from 0.9% to 7.3% for the various components of the fishery. Encounters (whales within 10 m of a net) with killer whales were reported, but not quantified, though no entanglements occurred.

In 1994, NMFS and WDFW conducted an observer program during the Puget Sound non-treaty chum salmon gillnet fishery (areas 10/11 and 12/12B). A total of 230 sets were observed during 54 boat trips, representing approximately 11% observer coverage of the 500 fishing boat trips comprising the total effort in this fishery, as estimated from fish ticket landings (Erstad et al. 1996). No interactions with killer whales were observed during this fishery. The Puget Sound treaty chum salmon gillnet fishery in Hood Canal (areas 12, 12B, and 12C) and the Puget Sound treaty sockeye/chum gillnet fishery in the Strait of Juan de Fuca (areas 4B, 5, and 6C) were also monitored in 1994 at 2.2% (based on % of total catch observed) and approximately 7.5% (based on % of observed trips to total landings) observer coverage, respectively (NWIFC 1995). No interactions resulting in killer whale mortalities were reported in either treaty salmon gillnet fishery.

Also in 1994, NMFS, WDFW, and the Tribes conducted an observer program to examine seabird and marine mammal interactions with the Puget Sound treaty and non-treaty sockeye salmon gillnet fishery (areas 7 and 7A). During this fishery, observers monitored 2,205 sets, representing approximately 7% of the estimated number of sets in the fishery (Pierce et al. 1996). Killer whales were observed within 10 m of the gear during 10 observed sets (32 animals in all), though none were observed to have been entangled.

Killer whale takes in the Washington Puget Sound Region salmon drift gillnet fishery are unlikely to have increased since the fishery was last observed in 1994, due to reductions in the number of participating vessels and available fishing time (see details in Appendix 1). Fishing effort and catch have declined throughout all salmon fisheries in the region due to management efforts to recover ESA-listed salmonids.

An additional source of information on the number of killer whales killed or injured incidental to commercial fishery operations is the self-reported fisheries information required of vessel operators by the MMPA. During the period between 1994 and 2004, there were no fisher self-reports of killer whale mortalities from any fisheries operating within the range of this stock. However, because logbook records (fisher self-reports required during 1990-94) are most likely negatively biased (Credle et al. 1994), these are considered to be minimum estimates. Logbook data are available for part of 1989-1994, after which incidental mortality reporting requirements were modified. Under the new system, logbooks are no longer required; instead, fishers provide self-reports. Data for the 1994-1995 phase-in period is fragmentary. After 1995, the level of reporting dropped dramatically, such that the records are considered incomplete and estimates of mortality based on them represent minimums (see Appendix 7 in Angliss and Lodge 2002 for details).

Due to a lack of observer programs, there are few data concerning the mortality of marine mammals incidental to Canadian commercial fisheries. Since 1990, there have been no reported fishery-related strandings of killer whales in Canadian waters. However, in 1994 one killer whale was reported to have contacted a salmon gillnet but did not entangle (Guenther et al. 1995). Data regarding the level of killer whale mortality related to commercial fisheries in Canadian waters are not available, though the mortality level is thought to be minimal.

During this decade there have been no reported takes from this stock incidental to commercial fishing operations (D. Ellifrit, pers. comm.), no reports of interactions between killer whales and longline operations (as occurs in Alaskan waters; see Yano and Dahlheim 1995), no reports of stranded animals with net marks, and no photographs of individual whales carrying fishing gear. The total fishery mortality and serious injury for this stock is zero.

Other Mortality

According to Northwest Marine Mammal Stranding Network records, maintained by the NMFS Northwest Region, no human-caused killer whale mortalities or serious injuries were reported from non-fisheries sources in 1998-2004. There was documentation of a whale-boat collision in Haro Strait in 2005 which resulted in a minor injury to a whale. In 2006, whale L98 was killed during a vessel interaction. It is important to note that L98 had become habituated to regularly interacting with vessels during its isolation in Nootka Sound. The annual level of human-caused mortality for this stock over the past five years is 0.2 animals per year (reflecting the vessel strike mortality of animal L98 in 2006).

STATUS OF STOCK

On November 15, 2005 NMFS listed Southern Resident killer whales as endangered under the ESA. Total annual fishery mortality and serious injury for this stock (0) is not known to exceed 10% of the calculated PBR (0.018) and, therefore, appears to be insignificant and approaching zero mortality and serious injury rate. The estimated annual level of human-caused mortality and serious injury of 0.2 animals per year exceeds the PBR (0.18). Southern Resident killer whales are formally listed as "endangered" under the ESA and consequently the stock is automatically considered as a "depleted" and "strategic" stock under the MMPA.

REFERENCES

- Angliss, R. P., and K. L. Lodge. 2002. Alaska marine mammal stock assessments, 2002. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-133. 224 pp.
- Baird, R. W., and P. J. Stacey. 1988. Variation in saddle patch pigmentation in populations of killer whales (*Orcinus orca*) from British Columbia, Alaska, and Washington State. Can. J. Zool. 66 (11):2582-2585.
- Baird, R. W., P. A. Abrams, and L. M. Dill. 1992. Possible indirect interactions between transient and resident killer whales: implications for the evolution of foraging specializations in the genus *Orcinus*. Oecologia 89:125-132.
- Barlow, J. 1995. The abundance of cetaceans in California waters. Part I: Ship surveys in summer and fall of 1991. Fish. Bull. 93:1 14.
- Barlow, J. 1997. Preliminary estimates of cetacean abundance off California, Oregon and Washington based on a 1996 ship survey and comparisons of passing and closing modes. Administrative Report LJ-97-11, Southwest Fisheries Science Center, National Marine Fisheries Service, P.O. Box 271, La Jolla, CA 92038. 25 pp.
- Bigg, M. A., P. F. Olesiuk, G. M. Ellis, J. K. B. Ford, and K. C. Balcomb III. 1990. Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. Pp. 386-406, *In:* Hammond, P. S., S. A. Mizroch, and G. P. Donovan (eds.), Individual Recognition of Cetaceans: Use of Photo-identification and Other Techniques to Estimate Population Parameters. Rep. Int. Whal. Commn. Special Issue 12.
- Black, N. A. P.O. Box 52001, Pacific Grove, CA 93950.
- Braham, H. W., and M. E. Dahlheim. 1982. Killer whales in Alaska documented in the Platforms of Opportunity Program. Rep. Int. Whal. Commn. 32:643-646.
- Brault, S., and H. Caswell. 1993. Pod-specific demography of killer whales (*Orcinus orca*). Ecology 74(5):1444-1454.
- Center for Whale Research, 1359 Smugglers Cove Rd., Friday Harbor, WA 98250.
- Committee on the Status of Endangered Wildlife in Canada (COSEWIC). 2003. Species Listing. Available at URL: http://www.cosewic.gc.ca/eng/sct0/index_e.cfm (access date October 2003).
- Credle, V. R., D. P. DeMaster, M. M. Merklein, M. B. Hanson, W. A. Karp, and S. M. Fitzgerald (eds.). 1994. NMFS observer programs: minutes and recommendations from a workshop held in Galveston, Texas, November 10-11, 1993. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-OPR-94-1. 96 pp.
- Dahlheim, M. E., D. K. Ellifrit, and J. D. Swenson. 1997. Killer whales of Southeast Alaska: a catalogue of photoidentified individuals. National Marine Mammal Laboratory, AFSC, NMFS, NOAA, 7600 Sand Point Way NE, Seattle, WA 98115. 79 pp.
- Ellifrit, D. Center for Whale Research, 1359 Smugglers Cove Rd., Friday Harbor, WA 98250.
- Erstad, P., S. J. Jeffries, and D. J. Pierce. 1996. 1994 Report for the Puget Sound fishery observer program in management areas 10/11 & 12/12B: nontreaty chum gill net fishery. Final Report, Washington Dept. Fish and Wildlife, Olympia, WA. 14 pp.
- Ford, J. K. B. Pacific Biological Station, Department of Fisheries and Oceans, Nanaimo, BC V9R 5K6.
- Ford, J. K. B., and H. D. Fisher. 1982. Killer whale (*Orcinus orca*) dialects as an indicator of stocks in British Columbia. Rep. Int. Whal. Commn. 32:671-679.

- Ford, J. K. B., G. M. Ellis, and K. C. Balcomb. 1994. Killer Whales: The Natural History and Genealogy of *Orcinus orca* in British Columbia and Washington State. University of British Columbia Press, Vancouver, BC, and University of Washington Press, Seattle. 102 pp.
- Ford, J. K. B., G. M. Ellis, and K. C. Balcomb. 2000. Killer Whales: The Natural History and Genealogy of *Orcinus orca* in British Columbia and Washington. 2nd edition. University of British Columbia Press, Vancouver, BC, and University of Washington Press, Seattle. 104 pp.
- Forney, K. A., J. Barlow, and J. V. Carretta. 1995. The abundance of cetaceans in California waters. Part II: Aerial surveys in winter and spring of 1991 and 1992. Fish. Bull. 93:15_26.
- Gearin, P. J. National Marine Mammal Laboratory, AFSC, NMFS, 7600 Sand Point Way NE, Seattle, WA 98115.
- Gearin, P. J., S. R. Melin, R. L. DeLong, H. Kajimura, and M. A. Johnson. 1994. Harbor porpoise interactions with a chinook salmon set-net fishery in Washington State. Rep. Int. Whal. Commn. Special Issue 15:427-438.
- Gearin, P. J., M. E. Gosho, J. L. Laake, L. Cooke, R. L. DeLong, and K. M. Hughes. 2000. Experimental testing of acoustic alarms (pingers) to reduce bycatch of harbour porpoise, *Phocoena phocoena*, in the state of Washington. J. Cetacean Res. Manage. 2(1):1-9.
- Green, G. A., J. J. Brueggeman, R. A. Grotefendt, C. E. Bowlby, M. L. Bonnel, and K. C. Balcomb. 1992. Cetacean distribution and abundance off Oregon and Washington, 1989-1990. Pp. 1-100, *In:* Brueggeman, J. J. (ed.), Oregon and Washington marine mammal and seabird surveys. Final Rep. OCS Study MMS 91-0093.
- Guenther, T. J., R. W. Baird, R. L. Bates, P. M. Willis, R. L. Hahn, and S. G. Wischniowski. 1995. Strandings and fishing gear entanglements of cetaceans on the west coast of Canada in 1994. Paper SC/47/O6 presented to the International Whaling Commission, May 1995 (unpublished). 7 pp.
- Hoelzel, A. R. 1991. Analysis of regional mitochondrial DNA variation in the killer whale; implications for cetacean conservation. Rep. Int. Whal. Commn. Special Issue 13:225-233.
- Hoelzel, A. R., and G. A. Dover. 1991. Genetic differentiation between sympatric killer whale populations. Heredity 66:191-195.
- Hoelzel, A. R., M. E. Dahlheim, and S. J. Stern. 1998. Low genetic variation among killer whales (*Orcinus orca*) in the Eastern North Pacific, and genetic differentiation between foraging specialists. J. Heredity 89:121-128
- Krahn, M. M., P. R. Wade, S. T. Kalinowski, M. E. Dahlheim, B. L. Taylor, M. B. Hanson, G. M. Ylitalo, R. P. Angliss, J. E. Stein, and R. S. Waples. 2002. Status review of Southern Resident killer whales (*Orcinus orca*) under the Endangered Species Act. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-NWFSC-54. 133 pp.
- Krahn, M. M., M. J. Ford, W. F. Perrin, P. R. Wade, R. P. Angliss, M. B. Hanson, B. L. Taylor, G. Ylitalo, M. E. Dahlheim, J. E. Stein, and R. S. Waples. 2004. 2004 Status review of Southern Resident killer whales (*Orcinus orca*) under the Endangered Species Act. U.S. Dep. Commer., NOAA Tech. Memo NMFS-NWFSC-62. 73 pp.
- Leatherwood, J. S., and M. E. Dahlheim. 1978. Worldwide distribution of pilot whales and killer whales. Naval Ocean Systems Center, Tech. Rep. 443:1-39.
- Leatherwood, S., C. O. Matkin, J. D. Hall, and G. M. Ellis. 1990. Killer whales, *Orcinus orca*, photo_identified in Prince William Sound, Alaska 1976 to 1987. Can. Field Nat. 104:362_371.
- Matkin, C., G. Ellis, E. Saulitis, L. Barrett-Lennard, and D. Matkin. 1999. Killer Whales of Southern Alaska. North Gulf Oceanic Society. 96 pp.
- Mitchell, E. D. 1975. Report on the meeting on small cetaceans, Montreal, April 1-11, 1974. J. Fish. Res. Bd. Can. 32:914-916.
- Northwest Indian Fisheries Commission (NWIFC). 1995. Monitoring of marbled murrelet and marine mammal interactions with 1994 tribal gillnet fisheries in northern Puget Sound, Hood Canal, and the Strait of Juan de Fuca. Final Report to NMFS, Contract No. 52ABNF400087, and U.S. Fish and Wildlife Service. Unpubl. report. 41 pp. Available at NWIFC, 6730 Martin Way E, Olympia, WA 98516.
- Olesiuk, P. F., M. A. Bigg, and G. M. Ellis. 1990. Life history and population dynamics of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. Rep. Int. Whal. Commn. Special Issue 12:209-242.
- Pierce, D. J., W. P. Ritchie, and R. Kreuziger. 1994. Preliminary findings of seabird interactions with the non-treaty salmon gill net fishery: Puget Sound and Hood Canal Washington. Unpubl. report. Washington Dept. Fish and Wildlife, Olympia, WA. 39 pp. Available at WDFW, 600 Capitol Way N, Olympia, WA 98501.

- Pierce, D. J., M. Alexandersdottir, S. J. Jeffries, P. Erstad, W. Beattie, and A. Chapman. 1996. Interactions of marbled murrelets and marine mammals with the 1994 Puget Sound sockeye gill net fishery. Final Report, Washington Dept. Fish and Wildlife, Olympia, WA. 21 pp.
- Reeves, R.R., W.F. Perrin, B.L. Taylor, C.S. Baker, and S.L. Mesnick. 2004. Report of the workshop on shortcomings of cetacean taxonomy in relation to needs of conservation and management, April 30 May 2, 2004, La Jolla, California. U.S. Department of Commerce NOAA Technical Memorandum NOAA-TM-NMFS-SWFSC-363. 94pp. Available from Southwest Fisheries Science Center, 8604 La Jolla Shores Drive, La Jolla, CA. 92037.
- Ross, P. S., G. M. Ellis, M. G. Ikonomou, L. G. Barrett-Lennard, and R. F. Addison. 2000. High PCB concentrations in free-ranging Pacific killer whales, *Orcinus orca*: effects of age, sex and dietary preference. Mar. Pollut. Bull. 40(6):504-515.
- Stevens, T. A., D. Duffield, E. Asper, K. Hewlett, A. Bolz, L. Gage, and G. Bossart. 1989. Preliminary findings of restriction fragment differences in mitochondrial DNA among killer whales (*Orcinus orca*). Can. J. Zool. 67:2592-2595.
- Wade, P. R., and R. P. Angliss. 1997. Guidelines for assessing marine mammal stocks: report of the GAMMS workshop April 3-5, 1996, Seattle, Washington. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-OPR-12. 93 pp.
- Yano, K., and M. E. Dahlheim. 1995. Killer whale, *Orcinus orca*, depredation on longline catches of bottomfish in the southeastern Bering Sea and adjacent waters. Fish. Bull. 93:355-372.
- Ylitalo, G. M., C. O. Matkin, J. Buzitis, M. M. Krahn, L. L. Jones, T. Rowles, and J. E. Stein. 2001. Influence of life-history parameters on organochlorine concentrations in free-ranging killer whales (*Orcinus orca*) from Prince William Sound, AK. Sci. Total Environ. 281:183-203.