TWELVE

Worldwide Distribution and Abundance of Killer Whales

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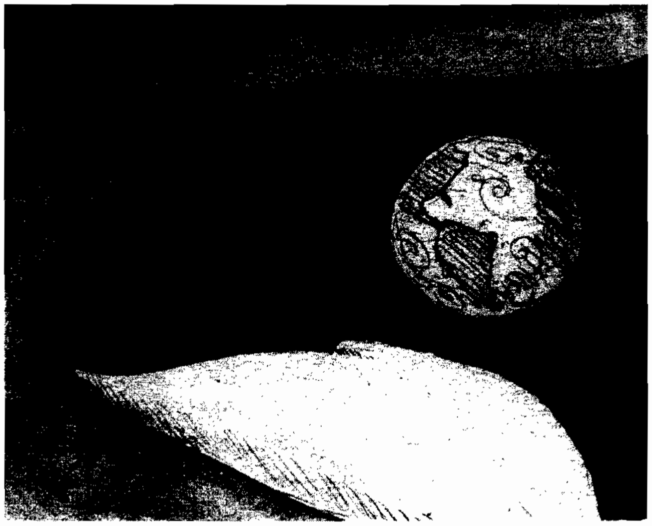

Killer whales have long been recognized as formidable predators in virtually all of the world's oceans (Leatherwood and Dahlheim 1978; Heyning and Dahlheim 1988). They are known to be common in many coastal areas, particularly at high latitudes, but they also occur in offshore and tropical waters (Leatherwood and Dahlheim 1978). Seasonal movement patterns, often associated with increased availability of prey species (Dahlheim 1981), have been documented or suggested in the eastern North Pacific (Braham and Dahlheim 1982; Baird and Dill 1995), the coast of Japan (Kasuya 1971), the North Atlantic and Norwegian waters (Sigurjónsson and Leatherwood 1988; Similä et al. 1996), the South Atlantic (Iñíguez 2001), and the Southern Hemisphere (Mikhalev et al. 1981; Kasamatsu and Joyce 1995). In a few coastal regions, most notably off British Columbia and the state of Washington, regularly occurring populations have been studied for decades, and much has been learned about their ecology, population structure, demography, social behavior, and genetics (see Bigg et al. 1990; Olesiuk et al. 1990; Ford et al. 1994, 1998; Baird and Dill 1995, 1996; Hoelzel et al. 1998, Barrett-Lennard 2000). In contrast, very little is known about killer whales in most other regions of the world. Several studies have suggested important functional roles for killer whale predation in the North Pacific and Southern Oceans, and killer whale predation has been implicated in various recent marine mammal declines in the North Pacific and Southern Ocean (Barrat and Mougin 1978; Estes et al. 1998; Springer et al. 2003). These processes are, however, controversial and not well substantiated. A first step toward gaining a better understanding of relevant processes is to evaluate patterns of killer whale abundance, distribution, and foraging habits.

In this chapter, we provide a review of the published literature on worldwide killer whale population structure, abundance, distribution, and known prey. We discuss differences in the methods that have been used to identify and assess killer whale populations, including sighting and whaling records, photo-identification methods, mark-recapture estimates, and distance sampling methods from shipboard and aerial platforms. Each method has limitations and strengths and provides somewhat different information on population size, structure, and distribution. When combined within a single region, these sources can complement one another to provide a clearer picture of killer whale biology; however, taken individually they make comparisons between regions difficult. Nonetheless, in the following sections we have attempted to synthesize some of the diverse literature on killer whale populations worldwide into a general overview.

Populations

Killer whales are presently considered to form a single cosmopolitan species, *Orcinus orca*, although separate species status has been suggested for different groups found in the Southern Ocean (Mikhalev et al. 1981; Berzin and Vladimirov 1983; Pitman and Ensor 2003) and for different forms found in the North Pacific (Baird et al. 1992; Baird 1994), based on color pattern, diet, and morphological traits. Substantial differences in food habits, behavior, genetics, morphology, and movement patterns have led to the description of distinct populations throughout the world (see Baird 2000; Dahlheim and Heyning 1999), including several sympatric populations that do not apparently interact or interbreed. The well-studied killer whales in the eastern North Pacific are known to consist of at least two and maybe three distinct types, commonly termed *resident, transient*, and *offshore* killer whales (Ford et al. 1994). They differ in their food habits and in a variety of morphological, ecological, and behavioral characteristics (Baird 2000). Recent genetic investigations have revealed marked differences between the *resident* and *transient* types of killer whales (Stevens et al. 1989; Hoelzel and Dover 1991; Hoelzel et al. 1998; Barrett-Lennard 2000; Barrett-Lennard and Ellis 2001). In addition, smaller genetic differences were shown between different communities of *resident* killer whales (Hoelzel et al. 1998; Barrett-Lennard 2000; Barrett-Lennard and Ellis 2001).

Although the terminology just mentioned refers only to the coastal eastern North Pacific killer whale populations, similar differences in food habits and ecology have been observed in other regions of the world. Antarctic killer whales comprise three types, provisionally termed Types A, B, and C, with clear differences in coloration, food habits, and some morphological traits (Pitman and Ensor 2003). Killer whale populations that forage primarily on marine mammals have been observed in all ocean basins of the world. Populations that forage primarily on fish and other invertebrates can be divided further into killer whales that exploit one or more seasonally abundant, high-latitude coastal fish species and those that forage widely on pelagic fish and invertebrates. To illustrate some of the differences in more detail, we provide a brief summary of information for these three general types of killer whales, with emphasis on the well-studied eastern North Pacific killer whale types.

Mammal-eaters

Mammal-eating killer whales have been documented worldwide in both coastal and offshore waters (Jefferson et al. 1991), but mammal-eating specialists have been confirmed only in the North Pacific and Southern Ocean. Eastern North Pacific *transient*-type killer whales are among the best-studied mammal-eating killer whales and are known to prey on a wide variety of marine mammals, including whales, dolphins, porpoises, and pinnipeds (Baird and Dill 1996). In inshore waters of British Columbia (Ford et al. 1998) and Prince William Sound, Alaska (Saulitis et al. 2000), two regions where *transient* predation has been studied systematically, the most frequently observed prey have been pinnipeds and porpoises. They have also occasionally been reported feeding on sea turtles and seabirds (Caldwell and Caldwell 1969; Ford et al. 1998; Baird and Dill 1996). Groups are generally small (<10) with a dynamic composition (Baird and Whitehead 2000). Individual *transient* killer whales have been documented to move great distances, reflecting large home ranges as the killer whales follow mobile prey resources (Goley and Straley 1994; Black et al. 1997). Some eastern North Pacific *transients* have been photographed in locations ranging from southeastern Alaska to California, a distance of at least 2,600 km. In the eastern North Pacific and in the Southern Ocean, mammal-eating killer whales are known to be sympatric with other forms of killer whales, but they have not been seen intermixing in social groups with other forms. In Antarctic waters there are two known types of mammal-eating killer whales (Pitman and Ensor 2003). Type A killer whales are thought to follow the seasonal migration of their main prey (Antarctic minke whales, *Balaenoptera borderensis*) and are generally found in open-water habitat. Type B killer whales may be found sympatrically with Type A whales in the open water around Antarctica, but they are more commonly observed in loose pack ice, where they prey upon seals.

Coastal Fish-eaters

Resident killer whales in the North Pacific feed primarily on salmon and other coastal fish species and are seen regularly during summer in the inland waterways of Alaska, British Columbia, and Washington state. Groups of *resident* whales can be distinguished from groups of sympatric *transient* or *offshore* killer whales based on differences in dorsal fin shape and saddle patch coloration. They include several distinct and well-known populations, including the Southern, Northern, and Gulf of Alaska *residents*. *Resident*-type killer whales are also found in the Aleutian Islands and the Bering Sea and are also thought to be found along the Kamchatka Peninsula of Russia, but population structure in these areas has not been fully determined. *Resident* whales are usually found in large groups ranging from approximately 5 to 50 whales, but they are occasionally found in even larger aggregations of 100 whales or more. Where well studied, it has been found that *resident*-type whales occur in stable social groups that are matrilines because offspring do not disperse from their mother's social group (Bigg et al. 1990). Seasonal movement patterns are not fully understood (Bigg et al. 1990; Ford et al. 1998), but during winter the southern *residents* have been reported along the outer coasts of British Columbia, Washington, and California.

Coastal fish-eating killer whales have also been documented in waters off Iceland, the Faroe Islands, the British Isles, and Norway, where they feed primarily on seasonally abundant herring, *Clupea harengus*, and other coastal fish species (Sigurjónsson et al. 1988, Jonsgård and Lyshoel 1970, Similä et al. 1996). Based on photo-identification studies, it has been suggested that the social system of coastal Norwegian whales is similar to that of eastern North Pacific *resident* whales, with stable pods comprising males and females with their offspring, and with no dispersal of either sex from their natal group (Bisther 2002). Pod sizes for Norwegian killer whales are reported to range from 6 to 30 whales with a median of 15. During the course of a 4-year study in northern Norway, pods with known individuals were seen repeatedly and regularly in the study area when herring were present (Similä et al. 1996).

The Antarctic Type C killer whale, known primarily from deep within the Antarctic pack ice, may also broadly be considered a coastal fish-eater. It is found in large groups of 10 to at least 150 (mean 46) and is known to feed on Antarctic toothfish *(Dissostichus mawsoni)*. Some reports suggest they may also take penguins and seals off the ice (Pitman and Ensor 2003), but no takes of these species have actually been observed. Stomach contents of 629 "yellow" killer whales taken in Soviet whaling operations during 1979–1980, which would have represented either Type B or C killer whales, contained 98.5% (by frequency of occurrence) fish, 1.1% squid, and 0.5% marine mammal prey (Berzin and Vladimirov 1983). Seasonal movement patterns are not well understood for the Type C killer whale (Pitman and Ensor 2003). Although some individuals have been reported to overwinter in Antarctic waters, there are also winter records of Type C whales at lower latitudes, including waters off New Zealand (Pitman and Ensor 2003).

Oceanic and Neritic Killer Whales

Killer whales have been reported from oceanic and neritic waters worldwide, but little is known about these whales. Killer whales are found at low densities throughout the eastern tropical Pacific (Wade and Gerrodette 1993), but their diet and population structure are little understood. One form, thought to be mostly neritic in distribution, occurs in the eastern North Pacific and is referred to as the *offshore*-type killer whale. Morphologically they are similar to *resident* whales (i.e., their dorsal fins appear to be more rounded at the tip than those of the *transient* type, and they share saddle patch coloration patterns), and they are commonly seen in groups ranging from 10 to 70 whales. *Offshore* killer whales have been found from central coastal Mexico to Alaska and are thought to occur mostly on the continental shelf, but they occasionally come into coastal waterways and have also been seen in offshore waters extending at least 200 miles from the U.S. West Coast (Black et al. 1997). Their main foraging target is assumed to be fish, but observational data on feeding events are extremely limited. *Offshore* whales are not known to intermingle in social groups with *resident* or *transient* whales. Genetic analyses suggest that *offshores* may be reproductively isolated, but they appear to be more closely related to *resident*-type whales (Hoelzel et al. 1998; Barrett-Lennard 2000). In other regions of the world, data on oceanic or neritic killer whales are scarce. Off Japan, killer whales are reported to feed on cod, flatfish, and cephalopods (Nishiwaki and Handa 1958), and these animals may represent a similar neritic form.

Methods of Population Estimation

Information on the abundance and distribution of killer whales ranges widely in age, reliability, detail, and quantitative nature. Population estimates are available for some areas of the eastern North Pacific, North Atlantic, and Southern Oceans and for scattered locations elsewhere in the world. However, methods used to assess populations of killer whales are not strictly comparable, because they estimate somewhat different population parameters and are subject to different biases. In this section we summarize the most common methods of assessing populations of killer whales and other cetaceans, along with an overview of strengths and weaknesses of each method (Table 12.1). After consideration of these differences, we have attempted to synthesize the available information to provide a worldwide summary of patterns of abundance and distribution of killer whales.

Photo-identification Catalogs (CAT)

Killer whales are amenable to long-term studies of local populations because individual whales can readily be identified on the basis of unique characteristics of their dorsal fins and saddle patches (Bigg et al. 1987), and whales often return to the same areas each year. Such studies provide a wealth of information on behavior, ecology, demography, genealogy, population structure, and movement patterns and can be used to establish a catalog of known individuals (see Bigg et al. 1990; Olesiuk et al. 1990; Ford et al. 1994). In cases where populations are small and individual whales are regularly seen in areas of photographic sampling, photo-identification catalogs can provide a minimum or actual population count, particularly if deaths can be documented through time. Such methods do not, however, work well in large, widely dispersed populations, because not all animals are likely to be photographed. For example, the catalog of eastern North Pacific *transient* killer whales contained 251 known individuals in 1999 (Ford and Ellis 1999; Matkin et al. 1999, summarized in Carretta et al. 2001), based on two decades of sampling off Washington state, British Columbia, and Alaska. Subsequently, photographs of killer whales seen off California between 1987 and 1996 were examined (Black et al. 1997), revealing ten matches to known *transient* whales and 95 previously unknown *transient* whales. The catalog count thus increased by 95 animals (38%) to 346 *transient* killer whales when photographs from a different part of this population's range were included. This suggests that not all individuals use the entire range, and catalogs developed within a subset of the entire population's range can underestimate total population size. Thus, photo-identification catalogs will provide

TABLE 12.1
Summary of Methods of Population Estimation for Killer Whales

Method	Information Type	Advantages	Disadvantages	Reference Examples
OBS: Anecdotal or descriptive information, such as whaling records, stranding data, incidental observations	Presence/absence; qualitative descriptions of occurrence, broad distribution patterns	Widely available in most inhabited/ exploited regions of the world; provides historical information	Non-quantitative and difficult to compare between records; limited information for many unexploited regions of the world	Diverse historical literature, whaling records, natural history notes; see for example summaries in Leatherwood et al. 1984; Sigurjónsson and Leatherwood 1988; Dahlheim et al. 1982
CAT: Photo-identification studies and catalogs	Individual-based information on behavior, birth/death rates, ecology and movement patterns; catalog of known individuals; long-term genealogical records	Provides detailed demographic data on population of interest	Photographic sampling may not capture entire population; takes many years and large effort to build comprehensive photo-identification catalog; if deaths are not documented, catalog can overestimate population size	Sigurjónsson et al. 1988; Leatherwood et al. 1990; Ford et al. 1994; Dahlheim et al. 1997; Dahlheim 1997; Heise et al. 1991; Black et al. 1997; Matkin et al. 1999; Iñíguez 2001; Guerrero-Ruiz et al. 1998; See also Hammond et al. 1990
MR: Mark-recapture methods	Estimate of the total number of whales that use a given study area during the study period; with sufficient data, demographic parameters can be estimated	Estimates proportion of unobserved whales to provide more complete estimate of population size; cost-effective method that can be carried out mostly from small boats; model selection and careful design of sampling sites can minimize biases	Requires at least two sampling periods to conduct analysis; if sampling not well-designed, can be negatively biased by individual heterogeneity in sighting probabilities	Poncelet et al. 2002; other cetacean mark-recapture studies: Hansen 1990; Wilson et al. 1999; Matthews et al. 2001; Read et al. 2003; Clapham et al. 2003; Calambokidis and Barlow 2004
SURV: Non-standardized surveys and observations with a measure of effort	Encounter rates, distribution information, instantaneous measure of relative abundance within surveyed region	Can be obtained incidentally to other surveys; semiquantitative data	Non-standardized effort; limited comparability between platforms, methods, regions, generally small sample sizes	Kasuya 1971; Eyre 1995; Miyashita et al. 1996; O'Sullivan and Mullin 1997; Aguayo et al. 1998; Gannier 2000; Garrigue and Greaves 2001; Kahn and Pet 2003; Ballance et al. 2001; Secchi et al. 2002
LTR: Line-transect surveys (Buckland et al. 1993)	Standardized estimate of instantaneous abundance and density	Comparable estimate across studies, as long as potential biases addressed	Costly, requires moderate number of sightings (>30) for analysis; does not provide movement data or information on animals outside of study area	Hammond 1984, Øien 1990; Wade and Gerrodette 1993; Barlow 1995; Forney et al. 1995; Branch and Butterworth 2001; Waite et al. 2002

accurate estimates of population size only if the animals are sampled throughout their range or if all members of the population are known to enter areas of photographic sampling during the study period.

Mark-recapture Methods (MR)

Mark-recapture methods (Seber 1982; Hammond 1986) can yield improved estimates of abundance based on photo-identification data, and they have been used successfully for a variety of individually recognizable cetacean species, including bottlenose dolphins (*Tursiops truncatus*; Hansen 1990; Wilson et al. 1999; Read et al. 2003), humpback whales (*Megaptera novaeangliae*; Clapham et al. 2003; Calambokidis and Barlow 2004), blue whales (*Balaenoptera musculus*; Calambokidis and Barlow 2004), and sperm whales (*Physeter macrocephalus*; Matthews et al. 2001). The method involves collecting a "mark" data set, in which a number of individuals are photographed and identified, and a "recapture" data set, from which a proportion of recaptured (previously identified) individuals is calculated. In the simplest form of the method (for a closed population) the population size is estimated as the number of individuals in the initial sample divided by the proportion of recaptured individuals. The result is an estimate of the total number of animals in the population during the study period. More sophisticated models are available for open populations (i.e., those with births, deaths, immigration, or emigration during the study period).

Mark-recapture methods are, however, sensitive to several assumptions. One is that all individuals in a population have equal capture probability within each sample. This assumption may be violated in various ways, such as if some individuals have indistinct identification characteristics or behave in a way that makes them less likely than others to be photographed, or if the population is not distributed homogeneously. These effects can be mitigated to a large extent by limiting the mark and recapture samples to the best photographs (to allow indistinct marks to be reliably identified, Friday et al. 2000), by making efforts to photograph all individuals in a sighted group, and by selecting broad geographic sampling locations throughout the population's range (Calambokidis and Barlow 2004). Other important assumptions are that marks are not lost through time and that marked animals can correctly be recognized upon recapture. If any of these assumptions are not met during sampling or addressed analytically, this can lead to substantial (usually downward) bias in the abundance estimates (see Hammond et al. 1990). Calambokidis and Barlow (2004) present a mark-recapture estimate for blue whales that was initially biased downward because of limited and uneven photographic sampling. This bias was largely eliminated once broader geographic sampling was achieved.

Despite the wealth of photographic data on killer whales in many regions of the world, there are no published mark-recapture estimates of abundance for this species except for that of Poncelet et al. (2002). Ongoing investigations in the eastern North Pacific are expected to include mark-recapture estimates in the future (J. Durban, personal communication).

Line-transect Surveys (LTR)

Dedicated line-transect surveys using established distance-sampling protocols (Buckland et al. 1993) have been used extensively to provide quantitative and reliable estimates of abundance for cetaceans at sea. Such surveys are generally conducted from medium-sized or large vessels or from aircraft, and the sighting efficiency of each platform is taken into account in estimating densities. The resulting abundance estimates represent a snapshot of the average number of animals within the study region during the study period. Many potential sources of bias can be accounted for during survey planning (e.g., spatial coverage and transect design) or during data analysis (e.g., correction factors for animals missed because of poor weather conditions or diving behavior). Line-transect methodology has been widely used to estimate the abundance of diverse cetacean species worldwide (Hammond 1984; Wade and Gerrodette 1993; Barlow 1995; Forney et al. 1995; Branch and Butterworth 2001) and is generally considered a reliable and effective technique when surveys are designed properly (Buckland et al. 1993). In a number of cases where both line-transect and mark-recapture estimates of abundance are available for a single population, as for blue whales and humpback whales off the U.S. West Coast (Calambokidis and Barlow 2004), abundance estimates from the two methods have been remarkably similar. In general, line-transect surveys yield the most directly comparable abundance estimates across studies. They do not, however, provide information on population identity or movement of individuals unless photo-identification or biopsy efforts are included in the survey.

Non-standardized Surveys (SURV)

In many cases marine mammal surveys are conducted incidentally during other marine investigations, such as by fishery observers, during seismic or oceanographic cruises, on ferry routes, or on other platforms of opportunity. As with dedicated line-transect surveys, opportunistic surveys provide a snapshot of the distribution and abundance of animals within the study area. Methodology has varied widely, however, and it is difficult or impossible to compare results directly from one study to another. Nonetheless, such surveys often provide new information on the distribution, relative abundance, and species composition of cetaceans, particularly in poorly studied regions (Ballance et al. 2001; Gannier 2000; Eyre 1995). Broad patterns of cetacean occurrence can be inferred if one takes into account characteristics of each platform, such as sighting efficiency and potential sources of bias. For example, the effective area surveyed will be greater for surveys conducted from large vessels, at greater height above the water, using multiple observers, and with high-powered binoculars than during surveys conducted from small boats, from platforms closer to the water surface, with a single observer, and without high-powered binoculars. Bias is introduced if animals avoid the platform from which observations are made (e.g., during seismic surveys; Stone 1997), or if they are attracted to the vessel while observations are underway (e.g., killer whales are known to depredate fish from longline vessels and may be attracted to longline survey vessels, particularly during set operations; Secchi and Vaske 1998, Pinedo et al. 2002).

Observations and Anecdotal Information (OBS)

The final category of information comprises a wide variety of descriptive, anecdotal, or incidental observations collected by whalers, fishermen, naturalists, oceanographers, biologists, and others. It may include, for example, presence/absence data, whaling or fishery catch records, or details of observations made (with or without measures of effort). Such observational information generally represents the least quantifiable source of data and is difficult to interpret in a broader context; however, in many regions of the world the only information available on killer whales is of this qualitative nature. In this study we have obtained descriptive information from published reviews (e.g., Sigurjónsson and Leatherwood 1988; Dahlheim et al. 1982), published notes and articles, and gray literature that was accessible in academic libraries or on the Internet. The quality and relevance of information from each source was evaluated individually before inclusion in the overall synthesis presented in the following section.

Patterns of Killer Whale Distribution and Abundance

Using information from all of the types of studies just presented, we have compiled a worldwide summary of patterns of abundance and distribution of killer whales (Table 12.2). Information fell into five general categories: observational information (OBS); photo-identification catalogs (CAT); mark-recapture estimates (MR); non-standardized surveys (SURV); and line-transect surveys (LTR). Because of the differences in accuracy and reliability of these methods, data were standardized into four broad categories of abundance (Table 12.2), defined as follows, based on the range of available line-transect estimates of killer whale densities:

- Rare (0–0.10 whales per 100 km^2)
- Uncommon (0.10–0.20 whales per 100 km^2)
- Common (0.20–0.40 whales per 100 km^2)
- Abundant (>0.40 whales per 100 km^2)

Encounter rates (sightings per linear distance) from non-standardized surveys were compared to encounter rates during line-transect surveys, bearing in mind differences in platform and methodologies, to allow classification of each survey result into one of the four density categories. For mark-recapture abundance estimates and photo-identification catalogs, the number of known or estimated killer whales was divided by the size of the area thought to be inhabited by the whales. This provided a crude density estimate, which was then used as a guideline for assigning an abundance category to each study region, taking into consideration uncertainties in whale movements or population size. Finally, anecdotal information was subjectively categorized on the basis of descriptions of killer whale occurrence (e.g., "seasonally common," "rare visitors"), reported frequency and regularity of sightings, and estimated numbers of killer whales seen within each study region. The assigned categories should be considered provisional for all regions that do not have quantitative estimates of killer whale density. Nonetheless, they provide a basis for examining patterns of distribution and abundance worldwide.

Killer whales have previously been described to be very widely distributed throughout the world's oceans (Leatherwood and Dahlheim 1978; Heyning and Dahlheim 1988). They are found in tropical, temperate, and high-latitude waters and in pelagic and coastal habitats (Dahlheim et al. 1982; Dahlheim and Heyning 1999). Whales inhabiting coastal areas often enter shallow bays, estuaries, and river mouths (Leatherwood et al. 1976). The global picture of killer whale distribution obtained in this study is largely consistent with these past observations but provides further detail and quantitative information. Killer whale densities increase by 1–2 orders of magnitude from the tropics to the highest sampled latitudes in the Arctic and Antarctic (Figure 12.1). The available data also support previous observations that killer whales are more common along continental margins (Dahlheim et al. 1982); however, there is some variation in this general pattern that appears linked to ocean productivity (Figure 12.2). Killer whales appear to be less common in western boundary currents, such as the Gulf Stream or the Kuroshio, than in more productive eastern boundary currents, such as the California Current (Figure 12.2). Known areas of locally higher density often coincide with greater productivity (e.g., off Argentina). Specific patterns are discussed in the following paragraphs for each oceanic region, based on published accounts. It is important to bear in mind, however, that whaling catches (e.g., Nishiwaki and Handa 1958; Rice 1974; Ohsumi 1975; Dahlheim 1981; Mikhalev et al. 1981; Reeves and Mitchell 1988b) may have reduced the size of some local killer whale populations prior to abundance assessments.

North Pacific Ocean and Adjacent Arctic Waters

In the North Pacific Ocean, killer whales have been documented as far north as the Chukchi and Beaufort Seas in the Arctic Ocean (Lowry et al. 1987). Killer whales occur commonly in the eastern Bering Sea (Braham and Dahlheim 1982; Waite et al. 2002) and are frequently observed near the Aleutian Islands (Scammon 1874; Murie 1959; Waite et al.

2002). They occur year-round in the waters of southeastern Alaska (Scheffer 1967) and the intracoastal waterways of British Columbia and Washington State (Balcomb and Goebel 1976; Bigg et al. 1987; Osborne et al. 1988). Killer whales are commonly found along the coast of Washington and Oregon and are regularly found but less abundant off California (Norris and Prescott 1961; Fiscus and Niggol 1965; Rice 1968; Black et al. 1997; Barlow 1995; Forney et al. 1995). Killer whales are distributed sparsely but continuously throughout the eastern tropical Pacific (Dahlheim et al. 1982; Wade and Gerrodette 1993), including both coasts of Baja California (Guerrero-Ruiz et al. 1998; Gerrodette and Palacios 1996). Data provided by Gerrodette and Palacios (1996), combined with detection function estimates from Wade and Gerrodette (1993), allow estimation of killer whale densities by the Exclusive Economic Zones (EEZs) of eastern tropical Pacific countries, ranging from Mexico to Ecuador. The overall pattern appears to be one of decreasing density as one approaches the equator from either hemisphere, with a rare occurrence overall.

In the western North Pacific, killer whales are common along the Russian coast in the Bering Sea, the Sea of Okhotsk, and the Sea of Japan and along the eastern side of Sakhalin and the Kurile Islands (Tomilin 1957; Berzin and Vladimirov 1989). There are accounts of their occurrence off China (Wang 1985) and Japan (Nishiwaki and Handa 1958; Kasuya 1971, Ohsumi 1975), but killer whale encounters are rare or uncommon. Whaling catches of killer whales in Japanese waters may have lowered their current abundance relative to pristine levels. Central Pacific records are quite rare, but sightings have been documented around the Hawaiian Islands (Mobley et al. 2001; Barlow 2006) and between Hawaii and California (NMFS, 1997 Sperm Whale Abundance and Population Structure Cruise, unpublished).

South Pacific

In contrast to the North Pacific, records of killer whales are considerably scarcer in the South Pacific, mostly as a reflection of more limited sampling effort. The most systematically sampled areas south of the equator are those covered during eastern tropical Pacific dolphin cruises between 1986 and 1993 (Wade and Gerrodette 1993, Gerrodette and Palacios 1996), extending southward to about 15°S. Patterns of occurrence are similar to those north of the equator, indicating that killer whales are widespread but rare. Waters off Ecuador (excluding the Galápagos Islands), were estimated to contain about 75 killer whales (derived from Gerrodette and Palacios [1996] using the detection function estimates from Wade and Gerrodette [1993]). Sighting records off Galápagos indicate that killer whales are regular but rare in waters surrounding the archipelago (Merlen 1999). The only other quantitative estimate of killer whale abundance within the South Pacific Ocean was derived from photo-identification studies around New Zealand (Visser 2000), where an estimated 119 whales were found.

In other South Pacific regions, records indicate that killer whales are rare or uncommon throughout most of their range. Killer whales were sighted on three occasions during nonstandard sighting surveys in 1993–1995 between waters of the Peru Current off Chile and oceanic waters surrounding Easter Island (Aguayo et al. 1998). Although the total distance searched is not provided, the number of days of search effort suggests that killer whales are rare in oceanic waters of the southeastern Pacific (Table 12.2), although they appear to be more common in the more coastal waters of the Peru Current (Aguayo et al. 1998; Miyashita et al. 1995). In the Solomon Islands a 1993 sighting survey aboard two large research vessels resulted in one killer whale sighting during 3,700 km of search effort (Shimada and Pastene 1995). Taking platform and observer efficiency into account, this indicates that killer whales are rare in waters around the Solomon Islands. Surveys in French Polynesia during 1996–2000 (Gannier 2000; Laran and Gannier 2001) resulted in only one sighting of killer whales during more than 11,000 km. Ling (1991) compiled records from 1982 to 1990 of killer whales in South Australia and reported that they appeared to be present in most South Australian waters. Seasonal concentrations have been reported off Tasmania and Macquarie Island and in association with pinniped breeding activities. The available descriptions suggest that killer whales are uncommon in most South Australian waters, with localized areas in which they may be considered common.

Indian Ocean

Records of killer whales in the Indian Ocean and adjacent seas are generally rare. Most information on their distribution and relative abundance has been obtained during nonstandard sighting surveys and opportunistic studies. They have been reported taking catches from longlines targeting tuna in the Indian Ocean (Sivasubramanian 1965). A 1993 east-west survey transect through the Indian Ocean, at about 12°S, yielded one sighting of killer whales roughly midway between the Seychelles and the east coast of Africa (Eyre 1995), indicating that killer whales are rare in these waters. No killer whales were seen during a 1998 survey covering about 1,700 km in waters of the Maldives (Ballance et al. 2001). Visual and acoustic surveys within Komodo National Park, Indonesia, indicate that killer whales are present but rare, with two sightings in over 8,700 km surveyed. Photo-identification studies conducted during 1964–2000 in waters of the Crozet Archipelago, Southern Indian Ocean, indicate a small, regularly occurring population (Poncelet et al. 2002). Killer whales are also regular visitors at Marion Island in the Southern Indian Ocean during the southern elephant seal *(Mirounga leonina)* breeding season, with about 30 individually identified whales (Keith et al. 2001; Pistorius et al. 2002). In a synthesis of 1965–1988 data from Japanese whale scouting and whale sighting surveys, Miyashita et al. (1995) suggest that killer whales are more abundant, perhaps uncommon to common, in the Southern Indian Ocean.

TABLE 12.2
Regional Population Estimates for Killer Whales

Region	Source of abundance information	Data Type	Years	Area size (km²)
Atlantic Ocean and Adjacent Seas				
Norwegian Sea	Øien 1990	LTR	1988	477,727
Northern Norway	Similä et al. 1996	CAT	1990–1993	67,000
Iceland & Faroe Islands	Gunnlaugsson and Sigurjónsson 1990; Sigurjónsson et al. 1989	LTR	1987	2,281,630
NW Scotland	MacLeod et al. 2003	LTR	1998	104,000
North Sea/West of Great Britain	Stone 1997	SURV	1996	
Newfoundland/Labrador	Lien et al. 1988	SURV	1979–1986	
Southeastern U.S. shelf/slope	Garrison et al. 2003	LTR	2002	263,564
Western North Atlantic (SE U.S.)	Mullin and Fulling 2003	LTR	1998	573,000
Gulf of Mexico (Oceanic Northern Gulf)	Derived from Mullin and Hoggard 2000	LTR	1991–1997	398,960
Gulf of Mexico (Oceanic Northern Gulf)	Mullin and Fulling 2004	LTR	1996–2001	380,432
Gulf of Mexico (GulfCet I area)	Derived from Mullin and Hoggard 2000	LTR	1991–1997	154,621
Gulf of Mexico (aerial surveys)	Mullin and Hoggard 2000	LTR	1996–1998	82,796
Gulf of Mexico (shelf waters)	Fulling et al. 2003	LTR	1998–2001	245,800
Northern Spain	López et al. 2004	SURV	1998–1999	9,842
Mediterranean	Notarbartolo-di-Sciara 1987	OBS	1985	
Southern Brazil	Pinedo et al. 2002	SURV		
Patagonia, Argentina	López and López 1985; Iñíguez 2001	CAT	1985–1997	20,002
Southern Ocean				
Area II	Hammond 1984	LTR	1981–1982	1,830,660
Area III	Hammond 1984	LTR	1979–1980	1,795,778
Area IV	Hammond 1984	LTR	1978–1979	1,431,045
Area V	Hammond 1984	LTR	1980–1981	1,868,464
S of 60°S	Branch and Butterworth 2001	LTR	1978–1983	9,935,989
S of 60°S	Branch and Butterworth 2001	LTR	1985–1990	11,655,723
S of 60°S	Branch and Butterworth 2001	LTR	1991–1997	10,922,924
Southern Ocean	Kasamatsu and Joyce 1995	LTR	1976–1988	28,765,576
Marion Island, Southern Ocean	Keith et al. 2001; Pistorius et al. 2002	OBS	1973–2000	
Pacific Ocean and Adjacent Arctic Waters				
Central Bering Sea	derived from Waite et al. 2002	LTR	1999	196,885
SE Bering Sea	Waite et al. 2002	LTR	2000	158,561
Aleutian Islands	Forney (unpublished data)	LTR	1994	634,042
Aleutian Islands, west of Unimak	Zerbini et al. 2006	LTR	2001–2003	109,933
Gulf of Alaska, east of Unimak	Zerbini et al. 2006	LTR	2001–2003	107,680
Gulf of Alaska *transients*	Matkin et al. 1999	CAT		214,307
Western Alaska (excluding Kodiak)	Dahlheim 1997; Waite, personal communication	CAT		*94,998*
BC/Washington *residents*, summer	Ford et al. 2000; Carretta et al. 2002	CAT	1970–2003	129,889
Alaska Southeast to Kodiak *residents*	Matkin et al. 1999; Dahlheim, personal communication; Angliss and Lodge 2002	CAT		150,515
U.S. West Coast *transients*	Matkin et al. 1999; Matkin, personal communication; Angliss and Lodge 2002	CAT		400,904

Effort (km)	No. Si	No. Ani	Si/1000 km	Abundance Estimate	CV	Density (Animals per 100 km²)	Catalog or Minimum count	Abundance Category
Atlantic Ocean and Adjacent Seas								
5,742	7	67	1.22	3,100	0.63	0.65		Abundant
						0.61	408	Abundant
21,827	25	199	1.15	6,618	0.32	0.29		Common
2,157	0	0	0.00	0		0.00		Rare
7100 hrs	17	120						Uncommon
85,273	58		0.68					
3,744	0	0	0.00	0		0.00		Rare
4,163	0	0	0.00	0		0.00		Rare
				246	0.39	0.06		Rare
12,162	5	12	0.41	133	0.49	0.03		Rare
				92	0.48	0.06		Rare
4,101	0	0	0.00	0		0.00		Rare
2,196	0	0	0.00	0		0.00		Rare
8,128	0	0	0.00	0		0.00		Rare
								Rare
3,324	5	15	1.50					Common
	408						30	Uncommon
Southern Ocean								
11,810	13	301	1.10	12,367	0.69	0.68		Abundant
12,812	22	1,608	1.72	38,278	0.63	2.13		Abundant
12,792	24	946	1.88	16,399	0.55	1.15		Abundant
10,014	24	6,014	2.40	136,500	0.69	7.31		Abundant
65,979	117	2,002	1.77	91,310	0.34	0.92		Abundant
67,550	114	817	1.69	27,168	0.26	0.23		Common
52,334	68	836	1.30	24,790	0.23	0.23		Common
130,036	129	1,135	0.99	80,400	0.15	0.28		Common
							25–30	
Pacific Ocean and Adjacent Arctic Waters								
1,761	2	10	1.14	121		0.06		Rare
2,194	11	50	5.01	391	0.43	0.25		Common
2,780	14	75	5.04	2,594	0.44	0.41		Abundant
3,560	16	113	4.49	584	0.51	0.54		Abundant
5,494	14	192	2.55	655	0.54	0.61		Abundant
				32		0.01	32	Rare
				180		0.19	180	Uncommon
				295		0.23	295	Common
				440		0.29	440	Common
				344		0.09	344	Rare

TABLE 12.2 (CONTINUED)

Region	Source of abundance information	Data Type	Years	Area size (km^2)
Pacific Ocean and Adjacent Arctic Waters				
Oregon/Washington	Barlow 2003	LTR	1996–2001	325,018
California	Barlow 2003	LTR	1991–2001	817,549
California (aerial surveys)	Forney et al. 1995	LTR	1991–1992	264,270
Mexico (Gulf of California)	Guerrero-Ruiz et al. 1998	CAT	1972–1997	210,000
Eastern Tropical Pacific	Wade and Gerrodette 1993	LTR	1986–1990	19,148,000
Mexico (Gulf of California)	Gerrodette and Palacios 1996	LTR	1986–1993	262,125
Mexico (Pacific Coast EEZ)	Gerrodette and Palacios 1996	LTR	1986–1993	2,054,192
Central America EEZ	Gerrodette and Palacios 1996	LTR	1986–1993	323,013
Costa Rica EEZ	Gerrodette and Palacios 1996	LTR	1986–1993	475,737
Panama EEZ	Gerrodette and Palacios 1996	LTR	1986–1993	188,045
Columbia EEZ	Gerrodette and Palacios 1996	LTR	1986–1993	329,492
Ecuador EEZ	Gerrodette and Palacios 1996	LTR	1986–1993	229,863
Galapagos	Merlen 1999	OBS	1948–1997	
Eastern Temperate Pacific	NMFS, 1997 Sperm Whale Abundance and Population Structure Cruise, unpublished	LTR	1997	7,786,000
Hawaii	Barlow 2006	LTR	2002	2,452,916
Sea of Okhotsk	Berzin and Vladimirov 1989	OBS	1979–1984	
Kamchatka and Commander Islands	Miranova et al. 2002	OBS	1992–2000	
Japan (aerial surveys)	Kasuya 1971	SURV	1959–1970	
Western North Pacific	Miyashita et al. 1996	SURV	1993–1995	
Marquesas Islands/French Polynesia	Laran and Gannier 2001	SURV	1998–2000	
Society Islands/French Polynesia	Gannier 2000	SURV	1996–1999	
New Zealand	Visser 2000	CAT	1992–1997	
Solomon Islands	Shimada and Pastene 1995	SURV	1993	
Eastern South Pacific (Chile to Easter Island)	Aguayo et al. 1998	OBS	1993–1995	
Indian Ocean and Adjacent Seas				
Indian Ocean	Eyre 1995	SURV	1993	
Maldives	Ballance et al. 2001	SURV	1998	
South Australia	Ling 1991	OBS	1982–1990	
Komodos Island, Indonesia	Kahn and Pet 2003	SURV	1999–2001	
Crozet Archipelago	Poncelet et al. 2002	M-R	1977–2000	

NOTE: Worldwide estimates of abundance and density of killer whales. (Si = Sightings, Ani = Animals, CV = Coefficient of Variation).

North Atlantic and Adjacent Seas

The first comprehensive summary of killer whale occurrence in the North Atlantic (Sigurjónsson and Leatherwood 1988) was based largely on whaling records, incidental sightings, anecdotal information, strandings, and some photo-identification efforts in coastal waters. Overall, killer whales are rare to uncommon in lower latitudes of the North Atlantic, becoming increasingly common at higher latitudes. Quantitative survey-based estimates of killer whale abundance have been made in the eastern North Atlantic and adjacent seas, including waters off Norway, Iceland, and the Faroe Islands (Sigurjónsson et al. 1989; Gunnlaugsson and Sigurjónsson 1990; Øien 1990). Killer whales appear common to very abundant in most of these waters and are seasonally well known as they follow herring in coastal areas off Norway (Sigurjónsson et al. 1988; Similä et al. 1996). Whaling catches of killer whales in Norwegian waters may have lowered their current abundance compared to pristine abundance levels. They have been documented infrequently in the North Sea north of Great Britain during seismic surveys (Stone 1997).

Information for the western North Atlantic is primarily qualitative, but killer whales appear to be common in areas of the Canadian Arctic (Reeves and Mitchell 1988a,

Effort (km)	No. Si	No. Ani	Si/1000 km	Abundance. Estimate	CV	Density (Animals per 100 km²)	Catalog or Minimum count	Abundance Category
Pacific Ocean and Adjacent Arctic Waters								
7,482	7	52	0.94	898	0.35	0.28		Common
33,327	11	64	0.33	511	0.35	0.06		Rare
13,042	2	2	0.15	65	0.69	0.02		Rare
	156	843				0.04	86	Rare
135,300	57	308	0.42	8,500	0.37	0.04		Rare
4,377	3	13	0.12	146		0.06		Rare
25,356	15	56	0.59	852		0.04		Rare
5,251	3	12	0.57	143		0.04		Rare
8,465	4	14	0.47	153		0.03		Rare
3,692	1	1	0.27	10		0.01		Rare
5,856	1	6	0.17	64		0.02		Rare
1,164	1	2	0.86	75		0.03		Rare
								Uncommon
8,100	4	31	0.49					Rare
17,050	2	13	0.12	349	0.98	0.01		Rare
								Common
	274	1,619					700–800	Common
318,190	26	151	0.08					Rare
20,179	7	31	0.35					Rare
4,896	1	–	0.20	0		0.00		Rare
6,452	0	–	0.00	0		0.00		Rare
				119	0.20		115	Uncommon
3,704	1	5	0.27					Rare
581 hrs	3	8						Rare
Indian Ocean and Adjacent Seas								
23,030	1	2	0.04					Rare
1,700	0	–	0.00	0		0.00		Rare
	26							Common
8,716	2	–	0.23					Rare
							43–93	

Mitchell and Reeves 1988), uncommon but seasonally regular in Labrador and Newfoundland (Lien et al. 1988), and rare in the Bay of Fundy and in U.S. Atlantic waters (Katona et al. 1988; Reeves and Mitchell 1988b; CeTAP 1982). During recent surveys conducted along mid-latitudes of the U.S. East Coast, there were no killer whale sightings (Mullin and Fulling 2003). Killer whales are considered rare in the Gulf of Mexico (O'Sullivan and Mullin 1997; Mullin and Hoggard 2000, Fulling et al. 2003), the Caribbean (Katona et al. 1988; Mitchell and Reeves 1988), and the Mediterranean Sea (Notarbartolo-di-Sciara 1987). López et al. (2004) report that killer whales are absent or rare in waters of the eastern North Atlantic, based on 1998–1999 sighting records from fishery observers onboard vessels off northwestern Spain. In the broader eastern North Atlantic, killer whales are considered widespread in coastal and offshore areas, but nowhere common (Hammond and Lockyer 1988).

South Atlantic

Although the presence of killer whales has been documented in the South Atlantic for decades (Budylenko 1981), quantitative estimates of abundance for this region are not

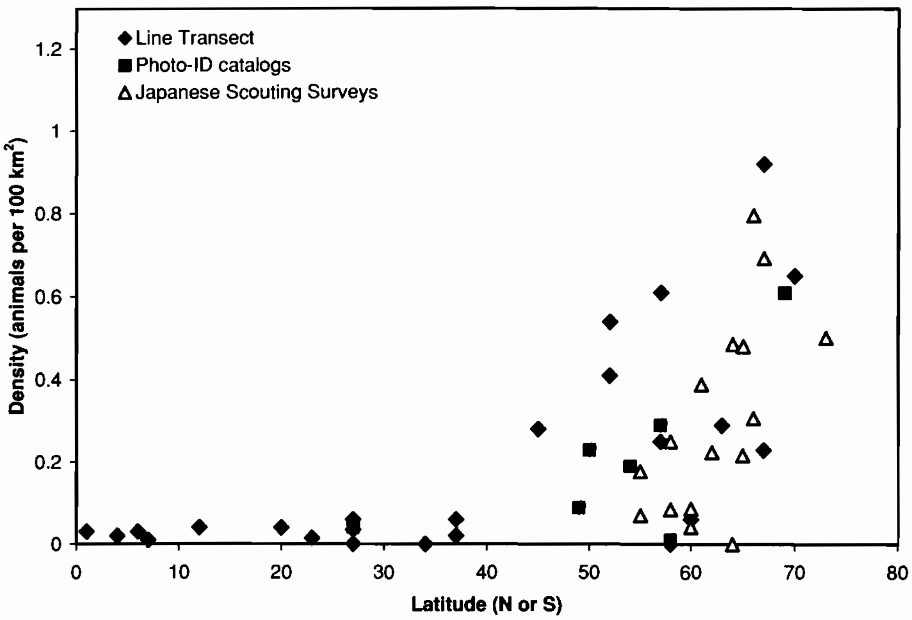

FIGURE 12.1. Worldwide killer whale density by latitude. Estimates are plotted separately for line-transect studies (diamonds), photo-identification catalog estimates of killer whale densities (squares), and Japanese whale scouting survey data (triangles; Kasamatsu and Joyce 1995), because the different types of estimates are not directly comparable.

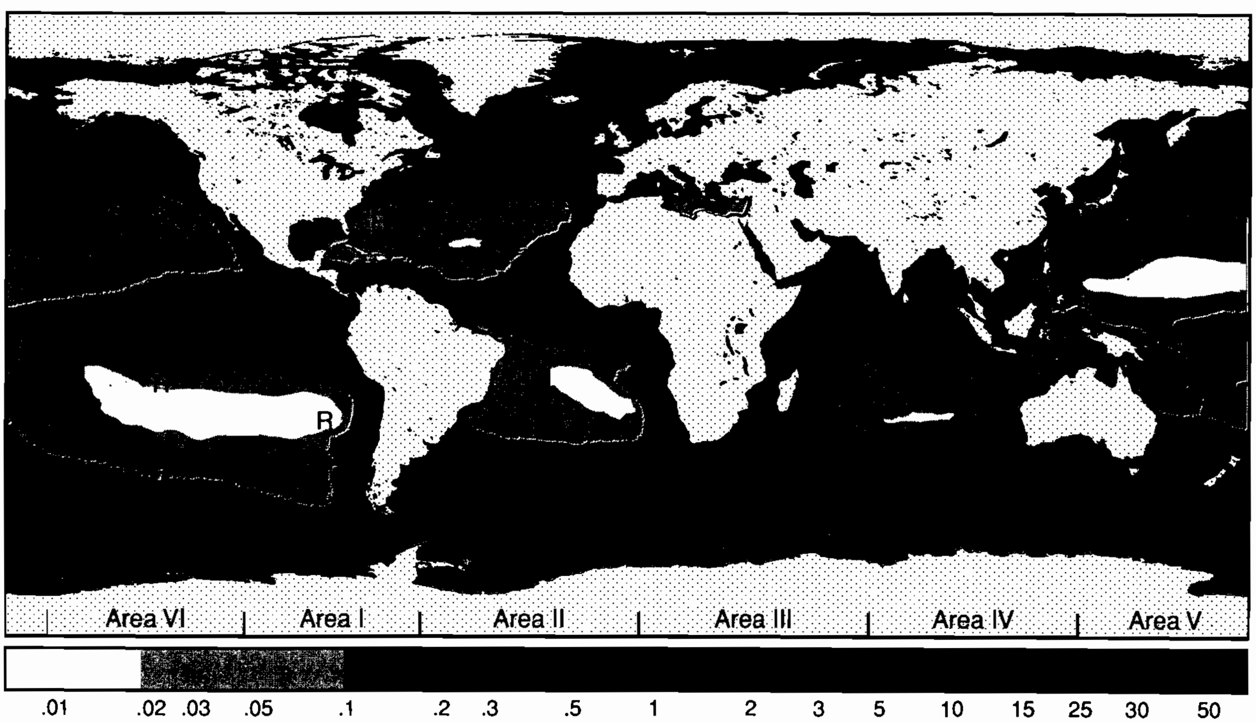

FIGURE 12.2. Worldwide killer whale densities, relative to ocean productivity as measured by the average chlorophyll-a concentration (mg/m^3) from SeaWiFS images, 1997–2002. Killer whale density categories are defined as (R) rare, 0–0.10 per 100 km^2; (U) uncommon, 0.10–0.20 per 100 km^2; (C) common, 0.20–0.40 per 100 km^2; and (A) abundant, >0.40 per 100 km^2. Labels in parenthesis represent greater uncertainty. Antarctic areas correspond to those used for IWC/IDCR surveys (Branch and Butterworth 2001). [Background image courtesy of NASA/Goddard Space Flight Center and ORBIMAGE, Inc.]

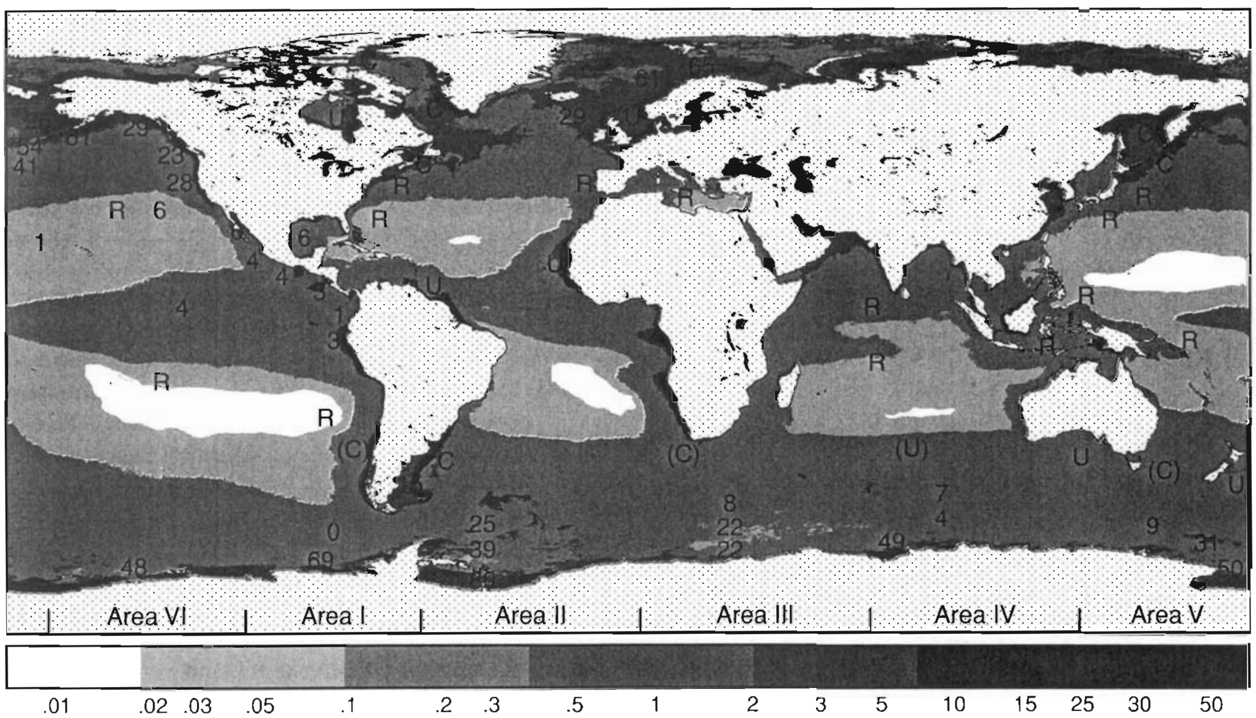

FIGURE 12.2. Worldwide killer whale densities, relative to ocean productivity as measured by the average chlorophyll-a concentration (mg/m^3) from SeaWiFS images, 1997–2002. Killer whale density categories are defined as (R) rare, 0–0.10 per 100 km^2; (U) uncommon, 0.10–0.20 per 100 km^2; (C) common, 0.20–0.40 per 100 km^2; and (A) abundant, >0.40 per 100 km^2. Labels in parenthesis represent greater uncertainty. Antarctic areas correspond to those used for IWC/IDCR surveys (Branch and Butterworth 2001). [Background image courtesy of NASA/Goddard Space Flight Center and ORBIMAGE, Inc.]

available. The best-studied population in the South Atlantic is regularly found off Patagonia, coincident with pinniped breeding activities, and is estimated to contain about 30 animals based on photo-identification efforts (López and López 1985; Iñíguez 2001). Killer whales are also known from pelagic waters off southern Brazil, where they have a history of depredation on tuna and swordfish longline catches (Secchi and Vaske 1998). During vessel of opportunity surveys conducted from fishing vessels off Southern Brazil in 1996–1999, killer whales were the second most common cetacean seen (Pinedo et al. 2002); however, it is possible that sighting rates were inflated because killer whales may have been attracted to the fishing vessels from which observations took place. When one takes into account only sightings that were made during vessel transits, not in association with longline operations, the overall encounter rate suggests that killer whales are nonetheless common off southern Brazil (Table 12.2). Sighting records and whaling catches indicate that killer whales are also found seasonally in the southeastern Atlantic (Budylenko 1981; Mikhalev et al. 1981), but insufficient effort data are available to categorize their abundance in this region. A map of data from Japanese whale scouting surveys (1964–1988) and whale sighting surveys (1972–1990) indicates that killer whales are common off the tip of Southern Africa (Miyashita et al. 1995).

Southern Ocean

Killer whales have long been known to be abundant in the Southern Ocean. Between 1961 and 1980, Soviet whaling operations are reported to have taken over 1,600 killer whales, including 906 killer whales during the 1979–1980 season (Mikhalev et al. 1981; Berzin and Vladimirov 1983). These operations may have reduced recent abundance in these areas. Several analyses of line-transect surveys have yielded abundance estimates for killer whales around Antarctica (Ohsumi 1981, Hammond 1984, Kasamatsu and Joyce 1995); however, some of the estimates were considered biased by methodology and survey coverage (Branch and Butterworth 2001). More recent estimates that account for some of these biases indicate that about 25,000 killer whales inhabit waters south of 60°S (Branch and Butterworth 2001); however, there are still uncertainties related to coverage of areas in the pack ice. Densities are known to vary locally within Antarctic waters, ranging from very abundant to uncommon (Secchi et al. 2002; Pitman and Ensor 2003), and it has been recognized that killer whale densities are higher closer to the ice edge, where Type B and C killer whales can occur in large aggregations of tens to hundreds of animals (Berzin and Vladimirov 1983, Pitman and Ensor 2003). Kasamatsu and Joyce (1995) calculated killer whale abundance separately for six east-west Antarctic areas and by distance from the ice edge. Although their absolute density values may be biased by the analytical methods used, their study provides a unique overview of relative patterns of Antarctic killer whale density by latitude; it is therefore included separately in the overall assessment of worldwide latitudinal patterns (Figure 12.1).

Conclusions

The abundance categories in this study should be considered provisional, particularly for areas with limited sampling. Overall, the observed patterns of worldwide killer whale distribution are in general agreement with previous descriptions, which indicate that killer whales are more common at higher latitudes and in coastal areas. Killer whale occurrence also appears broadly tied to regions of higher ocean productivity, as indicated by remotely sensed chlorophyll levels (Figure 12.2), and the latitudinal and inshore/offshore patterns of abundance may simply be a reflection of the higher productivity in coastal and high-latitude areas. Regions of similar latitude exhibit differences in abundance that may be tied to patterns of productivity and prey availability; for example, killer whales are rare along the U. S. northeast coast although they are common along the coast of Oregon and Washington, at a similar latitude.

Many portions of the world's ocean have not been adequately studied, but it is noteworthy that fish-eating specialists appear to occur only at high latitudes in the Pacific, Atlantic, and Southern Oceans. In both the Pacific and Southern Oceans, fish-eating specialists occur in sympatry or parapatry with other types of killer whales that appear to specialize on marine mammal prey, suggesting that in high-productivity areas killer whales have undergone a form of niche separation to take advantage of relatively abundant prey, and this may have occurred independently several times. Although relatively fewer studies have occurred at lower latitudes and in less productive areas, there is some suggestion that killer whales in these areas may be more generalist predators (Baird 2002). For example, killer whales that are thought to represent a single population in the Gulf of California have been observed to take both marine mammal and fish prey (Silber et al. 1990, Guerrero-Ruiz et al. 2002).

Although the available data are far from complete, abundance estimates for the areas that have been sampled provide a *minimum* worldwide abundance estimate of about 50,000 killer whales. It is likely that the total abundance is considerably higher, because estimates are not available for many high-latitude areas of the northern hemisphere and for large areas of the South Pacific, South Atlantic, and Indian Oceans. The impact of killer whales on the oceanic ecosystem is difficult to evaluate without further targeted studies, particularly given their broad range of prey species. Ultimately, their impact depends fundamentally on four things: how many there are, where they are, what they eat, and how much they eat. This study has provided a worldwide overview of the first two of these issues and provided limited information on the third. Combined with more detailed studies on diet, energetics, and foraging ecology of individual populations, this represents a step towards gaining a better understanding of the role of killer whales in the ecosystem.

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Cover photograph: Predator-prey interactions between killer whales and baleen whales, and how such behavioral interactions may have been altered by modern industrial whaling, has emerged as an intriguing and controversial topic of research. Detail of "The Greenland whale." © The New Bedford Whaling Museum.

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