Prevalence of the commensal barnacle *Xenobalanus globicipitis* on cetacean species in the eastern tropical Pacific Ocean, and a review of global occurrence

Emily A. Kane (contact author)[1, 2]

Paula A. Olson [2]

Tim Gerrodette[2]

Paul C. Fiedler[2]

Email address for E. A. Kane: ekane@tamu.edu

[1] Southampton College
239 Montauk Highway
Southampton, New York 11968

[2] National Marine Fisheries Service, NOAA
Southwest Fisheries Science Center
8604 La Jolla Shores Dr.
La Jolla, California 92037

Present address for contact author (E. A. Kane): Texas A&M University at Galveston
5007 Avenue U
Galveston, Texas 77551

Abstract—Distribution and prevalence of the phoretic barnacle *Xenobalanus* on cetacean species are reported for 22 cetaceans in the eastern tropical Pacific Ocean (21 million km^2). Four cetacean species are newly reported hosts for *Xenobalanus*: Bryde's whale (*Balaenoptera edeni*), long-beaked common dolphin (*Delphinus capensis*), humpback whale (*Megaptera novaeangliae*), and spinner dolphin (*Stenella longirostris*). Sightings of *Xenobalanus* in pelagic waters are reported for the first time, and concentrations were located within three productive zones: near the Baja California peninsula, the Costa Rica Dome and waters extending west along the 10°N Thermocline Ridge, and near Peru and the Galapagos Archipelago. Greatest prevalence was observed on blue whales (*Balaenoptera musculus*) indicating that slow swim speeds are not necessary for effective barnacle settlement. Overall, prevalence and prevalence per sighting were generally lower than previously reported. The number of barnacles present on an individual whale was greatest for killer whales, indicating that *Xenobalanus* larvae may be patchily distributed. The broad geographic distribution and large number of cetacean hosts, indicate an extremely cosmopolitan distribution. A better understanding of the biology of *Xenobalanus* is needed before this species can be used as a biological tag.

Manuscript submitted 28 January 2008.
Manuscript accepted 17 June 2008.
Fish. Bull 106:395–404 (2008).

Barnacles of the superfamily Coronuloidea live as obligate commensals on sea turtles, cetaceans, sirenians, sea snakes, and crustaceans (Newman and Ross, 1976). The monotypic *Xenobalanus globicipitis* Steenstrup, 1851 (herein referred to by genus) is specialized for living as a commensal on whales and dolphins (Darwin, 1854). The typical six-plate balanomorph shell is small and is imbedded into the skin of the cetacean host. The membrane supporting the operculum is greatly elongated, so that externally *Xenobalanus* resembles a pedunculate barnacle. This species is most commonly observed on the trailing edges of the dorsal fin, pectoral flippers, and tail fluke of the host, although it has been reported in areas such as the rostrum and the area between the teeth (Samaras, 1989). *Xenobalanus* does not receive nutrition from its cetacean host and therefore is not considered a parasite. Instead, as a suspension-feeding cirriped, it uses the water flow around swimming cetaceans and benefits from being transported by its host (phoresis). This species is highly specialized to live on cetaceans (Seilacher, 2005) and it has been suggested that its hermaphroditic reproduction may be synchronized with that of its host (Dollfus, 1968; Fertl, 2002). A five- to six-month reoccurrence cycle has been reported for *Xenobalanus* (Van Waerebeek et al., 1993; Orams and Schuetze, 1998), which may indicate that its life span may be of similar length or that occurrence is correlated with seasonal environmental conditions. *Xenobalanus* has been reported on 30 cetacean species worldwide and has a prevalence ranging from 0.5% to 55% of individuals in each sighting. However, intensity is highly variable, and there are some reports of greater than 100 barnacles on a single host (Aznar et al., 2005).

We examined the presence of *Xenobalanus* on cetaceans in the eastern tropical Pacific Ocean (ETP). Based on photographs taken during research cruises from 1977 through 2003, mean prevalence, mean intensity, and geographic distribution are described for *Xenobalanus* on 22 host cetacean species. In addition, peer-reviewed literature on this subject is examined, updating a previous summary of the cetacean hosts of this barnacle (Rajaguru and Shantha, 1992).

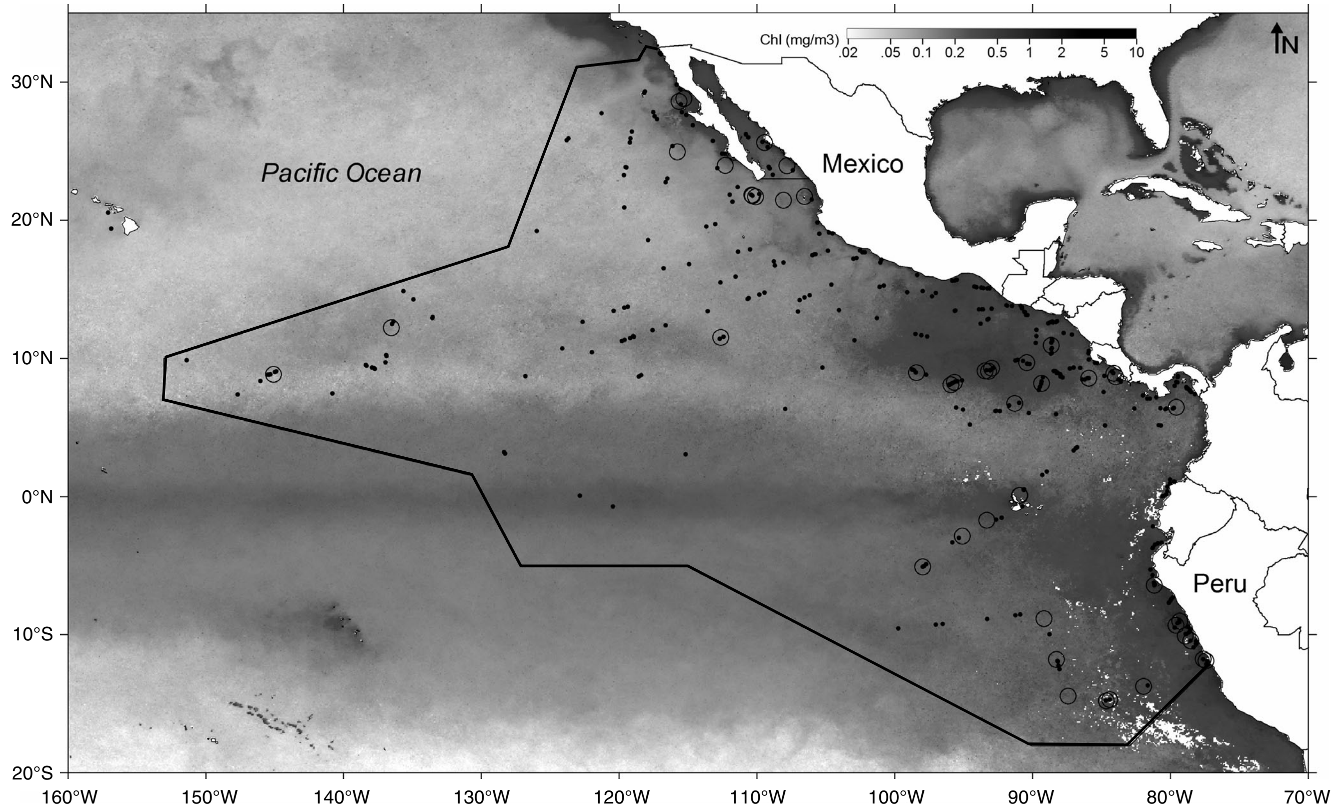

Figure 1

Xenobalanus presence or absence for 445 cetacean sightings in the eastern tropical Pacific Ocean (ETP) in 2003 as determined from analysis of identification photographs. Dots (●) indicate cetacean sightings with no *Xenobalanus* observed; circles (○) indicate sightings with one or more barnacles observed; the solid line indicates the border of the ETP study area. Presence or absence is overlaid on a background of graded shading representing the volume of chlorophyll-*a* (mg/m^3) averaged from September to November 2003.

Materials and methods

Data collection

Cetaceans were photographed during a 2-ship, 4-month research cruise in 2003, covering 26,000 km of transects surveyed for marine mammals (boundaries shown in Figs. 1 and 2). Camera equipment included Canon EOS 10D and D60 digital cameras (Canon USA, Lake Success, NY) with 75–300 mm image-stabilized zoom and 400-mm fixed lenses. Date, latitude and longitude, cetacean species (as identified by trained cruise personnel), and unique sighting number per cetacean group were recorded with each photograph. In the laboratory, additional data were recorded upon examination of photographs, including the number of usable photographs in the sighting (as described below), number of individual cetaceans identified in the sighting, number of individuals infested with *Xenobalanus*, and number of *Xenobalanus* present. If barnacles were clumped in such a way as to compromise the accuracy of the count, the maximum number of discernible barnacles was recorded. The resolution of the digital photographs was such that in most cases, individual barnacles were easily identified.

In external appearance, *Xenobalanus* may be confused with the parasitic copepod *Pennella balaenoptera* (Evans, 1994) or the stalked barnacle *Conchoderma virgatum* (Ruppert et al., 2004). However, the much larger *P. balaenoptera* usually occurs along the flanks, whereas *Xenobalanus* is generally found along the trailing edges of the dorsal fin, pectoral flippers, and the fluke, as has been described for stranded and live cetaceans. Similar to *P. balaenoptera*, *C. virgatum* requires a less specific position for attachment, requiring any hard substrate (such as another barnacle, a tooth, or exposed bone), and *C. virgatum* is considerably lighter in coloration than *Xenobalanus*. Digital photographic quality was sufficient for accurate identification of the commensal *Xenobalanus*; no specimens were obtained for direct examination.

During the cruise, typically many photographs were taken for each sighting. For our study, usable photographs had 1) to be in focus, 2) to be of sufficient resolution to identify a barnacle if present, and 3) to include at least one cetacean dorsal fin. For large schools, only one photograph per school was used in order to prevent recounting individuals. For small schools, only photographs of animals identifiable as individuals, either from field notes or from unique markings or pigmen-

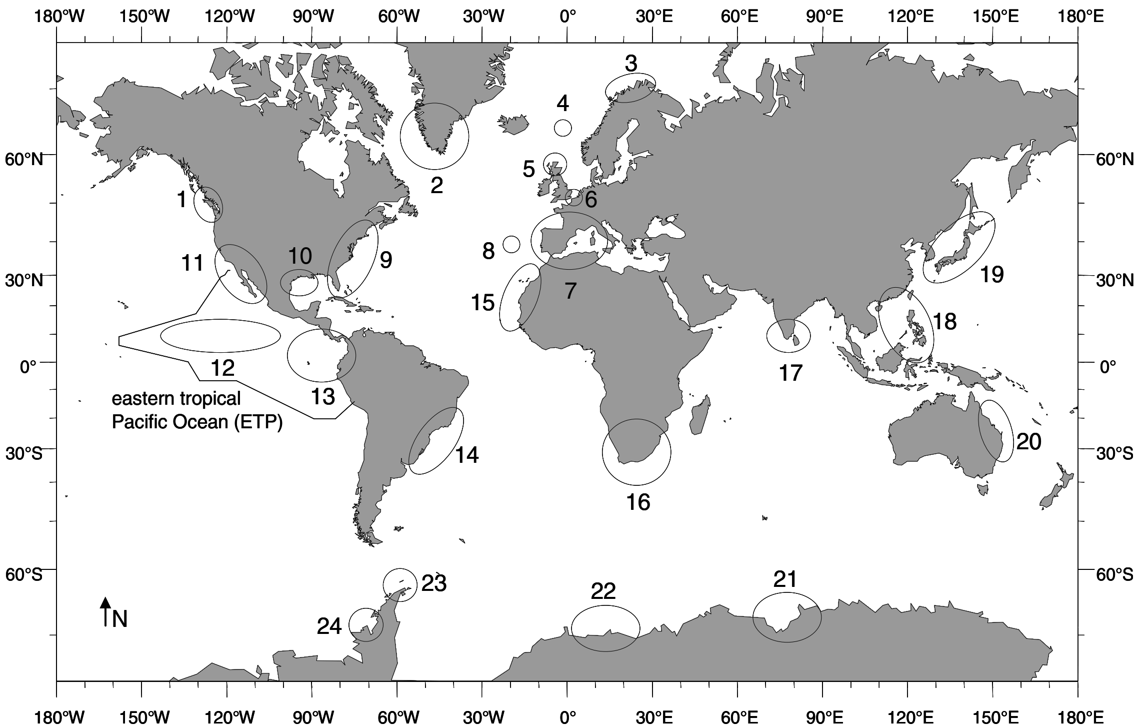

Figure 2

Documented sightings of *Xenobalanus* worldwide on various cetacean hosts compiled from literature review, and an outline of the current study area (eastern tropical Pacific Ocean). Ovals indicate the geographic region where barnacles have been reported and their size does not indicate intensity of infestation. Refer to Table 3 for the corresponding citations for each region.

tation, were used. Photographs used represent a subsample of individuals and did not include every animal observed. Killer whales (*Orcinus orca*) were studied in additional detail, by using photographs taken on previous cruises dating back to 1977, and including photographs from the ETP in the California and Mexico killer whale catalog (Black et al., 1997).

Data analysis

Two measures of prevalence of *Xenobalanus* were calculated for each cetacean species with at least three sightings with usable photographs. Prevalence was calculated for each sighting by dividing the number of individual whales or dolphins with barnacles by the total number of individual cetaceans identified. Mean prevalence and its standard error for each species were calculated from these values. Prevalence per sighting was calculated for each species by dividing the number of sightings with barnacles present by the total number of sightings. Mean barnacle intensity was calculated as the total number of barnacles observed on a host species divided by the number of infested hosts of the same species (Bush et al., 1997). To relate barnacle presence to primary productivity, the presence or absence of *Xenobalanus* at each cetacean sighting in 2003 was plotted on a map of average surface chlorophyll concentration in the ETP that was based on data provided by the SeaWiFS Project, NASA/Goddard Space Flight Center, and GeoEye.

Several statistical tests were performed to determine significant differences among the data. A nonparametric Mann Whitney-U test was used to determine if the rates of prevalence differed between Mysticetes and Odontocetes and a nonparametric Kruskal-Wallace test was used to determine if the prevalence rates differed significantly among species. Chi-square goodness-of-fit test was used to determine if the number of barnacles per killer whale followed a Poisson distribution. After normalization, linear regression was used to determine if the number of barnacles observed was predicted by the total number of animals observed in the sighting.

Results

Within the ETP over 10,000 photographs of 22 cetacean species and 2510 individuals revealed that 132 individuals of 14 species were host to *Xenobalanus* (Table 1). Out of 497 photographed sightings, 445 were determined to be usable in the analysis, and of these sightings, 47 displayed *Xenobalanus*: 38 odontocete sightings and 9 mysticete sightings. *Xenobalanus* was not observed on seven cetacean species and on one genus for which the species could not be identified: pygmy killer whale

Table 1

Summary of photographic data collected for cetaceans in the eastern tropical Pacific Ocean from 1977 through 2003, including the number of usable photographs ("photographs"), number of sightings ("sightings"), number of identifiable individual cetaceans ("individuals"), and number of identifiable individuals infested with *Xenobalanus* ("infested individuals"). ♦ Denotes newly reported hosts of *Xenobalanus* that were determined from this study.

Species	Common name	Years	Photographs	Sightings	Individuals	Infested individuals
Balaenoptera edeni♦	Bryde's whale	2003	415	30	43	3
Balaenoptera musculus	blue whale	2003	513	17	24	9
Balaenoptera physalus	fin whale	2003	92	4	6	1
Delphinus capensis♦	long-beaked common dolphin	2003	228	13	69	2
Delphinus delphis	short-beaked common dolphin	2003	1146	48	287	3
Feresa attenuata	pygmy killer whale	2003	25	1	11	0
Globicephala macrorhynchus	short-finned pilot whale	2003	1551	34	297	9
Grampus griseus	Risso's dolphin	2003	155	12	58	1
Lagenodelphis hosei	Fraser's dolphin	2003	34	1	6	0
Lagenorhynchus obliquidens	Pacific white-sided dolphin	2003	5	1	2	0
Lagenorhynchus obscurus	dusky dolphin	2003	245	11	68	4
Megaptera novaeangliae♦	humpback whale	2003	504	12	34	1
Mesoplodon spp.	unidentified *Mesoplodon*	2003	40	2	3	0
Orcinus orca	killer whale	1977–2003	1160	49	354	69
Peponocephala electra	melon-headed whale	2003	17	1	9	0
Physeter macrocephalus	sperm whale	2003	215	9	19	0
Pseudorca crassidens	false killer whale	2003	49	2	11	0
Stenella attenuata	pantropical spotted dolphin	2003	1281	76	326	4
Stenella coeruleoalba	striped dolphin	2003	845	51	319	18
Stenella longirostris♦	spinner dolphin	2003	770	39	271	3
Steno bredanensis	rough-toothed dolphin	2003	118	12	41	0
Tursiops truncatus	bottlenose dolphin	2003	600	61	252	5
Total			10,008	486	2510	132

(*Feresa attenuata*); Fraser's dolphin (*Lagenodelphis hosei*); Pacific white-sided dolphin (*Lagenorhynchus obliquidens*); melon-headed whale (*Peponocephala electra*); sperm whale (*Physeter macrocephalus*); false killer whale (*Pseudorca crassidens*), rough-toothed dolphin (*Steno bredanensis*); and three unidentified beaked whale individuals (*Mesoplodon* spp.) Of these, the barnacle has been previously reported throughout its worldwide range on pygmy killer whale, false killer whale, two species of beaked whales (*Mesoplodon* spp., Rajaguru and Shantha, 1992), Pacific white-sided dolphin (Dailey and Walker, 1978), and rough-toothed dolphin (Addink and Smeenk, 2001).

Four cetacean species seen in the ETP had not previously been reported as hosts of *Xenobalanus*: Bryde's whale (*Balaenoptera edeni*), long-beaked common dolphin (*Delphinus capensis*), humpback whale (*Megaptera novaeangliae*), and three forms of spinner dolphin (*Stenella longirostris*): eastern (*S. longirostris orientalis*) and the forms known commonly as whitebelly and southwestern spinner dolphins (Table 2). For Bryde's whales and humpback whales, the dorsal fin was the only visible appendage, as opposed to the long-beaked common dolphins and spinner dolphins for which pectoral flippers and tail flukes were also visible. The humpback whale individual that displayed a single specimen of *Xenobalanus* appeared to have a damaged dorsal fin.

Prevalence and intensity of the barnacle

Blue whales (*Balaenoptera musculus*) had the highest mean prevalence of the barnacle, followed by fin whales (*B. physalus*) and killer whales (Fig. 3A). There was a significant difference in mean prevalence among species (χ^2_{30}=50.6, P<0.01) and Mysticetes had a higher mean prevalence of the barnacle than Odontocetes (5.1% vs. 0.8%). Standard error was greatest for blue (13.8) and fin whales (16.5); all other species had a standard error less than 1.5. Blue, fin, and killer whales also had the highest prevalence per sighting, and 38% of killer whale sightings had barnacles (Fig. 3B). Prevalence per sighting was similar for Mysticetes and Odontocetes (12.7% vs. 14.0%)—a nonsignificant difference (P=0.19). Of the three species most often infested, killer whales repre-

Table 2

Dates and geographic locations (latitude and longitude) for sightings of newly documented cetacean hosts of *Xenobalanus* in the eastern tropical Pacific Ocean in 2003. Data are the following: total number of individuals of the species photographed ("individuals"), total number of these individuals observed with barnacles ("infested individuals"), and barnacle intensity and anatomical location on the host ("intensity and location on the host").

Host	Individuals	Infested individuals	Intensity and location on the host	Date	Geographic location
Balaenoptera edeni Bryde's whale	64	3	4 on dorsal fin	03 November 2003	09.012°S 079.302°W
Delphinus capensis long-beaked common dolphin	69	1	1 on right pectoral flipper	12 August 2003	25.620°N 109.456°W
Megaptera novaeangliae humpback whale	34	1	1 on dorsal fin	05 November 2003	06.414°S 081.176°W
Stenella longirostris orientalis eastern spinner dolphin	99	1	1 on left pectoral flipper	15 August 2003	21.448°N 108.084°W
Stenella longirostris hybrid whitebelly spinner dolphin	91	1	1 on dorsal fin	20 August 2003	08.857°N 145.098°W
Stenella longirostris southwestern southwestern spinner dolphin	32	1	2 or more on right pectoral flipper	14 October 2003	05.084°S 097.974°W

sented the majority of individuals used in the analysis (14%), whereas blue whales (1%) and fin whales (0.2%) were rarely encountered. The number of barnacles was, therefore, independent of number of individuals observed (R^2=0.00, F=0.10, P=0.08).

Xenobalanus was found in coastal as well as offshore waters of the ETP (Fig. 1). All 22 species were represented in offshore sightings and 28% of individuals encountered were seen in waters greater than 600 km from land, and at a maximum distance of 4287 km from land. Of these offshore occurrences, 39 *Xenobalanus* were observed on 18 individuals comprising seven species. *Xenobalanus* was primarily observed in three areas: 1) waters around the Baja California peninsula, 2) the Costa Rica Dome and waters extending west along the 10°N Thermocline Ridge, and 3) waters off Peru and the Galapagos Archipelago. All three areas are known as areas of increased primary productivity within the ETP (Fig. 1, Fiedler et al., 1991; Pennington et al., 2006).

For killer whales, which were examined in more detail, of the 68 whales infested with 130 barnacles, the mean intensity of infestation was 1.9 barnacles per whale. The greatest numbers of killer whales were photographed in 1998–2003, and these whales also had the greatest intensity of barnacles. This observed increase in intensity was most likely the result of improved photographic techniques. The observed numbers of killer whales with 0, 1, 2, 3, and >3 barnacles were 286, 38, 15, 7, and 8, respectively. This is significantly different from the expected 245, 90, 17, 2, and 0 infested whales, respectively, as predicted by a Poisson distribution with mean 130/354 = 0.367 (χ^2_5>300, P<0.00001). The variance (0.941) was much larger than the mean (0.367).

Literature review

A chart of the worldwide distribution of *Xenobalanus* was generated from a review of the literature documenting regional occurrences of this genus (Fig. 2). Except for the ETP, *Xenobalanus* has been reported only within approximately 600 km from land, including the Faröe Islands and the Azores (sites 4 and 8). Figure 2 also demonstrates that *Xenobalanus* is highly cosmopolitan and has been reported in all oceans, namely in tropical, temperate, and polar waters.

The literature review updates a previous review conducted by Rajaguru and Shantha (1992). Eighteen peer-reviewed accounts have been published since that review, including that of the present study (Table 3). Additionally, ten records of *Xenobalanus* had not been included in Rajaguru and Shantha's (1992) review. An additional 14 cetacean species are now included: minke whale (*Balaenoptera acutorostrata*), Bryde's whale, long-beaked common dolphin, Pacific white-sided dolphin, dusky dolphin (*Lagenorhynchus obscurus*), right whale dolphin (*Lissodelphis borealis*), humpback whale, vaquita (*Phocoena sinus*), Burmeister's porpoise (*Phocoena spinipinnis*), franciscana (*Pontoporia blainvillei*), clymene dolphin (*Stenella clymene*), spinner dolphin,

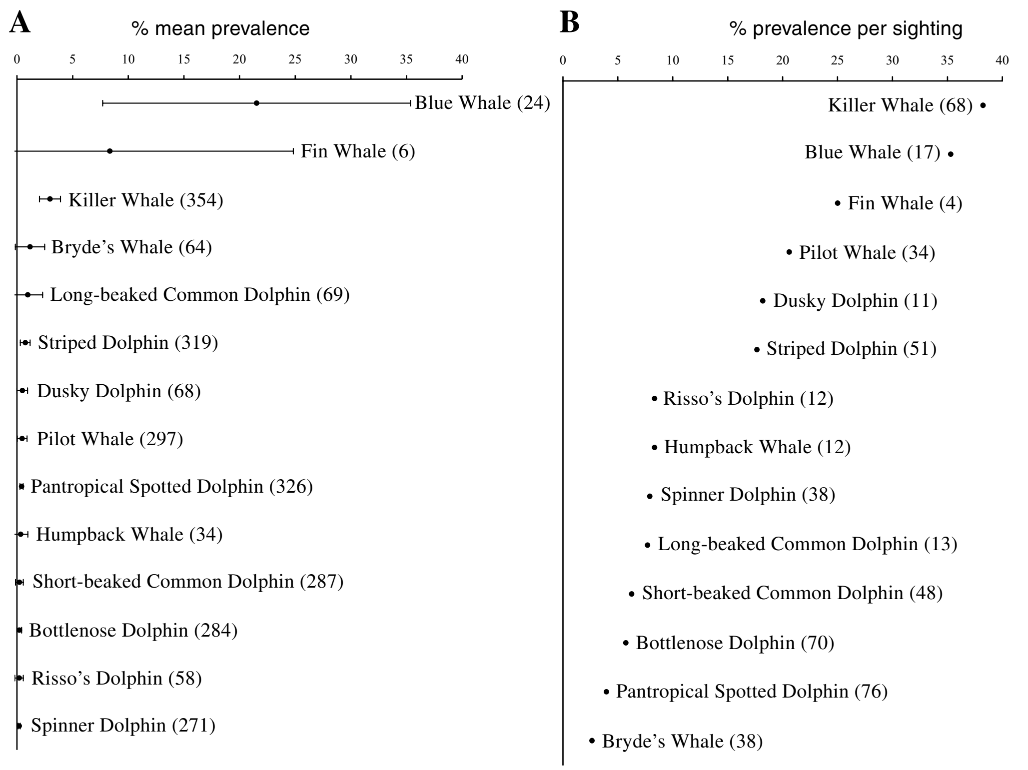

Figure 3

Prevalence of *Xenobalanus* on cetaceans in the eastern tropical Pacific Ocean in 2003 as determined from cetacean identification photographs; (**A**) percent mean prevalence of *Xenobalanus* ±2 standard errors, and (**B**) percent prevalence of *Xenobalanus* per sighting (number of sightings with barnacles/total number of sightings of a species). The number in parentheses (n) represents the total number of individuals and sightings, respectively, observed for each cetacean species on which *Xenobalanus* was observed.

rough-toothed dolphin, and Indo-Pacific bottlenose dolphin (*Tursiops aduncus*).

Discussion

Prevalence and intensity of the barnacle

We describe four new host species for the cetacean-specific phoretic barnacle *Xenobalanus* and document that the barnacle is present on cetaceans far offshore as well as in coastal areas. The fact that *Xenobalanus* has now been reported on 34 species of cetaceans in both coastal and offshore waters, from the Arctic to Antarctic, either 1) indicates that the barnacle is extremely cosmopolitan (Newman and Ross, 1976; Spivey, 1981), or 2) may suggest that more than one species of the genus *Xenobalanus* is involved.

Mean prevalence results from this study were lower than those from previous published accounts: 0.2% vs. 4–19% for short-beaked common dolphins (*Delphinus delphis*) (Pilleri, 1970; Dailey and Walker, 1978), 0.2% vs. 43–56% for bottlenose dolphins (*Tursiops truncatus*) (Di Beneditto and Ramos, 2004; Toth-Brown and Hohn, 2007), and 0.7% vs. 33–43% for striped dolphins (*Stenella coeruleoalba*) (Pilleri, 1970; Aznar et al., 2005). Two striped dolphins have been reported with an intensity of more than 100 *Xenobalanus* (Aznar et al., 2005), but the greatest intensity observed in our study was seven, on killer whales.

Although some differences in prevalence are due to previous reports of maximum, rather than mean, rates, the prevalence of *Xenobalanus* infestation reported in this study is underestimated because not all barnacles present on the animals were visible in our photographs. Only one side of the animal was photographed, and often part of the body was in the water. On the other hand, prevalence reported in many previous studies may have been overestimated when rates were based on mortality events and strandings. Because stranded animals are not usually healthy, the reported rates could represent an abnormal presence of the barnacle, as was observed in Aznar et al. (2005). Differences may also be related to habitat. Moreover, previous reports have

Table 3

Geographic regions and corresponding citations for each region where *Xenobalanus* has been documented on cetaceans worldwide. "Circle" refers to the regions encircled in Figure 2. References cited in Rajaguru and Shantha (1992) have been omitted individually, but are included under the citation for Rajaguru and Shantha (1992). Additional data about new hosts determined in the present study are available in Table 2.

Circle	Geographic region	Citation
1	Pacific Northwest United States and Canada	Rajaguru and Shantha (1992)
2	Greenland	Rajaguru and Shantha (1992)
3	Northern Scandanavian peninsula	Rajaguru and Shantha (1992)
4	Feröe Islands	Rajaguru and Shantha (1992)
5	Scotland and Shetland Islands	Rajaguru and Shantha (1992)
6	Belgium	Rajaguru and Shantha (1992)
7	Western Mediterranean and Iberian Peninsula	Raga and Carbonell (1985), Rajaguru and Shantha (1992), Aguilar and Raga (1993), Resendes et al. (2002), Aznar et al. (2005)
8	Azores	Rajaguru and Shantha (1992)
9	East coast United States and the Bahamas	Rajaguru and Shantha (1992), Toth-Brown and Hohn (2007)
10	Gulf of Mexico	Spivey (1981), Jefferson et al. (1995)
11	Southern California and Baja Peninsula	Dailey and Walker (1978), Brownell et al. (1987), Samaras (1989), This study
12	Pelagic ETP	This study
13	Costa Rica Dome, Galapagos, and Peru	Van Waerebeek et al. (1990, 1993), Reyes and Van Waerebeek (1995), Palacios et al. (2004), This study
14	Southeast coast of Brazil and Uruguay	Brownell (1975), Young (1991), Rajaguru and Shantha (1992), Di Beneditto and Ramos (2000, 2001, 2004)
15	Northwestern coast of Africa	Van Bree (1971), Rajaguru and Shantha (1992), Addink and Smeenk (2001)
16	South Africa and Namibia	Rajaguru and Shantha (1992)
17	Southern India	Rajaguru and Shantha (1992), Karuppiah et al. (2004)
18	Philippines, South China Sea, Hong Kong	Parsons et al. (2001)
19	Japan	Uchida and Jun (2000), Sakai et al. (2006)
20	East coast of Australia	Rajaguru and Shantha (1992), Orams and Schuetze (1998)
21	Mawson and Davis seas, Antarctica	Bushev (1990)
22	Riiser-Larsen and Lazarev Seas, Antarctica	Bushev (1990)
23	Shetland Islands, northwest Weddell Sea, Antarctica	Bushev (1990)
24	Bellinghausen Sea, Antarctica	Bushev (1990)

primarily been composed of data from coastal areas, whereas our study was focused on pelagic waters.

Factors affecting the presence of *Xenobalanus*

Other behavioral and environmental factors may also affect barnacle presence on cetaceans within the ETP. Swimming speed of the host has been shown to correlate negatively with intensity of the whale lice *Isocyamus delphini* (Balbuena and Raga, 1989) and has been hypothesized as an inversely proportional factor in *Xenobalanus* settlement (Orams and Schuetze, 1998; Aznar et al., 2005). In our study, blue whales had the greatest mean intensity of *Xenobalanus* and have been shown to sustain cruising speeds up to 33 km/hr (Yochem and Leatherwood, 1985), indicating that swimming speed may not be a primary factor in host species selection for *Xenobalanus*. Abrasive breaching and slapping behavior of the host may scour barnacles and inhibit settlement; however, some barnacles appear resistant (Felix et al., 2006; Sakai et al., 2006). In the ETP, deep-diving sperm whales (*Physeter macrocephalus*) and beaked whales (*Mesoplodon* spp.) were not hosts, indicating that dive depth of the host may limit the settlement of the barnacle on these species. Orams and Schuetze (1998) and Toth-Brown and Hohn (2007) have suggested an environmental correlation in the distribution of *Xenobalanus* that is similar to that observed between primary production and barnacle presence in the ETP. Plankton abundance in oligotrophic areas of the ETP may be below a critical threshold for the filter-feeding barnacles and may thus indirectly limit the presence of *Xenobalanus*.

The intensity of barnacles on killer whales in the ETP was not randomly distributed. There were more whales with no barnacles and with three or more barnacles than would be expected if barnacles settled randomly on killer whales, indicating that if *Xenobalanus* larvae settle, it is most often in groups of three or more. This aggregated or contagious distribution could occur as a result of: 1) a chemical cue emitted from the host that induces settlement (Nogata and Matsumura, 2005), 2) a chemical cue emitted from conspecifics that induces settlement (Knight-Jones, 1953), which was suggested for *Xenobalanus* by Aznar et al. (2005), 3) patchily distributed barnacle larvae, or 4) an inability of the host to slough newly settled larvae (Ridgway et al., 1997). The low variance in prevalence and the nonuniform distribution of *Xenobalanus* sightings within the ETP indicate that most species are equally selected and that barnacle recruitment may be the result of patchily distributed larvae.

Xenobalanus has been reported on a wide variety of cetacean hosts, and this apparent lack of specialization could provide insight into evolutionary age of *Xenobalanus*. Various species of cyamid whale lice are highly specialized for a particular species of right whale (*Eubalaena* spp., Kaliszewska et al., 2005). *Xenobalanus* is more of a generalist than whale lice, given its apparent ability to settle on various cetacean hosts, which may indicate that its evolution and relationship with cetaceans may be more recent than that of other cetacean commensals, and that its specialization to host species has not yet occurred. Coronulid whale barnacles did not appear in the fossil record until approximately 23 million years ago (Newman and Ross, 1976; Seilacher, 2005), after the appearance of Mysticetes and Odontocetes in the fossil record approximately 35 million years ago. However, it is unknown at what point the genus *Xenobalanus* arose, and presently no data exist on the evolutionary age of cyamids for comparison. In the ETP, *Xenobalanus,* appearing on almost every cetacean species encountered*,* did not exhibit the degree of host specialization observed in whale lice. With a lack of data on evolutionary age, these findings support only the hypothesis that *Xenobalanus* is a generalist cetacean barnacle.

Biological tags

The relationship between commensals and their hosts, which can indicate host movement and host distributional patterns, is often used to make inferences into the biology and ecology of the host. Comparison of internal parasite fauna has helped distinguish stocks, determine stock associations, track large-scale movements, and identify new recruits to populations in many species of fish, elasmobranchs, invertebrates, and marine mammals (Williams et al., 1992). Among marine mammals, intestinal parasites, whale lice, and barnacles have proven useful for tracking migrations of gray whales (*Eschrichtius robustus*; Killingley, 1980) and identifying stocks and the social structure of pilot whales (*Globicephala melas*; Balbuena and Raga, 1993), and have been useful for tracking general movement patterns of wide ranging, elusive cetacean populations without the use of expensive tagging equipment.

Our results indicate that *Xenobalanus*, however, would not be useful as a biological tag. Within the ETP, *Xenobalanus* is widely distributed and a single, definitive source or home range was not determined for this species. However, this is the first study where distribution of *Xenobalanus* has been systematically examined on a large scale and it is possible that the few offshore observations within the ETP are not representative of global distribution. Although *Xenobalanus* could not be used as a biological tag to track the movements of cetaceans within the ETP in this study, the potential use of *Xenobalanus* as a biological tag should not be abandoned completely. Increased knowledge of the biology of the barnacle, such as host-selection criteria, environmental tolerance limits, and early life history strategies could provide a finer resolution of the phoretic relationship with cetacean species that would enable the use of *Xenobalanus* as a biological tag in future studies. This and other research on *Xenobalanus* will form a useful part of the study of cetacean biology and ecology.

Acknowledgments

Funding for travel and living expenses for E. A. Kane was provided by the Evan Frankel Foundation. We thank J. Barlow, M. Kretzmann, and W. Perrin for reviewing the manuscript before submission, as well as D. Fertl and two anonymous reviewers for their helpful comments. We also thank N. Black and the many scientists and researchers who donated photographs, references, and information for the project.

Literature cited

Addink, M. J., and C. Smeenk.
2001. Opportunistic feeding behavior of rough-toothed dolphins *Steno bredanensis* off Mauritania. Zool. Verh. (Leiden) 334:37–48.

Aguilar, A., and J. A. Raga.
1993. The striped dolphin epizootic in the Mediterranean Sea. Ambio 22:524–528.

Aznar, F. J., D. Perdiguero, A. Perez del Olmo, A. Repulles, C. Agusti, and J. A. Raga.
2005. Changes in epizoic crustacean infestations during cetacean die-offs: the mass mortality of Mediterranean striped dolphins *Stenella coeruleoalba* revisited. Dis. Aquat. Org. 67:239–247.

Balbuena, J., and J. A. Raga.
1989. Ecology and host relationships of the whale-louse

Isocyamus delphini (Amphipoda: Cyamidae) parisitizing long-finned pilot whales (*Globicephala melas*) off the Faroe Islands (Northeast Atlantic). Can. J. Zool. 69:141–145.

1993. Intestinal helminths as indicators of segregation and social structure of pods of long-finned pilot whales (*Globicephala melas*) off the Faroe Islands. Can. J. Zool. 72:443–448.

Black, N., A. Schulman-Janiger, R. Ternullo, and M. Guerrero-Ruiz.

1997. Killer whales of California and western Mexico: a catalog of photo-identified individuals. NOAA Tech. Rep. NMFS-SWFSC 247, 174 p.

Brownell, R.

1975. Progress report on the biology of the Franciscana, *Pontoporia blainvillei*, in Uruguayan waters. J. Fish. Res. Board Can. 32:1073–1078.

Brownell, R. L., L. T. Findley, O. Vidal, A. Robles, and S. Manzanilla.

1987. External morphology and pigmentation of the vaquita, *Phocoena sinus* (Cetacea, Mammalia). Mar. Mamm. Sci. 3:22–30.

Bush, A. O., K. D. Lafferty, J. M. Lotz, and A. W. Shostak.

1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. J. Parasitol. 83:575–583.

Bushev, S.

1990. A study of the population structure of the southern minke whale (*Balaenoptera acutorostrata* Lacépède) based on morphological and ecological variability. Rep. Int. Whal. Comm. 40:317–324.

Dailey, M. D., and W. A. Walker.

1978. Parasitism as a factor **(?)** in single strandings of southern California cetaceans. J. Parasitol. 64:593–596.

Darwin, C.

1854. A monograph on the subclass Cirripedia, II the Balanidae, Verrucidae, etc., 684 p. Royal Soc. Publs., London, England.

Di Beneditto, A. P. M., and R. M. A. Ramos.

2000. Records of the barnacle *Xenobalanus globicipitis* (Steenstrup, 1851) on small cetaceans of Brazil. Biotemas 13:159–165.

2001. Biology and conservation of the franciscana (*Pontoporia blainvillei*) in the north of Rio de Janeiro State, Brazil. J. Cetacean Res. Manag. 3:185–192.

2004. Biology of the marine tucuxi dolphin (*Sotalia fluviatilis*) in south-eastern Brazil. J. Mar. Biol. Assoc. UK 84:1245–1250.

Dollfus, R.

1968. *Xenobalanus globicipitis* Steenstrup (Cirripedia, Thoracica): collected on *Tursiops truncatus* (Montagu) near the northern coast of Morocco. Bull. Inst. Pêches Marit. Maroc. 16:55–59. [In French.]

Evans, W. E.

1994. Common dolphin, white-bellied porpoise *Delphinus delphis* Linnaeus, 1758. *In* Handbook of marine mammals, vol. 5: The second book of dolphins and the porpoises (S. H. Ridgway, and R. Harrison, eds.), p. 216–217. Academic Press, San Diego, CA.

Felix, F., B. Bearson, and J. Falconi.

2006. Epizoic barnacles removed from the skin of a humpback whale after a period of intense surface activity. Mar. Mamm. Sci. 22:979–984.

Fertl, D.

2002. Barnacles. *In* Encyclopedia of Marine Mammals (W. F. Perrin, B. Würsig, and J. G. M. Thewissen, eds.), p. 75–78. Academic Press, San Diego, CA.

Fiedler, P. C., V. Philbrick, and F. P. Chavez.

1991. Oceanic upwelling and productivity in the eastern tropical Pacific. Limnol. Oceanogr. 36:1834–1850.

Jefferson, T. A., D. Odell, and K. Prunier.

1995. Notes on the biology of the clymene dolphin (*Stenella clymene*) in the northern Gulf of Mexico. Mar. Mamm. Sci. 11:564–573.

Kaliszewska, Z. A., J. Seger, V. J. Rowntree, S. G. Barco, R. Benegas, P. B. Best, M. W. Brown, R. L. Brownell, A. Carribero, R. Harcourt, A. R. Knowlton, K. Marshall-Tilas, N. J. Patenaude, M. Rivarola, C. M. Schaeff, M. Sironi, W. A. Smith, and T. K. Yamada.

2005. Population histories of right whales (Cetacea: Eubalaena) inferred from mitochondrial sequence diversities and divergences of their whale lice (Amphipoda: Cyamus). Mol. Ecol. 14:3439–3456.

Karuppiah, S., A. Subramanian, and P. Obbard.

2004. The barnacle *Xenobalanus globicipitis* (Cirripedia, Coronulidae) attached to the bottlenose dolphin *Tursiops truncatus* (Mammalia, Cetacea) on the southeastern coast of India. Crustaceana 7:879–882.

Killingley, J. S.

1980. Migrations of California gray whales tracked by oxygen-18 variations in their epizoic barnacles. Science 207:759–760.

Knight-Jones, E. W.

1953. Laboratory experiments on gregariousness during settling in *Balanus balanoides* and other barnacles. J. Exp. Biol. 30:584–598.

Newman, W. A., and A. Ross.

1976. Revision of the Balanomorph barnacles; including a catalog of species. S. Diego Soc. Nat. Hist. Mem. 9:1–108.

Nogata, Y., and K. Matsumura.

2005. Larval development and settlement of a whale barnacle. Biol. Lett. 2:92–93.

Orams, M. B., and C. Schuetze.

1998. Seasonal and age/size-related occurrence of a barnacle (*Xenobalanus globicipitis*) on bottlenose dolphins (*Tursiops truncatus*). Mar. Mamm. Sci. 14:186–189.

Palacios, D. M., S. K. Salazar, and D. Day.

2004. Cetacean remains and strandings in the Galápagos Islands, 1923–2003. Lat. Am. J. Aquat. Mamm. 3:127–150.

Parsons, E. C. M., R. M. Overstreet, and T. A. Jefferson.

2001. Parasites from Indo-Pacific hump-backed dolphins (*Sousa chinensis*) and finless porpoises (*Neophocaena phocaenoides*) stranded in Hong Kong. Vet. Rec. 148:776–780.

Pennington, J. T., K. L. Mahoney, V. S. Kuwahara, D. D. Kolber, R. Calienes, and F. P. Chavez.

2006. Primary production in the eastern tropical Pacific: a review. Prog. Oceanogr. 69:285–317.

Pilleri, G.

1970. *Xenobalanus globicipitis* Steenstrup on *Delphinus delphus*, *Stenella styx*, *Tursiops truncatus* in the western Mediterranean. *In* Investigations on Cetacea, vol. 2 (G. Pilleri, ed.), p. 248–249. Waldau-Berne, Berne, Switzerland.

Raga, J. A., and E. Carbonell.

1985. New dates about parasites on *Stenella coeruleoalba* (Meyen, 1833) (Cetacea: Delphinidae) in the western Mediterranean Sea. *In* Investigations on Cetacea, vol. 17 (G. Pilleri, ed.), p. 207–213. Waldau-Berne, Berne, Switzerland.

Rajaguru, A., and G. Shantha.
1992. Association between the sessile barnacle *Xenobalanus globicipitis* (Coronulidae) and the bottlenose dolphin *Tursiops truncatus* (Delphinidae) from the Bay of Bengal, India, with a summary of previous records from cetaceans. Fish. Bull. 90:197–202.

Resendes, A., C. Juan-Sallés, S. Almeria, N. Majó, M. Domingo, and J. Dubey.
2002. Hepatic sarcocystosis in a striped dolphin (*Stenella coeruleoalba*) from the Spanish Mediterranean coast. J. Parasitol. 88:206–209.

Reyes, J. C., and K. Van Waerebeek.
1995. Aspects of the biology of the Burmeister's porpoise from Peru. Rep. Int. Whaling Comm. Spec. Issue 16:349–364.

Ridgway, S. H., E. Lindner, K. A. Mahoney, and W. A. Newman.
1997. Gray whale barnacles *Cryptolepas rhachianecti* infest white whales, *Delphinapterus leucas*, housed in San Diego Bay. Bull. Mar. Sci. 61:377–385.

Ruppert, E., R. Fox, and R. Barnes.
2004. Invertebrate zoology: a functional evolutionary approach, 963 p. Brooks/Cole, Belmont, CA.

Sakai, M., T. Hishii, S. Takeda, and S. Kohshima.
2006. Flipper rubbing behaviors in wild bottlenose dolphins (*Tursiops aduncus*). Mar. Mamm. Sci. 22:966–978.

Samaras, W.
1989. New host record for the barnacle *Cryptolepas rhachianecti* Dall, 1872 (Balanomorpha, Coronulidae). Mar. Mamm. Sci. 5:84–87.

Seilacher, A.
2005. Whale barnacles: exaptational access to a forbidden paradise. Paleobiology 31:27–35.

Spivey, H. R.
1981. Origins, distribution, and zoogeographic affinities of the Cirripedia (Crustacea) of the Gulf of Mexico. J. Biogeogr. 8:153–176.

Toth-Brown, J., and A. A. Hohn.
2007. Occurrence of the barnacle, *Xenobalanus globicipitis*, on coastal bottlenose dolphins (*Tursiops truncatus*) in New Jersey. Crustaceana 80:1271–1279.

Uchida, A., and A. Jun.
2000. The ectoparasites and endoparasites in the minke whale, *Balaenoptera acutorostrata*, from the western north Pacific Ocean. J. Jap. Vet. Med. Assoc. 53:85–88.

Van Bree, P.
1971. The rabbit-eared barnacle, *Conchoderma auritum*, on the teeth of the dolphin *Stenella frontalis*. Rep. J. Mamm. 36:316–317. [In German.]

Van Waerebeek, K., J. C. Reyes, and J. Alfaro.
1993. Helminth parasites and phoronts of dusky dolphins *Lagenorhynchus obscurus* (Gray, 1828) from Peru. Aquat. Mamm. 19:159–169.

Van Waerebeek, K., J. C. Reyes, A. J. Read, and J. S. McKinnon.
1990. Preliminary observations of bottlenose dolphins from the Pacific coast of South America. *In* The bottlenose dolphin (S. Leatherwood, and R. Reeves, eds.), p. 143–154. Academic Press, San Diego, CA.

Williams, H. H., K. MacKenzie, and A. M. McCarthy.
1992. Parasites as biological indicators of the population biology, migrations, diet, and phylogenetics of fish. Rev. Fish Biol. Fish. 2:144–176.

Yochem, P. K., and S. Leatherwood.
1985. Blue Whale *Balaenoptera musculus* (Linnaeus, 1758). *In* Handbook of marine mammals, vol. 3: The sirenians and baleen whales (S. H. Ridgway, and R. Harrison, eds.), p. 193–240. Academic Press, San Diego, CA.

Young, P. S.
1991. The superfamily Coronuloidea Leach (Cirripedia, Balanomorpha) from the Brazilian coast, with redescription of *Stomatolepas* species. Crustaceana 61:190–212.