





# Some like it hot: Temperature and hydrodynamic factors influence *Xenobalanus globicipitis* attachment to cetaceans

Milan M. Dolezal<sup>1</sup>  | Vivienne Foroughirad<sup>1</sup>  | Frank E. Fish<sup>2</sup> |  
Ann-Marie Jacoby<sup>3</sup> | Melissa A. Collier<sup>1</sup> | Colin J. Murphy<sup>1</sup> |  
Keith A. Rittmaster<sup>4</sup> | Janet Mann<sup>1</sup>

<sup>1</sup>Department of Biology, Georgetown University, Washington, District of Columbia

<sup>2</sup>Department of Biology, West Chester University, West Chester, Pennsylvania

<sup>3</sup>Marine Science and Conservation Division, Duke University, Beaufort, North Carolina

<sup>4</sup>North Carolina Maritime Museum/Bonehenge Whale Center, Beaufort, North Carolina

## Correspondence

Janet Mann, Department of Biology, Georgetown University, 3700 O Street NW, Regents Science Hall, Washington, DC 20057.  
Email: [mannj2@georgetown.edu](mailto:mannj2@georgetown.edu)

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## Abstract

Barnacles can reveal much about the physiology, health, and spatial ecology of their cetacean hosts. Here, we examine how temperature and hydrodynamic factors impact presence of *Xenobalanus globicipitis*, a pseudo-stalked barnacle that attaches exclusively to cetaceans. We hypothesized that temperature is a key environmental factor (i.e., water temperature) and physiological factor, in that *X. globicipitis* prefers the warmest skin temperature for attachment, possibly as a mechanism for survival in colder waters. First, we demonstrate a global relationship between spatial ecology of host species and presence of *X. globicipitis*. Notably, *X. globicipitis* is absent in the four species occupying waters with the lowest sea surface temperature (SST) year-round, but present in migratory species that likely acquire the barnacle in waters with higher SST. Second, barnacle attachment location on common bottlenose dolphin (*Tursiops truncatus*) dorsal fins corresponds with fin temperature and hydrodynamics. Although body temperature may influence attachment location on the body of the animal, hydrodynamic forces, as previously proposed, determine how well barnacles can remain attached during the adult stage. *X. globicipitis* prevalence likely provides important bioindicator, ecological, and physiological information about its host. As parasitic infestation has some cost, these results have implications for cetacean health in warming seas.

## KEYWORDS

bottlenose dolphins, ectoparasites, hydrodynamics, temperature, *Tursiops truncatus*, vortices, *Xenobalanus globicipitis*

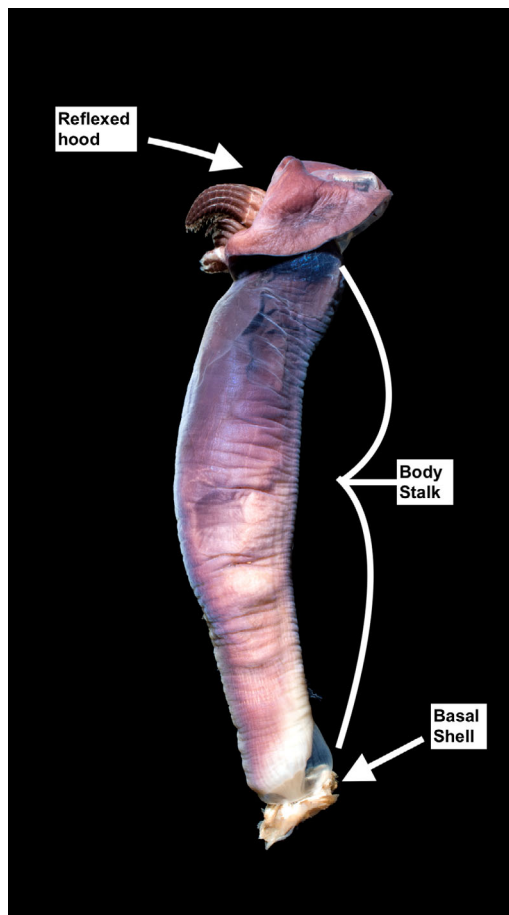
## 1 | INTRODUCTION

Since Darwin's (1854) initial observations of barnacles on cetaceans, scientists have identified multiple barnacle species that attach to cetaceans including *Coronula complanata*, *Coronula diadema*, *Tubicinella major*, *Cryptolepas rhachianecti*, and *Xenobalanus globicipitis* (Seilacher, 2005). *X. globicipitis* is of particular interest because it is exclusive to cetaceans, suggesting a complex and obligate relationship. While the presence of this barnacle can be an indicator of the health status and population membership of its host (e.g., Aznar et al., 2005; Urian et al., 2019), very little is known about what environmental factors affect the presence and absence of barnacles on cetaceans. Here we examine how skin temperature and fin hydrodynamics influence the location of *X. globicipitis* attachments on the dorsal fin of common bottlenose dolphins (*Tursiops truncatus*), and the role of sea surface temperature (SST) in its global distribution on cetaceans.

*X. globicipitis* is distinguished in its appearance by two distinct parts: the star-shaped basal shell and the body stalk, which holds internal organs under a reflexed hood (Figure 1; Seilacher, 2005). Despite this body stalk, *X. globicipitis* is considered pseudo-stalked and sessile, because the shell, rather than the stalk, attaches directly to the skin of the host (Fertl & Newman, 2018; Pugliese et al., 2012). *X. globicipitis* grows from the base at the basal shell and sheds old layers from the top of the stalk. As this body stalk lengthens, the basal shell widens (Seilacher, 2005) enabling use of the basal shell diameter as an indicator of barnacle age (Aznar et al., 2005). The basal shell interdigitates with the stratum corneum of the epidermis of the cetacean to anchor the barnacle in place (Pugliese et al., 2012). Although difficult to track, the normal life cycle of the barnacle on a living cetacean is 5–6 months from the time of attachment (Toth-Brown & Hohn, 2007). While it is not known whether *X. globicipitis* harms their hosts, they do increase drag and can be characterized as hydrodynamic parasites (Pugliese et al., 2012).

Most studies report attachment to the dorsal fin, pectoral flippers, and the caudal flukes (Carrillo et al., 2015). The primary hypothesis offered to explain attachment location on the cetacean is water flow and filtration, with the caudal flukes having the greatest volume of water flow (Carrillo et al., 2015). Seilacher (2005) observed high colonization rates on the trailing edge of caudal flukes and suggested that the vortices created by the caudal flukes allow for greater food filtration for the barnacles. As opposed to the body surface of cetaceans, where the high rate of skin sloughing deters the attachment of barnacles (Fish & Hui, 1991; Garten & Fish, 2020), the flippers, flukes, and dorsal fin can generate hydrodynamically derived vortices and eddies, which could foster low velocity flows permitting the attachment of barnacles (Carrillo et al., 2015; Fish et al., 2014; Fish & Lauder, 2017; Fish & Rohr, 1999; Moreno-Colom et al., 2020; Pugliese et al., 2012). Further, Moreno-Colom et al. (2020) suggested that greater aggregation of *X. globicipitis* on the dorsal, as opposed to ventral, side of the propulsive flukes provided a suitable settlement spot that would enhance survival, growth, and reproduction.

Additionally, variation in skin temperature may impact *X. globicipitis* attachment in cetaceans. These barnacles are broadly temperature dependent in their distribution based on higher infestation rates in warmer months for coastal bottlenose dolphin stocks (Urian et al., 2019), and *X. globicipitis* larval stages are hypothesized to need warmer waters (Kane et al., 2008). Indeed, on a common bottlenose dolphin's dorsal fin there lies a considerable temperature range (26.4–35.6; Meagher et al., 2002), which may affect where on the fin the barnacles prefer to attach; settlement on warmer parts of the fin could enable the barnacle to survive in colder waters. Despite these hypotheses, the role of hydrodynamics and skin temperature on *X. globicipitis* attachment preferences has not been investigated empirically. In addition to attachment preferences, we also know very little about what factors influence the distribution of *X. globicipitis* in cetacean species worldwide.



**FIGURE 1** Specimen of *Xenobalanus globicipitis* removed from a deceased *Tursiops truncatus* and photographed by Scott Smith using a Nikon D7200, with a Nikon AF-S DX Micro-NIKKOR 40 mm f/2.8G lens, and a single Nikon SB-700 Speedlight.

Earlier work has documented *X. globicipitis* in 34 cetacean species, spanning every ocean (Kane et al., 2008). Here, we update *X. globicipitis* occurrence on cetacean species, with a literature review. While *X. globicipitis* is clearly widespread, its *absence* in a species or population is difficult to document due to the likelihood of false negatives (Tyre et al., 2003). Long-term studies and extensive photographic evidence can reduce error since *X. globicipitis* is both distinctive and highly visible. Seasonal variation can also complicate infestation probability (e.g., Urian et al., 2019; Van Waerebeek et al., 1993); a migratory population might acquire *X. globicipitis* in one location, and carry it to another, therefore where the attachments occur (e.g., in the summer breeding grounds before migration) is not known.

In this study, we add to the understanding of *X. globicipitis* host attachment locations and global distribution by first investigating the effect of hydrodynamics and skin temperature on barnacle infestation on bottlenose dolphin dorsal fins and then characterizing the distribution of *X. globicipitis* in relation to ocean temperature. We combine our skin temperature and hydrodynamic hypotheses to test a collaboration between the two in barnacle settlement. We predict that water flow and eddies may determine where the *X. globicipitis* first land, but the barnacles are better able to survive and grow on warmer locations of the fin. Next, we examine two predictions based on the temperature-dependence hypothesis for *X. globicipitis*: (1) warmer places on cetaceans' bodies are more favorable for

barnacle survival following attachment; and (2) *X. globicipitis* attachment occurs more frequently in warmer waters (based on sea surface temperature, SST), where the larvae are able to survive prior to attachment. Attached *X. globicipitis* can then survive in colder waters (e.g., withstanding diving and migration) for the remainder of their life cycle. The temperature-dependence hypothesis has implications for barnacle distribution in warming oceans; we might expect to see higher latitude species become hosts for *X. globicipitis* when ocean temperatures rise to a level that supports the larval phase of the barnacle.

## 2 | METHODS

### 2.1 | Dorsal fin attachment location

#### 2.1.1 | Hydrodynamic analysis and distribution

To assess the relationship between *X. globicipitis* and hydrodynamics, photographic images were solicited from researchers and citizen scientists through the email list MARMAM (University of Victoria, British Columbia, Canada). Images were selected based on clarity (i.e., the numbers of *X. globicipitis* could be counted), the dolphin's fin was not damaged (i.e., fin tip was present, there were no gashes distorting the outline of the fin), attachment to the body was visible, and the fin was oriented perpendicular to the camera, providing a planar view. Of 197 images showing *X. globicipitis*, 151 dorsal fin images for bottlenose dolphins and one melon-headed whale (*Peponocephala electra*) were usable for analysis.

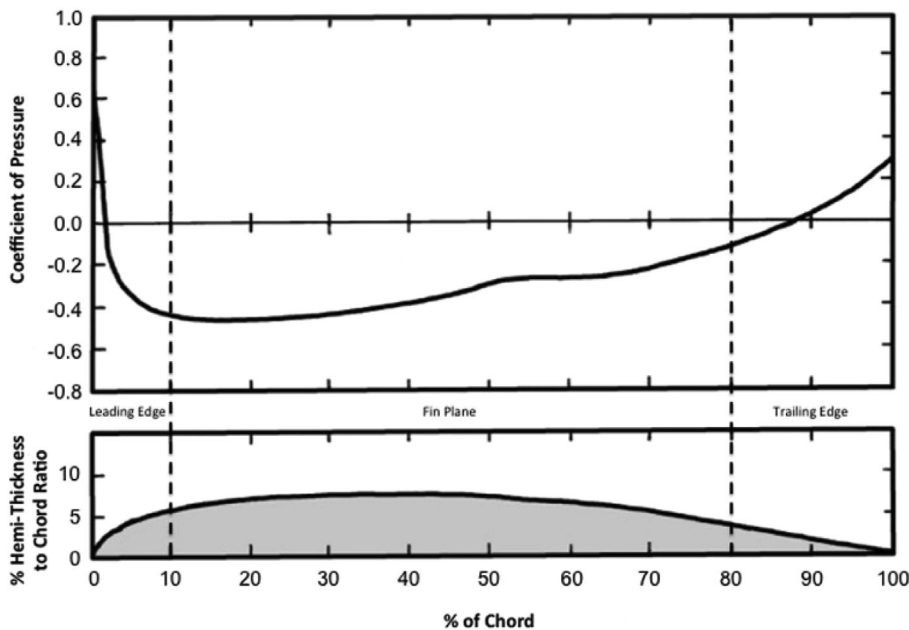
Based on the hydrodynamic analysis of the pressure distribution of a Dall's porpoise (*Phocoenoides dalli*) dorsal fin (Lang, 1966), these fin images were divided into three areas: the leading edge, fin plane, and trailing edge. The leading-edge area was the anterior 10% of the fin chord starting from the leading edge, where the chord is the linear distance from the leading to trailing edge. In this area, the pressure drops from its highest point to a plateau encompassing the minimum pressure over the fin surface (Figure 2). As the dorsal fin is swept back, the posterior margin of the leading-edge area follows the 10% contour of the fin. The trailing-edge area was the posterior 20% of the dorsal fin margin, where the pressure increases from the low-pressure plateau region (Figure 2). The remaining 70% of the chord in between the leading- and trailing-edge areas was the fin-plane area. The fin-plane area encompasses the low-pressure plateau (Figure 2).

As the dorsal fins of dolphins have finite profiles with low aspect ratios ( $= \text{span}^2/\text{planar area}$ ; Fish & Rohr, 1999), the fin tip will have a hydrodynamic effect that must be accounted for, as the fin top can produce a tip vortex (Fish, 1998; Hoerner, 1965; Vogel, 1994; Wegener, 1991). Therefore, the distal 20% of span (i.e., vertical distance from dorsal fin insertion on the body to the fin tip) was designated as the tip area.

Data were collected for each fin as the number of barnacles attached to each section. The barnacle density for each section was calculated as the number of attached barnacles divided by the planar surface area. As there was no scale in each of the images of the dolphin dorsal fins the planar surface area was determined as the percent area of the total fin area ( $= 100\%$ ). Mean planar surface areas for each section were calculated  $\pm$ one standard deviation. Statistical differences among the sections were determined with a nonparametric Friedman Test and Wilcoxon Signed Ranks Test with Bonferroni adjustments using SPSS. Differences were considered statistically significant at  $p \leq .05$ .

#### 2.1.2 | Temperature-hydrodynamic attachment model

To examine the fine-scale effects of fin surface temperature, we used survey data from a single population of live common bottlenose dolphins with low *X. globicipitis* attachment rates. Images of *X. globicipitis* dorsal fin attachment to common bottlenose dolphins were collected as part of photo-ID data collection for the Potomac-Chesapeake



**FIGURE 2** Pressure distribution (top) with respect to percent of chord for the dorsal fin of a Dall's porpoise redrawn from Lang (1966). The profile of the fin is illustrated as the hemi-thickness distribution as a percent of chord (below). For analysis based on the pressure distribution, the fin was divided into leading edge (0%–10% of chord), fin plane (10%–80% of chord), and trailing edge (80%–100% of chord) sections.

Dolphin Project (<https://www.pcdolphinproject.org>). Between July 2015 and October 2021, 357 surveys were conducted in a 210 km<sup>2</sup> area at the mouth of the Potomac River and middle Chesapeake Bay. Dolphins infested with *X. globicipitis* were observed in 13% of our surveys. We examined dorsal fin attachment, as this was the focus of photo-ID data collection and therefore the primary data set available.

Fifty-three individual dolphins were identified with *X. globicipitis* attachments and included in analyses. Individual dolphins were distinguished from one another using dorsal fin features, including markings, notches, mutilations, scarring, and shape (Würsig & Würsig, 1977). We selected and graded the best photograph of an individual's dorsal fin using a photographic quality grading scale of 0–3, where 0 is poor and 3 is excellent quality based on focus, contrast, angle, and visibility (Supplemental Data S4; Urian et al., 2015). For photographs to be included in analysis, an image quality score of 2 or 3 and a sufficient number of dorsal fin reference points were required. All individuals had visible front and back dorsal fin-to-body insertion points as well as a fully visible dorsal fin tip, in order to apply a scale and tip reference point. The infestation rate was low, with 87% of the 53 dolphins having one or two barnacles. Only one dolphin had four barnacles (Supplemental Data S2). Low infestation rates on individual dolphins minimizes the role of competition in settlement location. Species with high *X. globicipitis* infestation rates are not the best indicators of barnacle attachment preference. Preferred or optimal locations will be influenced by the available “real estate,” reproductive opportunities, availability of food for the barnacles, and how the degree of infestation impacts water flow. We checked for each of the 53 dolphins in other surveys but did not find any repeat sightings.

To mark *X. globicipitis* attachment points in relation to the dorsal fin space, we constructed a program with Python 3 using the OpenCV (Bradski, 2000) and PyQt5 (Summerfield, 2008) libraries. The program allows users to load an image in relation to a standardized grid and mark and export points to a spreadsheet for each image. For each dorsal fin image, we marked the fin's front insertion point, back insertion point, and tip. These three fin points served as reference points that were scaled to the same location on a two-dimensional grid for each individual using an affine

transformation from the *vec2dtransf* package in R (Carrillo, 2022). We then marked and exported 85 *X. globicipitis* attachment points on each of the 53 images and plotted all attachments relative to our transformed reference points.

We aligned our *X. globicipitis* attachment coordinates to a thermal image of a wild bottlenose dolphin dorsal fin at the surface in Sarasota, Florida (FLIR systems AGEMA 570 IR Camera; Meagher et al., 2002). We used the raster package (Hijmans, 2022) to rasterize the thermal image and extract temperature values for each attachment location. Points that did not land on the fin image after transformation were assigned the temperature and location of the nearest grid cell. In order to include hydrodynamics into our model, we used the fin-zone classifications described above (trailing edge, leading edge, tip, and fin plane). The grid cell size was set to approximate the size of a single *X. globicipitis* attachment (~1 cm), assuming an average size dorsal fin (600 cm<sup>2</sup>; Tolley et al., 1995). We then recorded the number of *X. globicipitis* in each cell across all 53 animals to be used as our response variable in a generalized linear Poisson model that examined the effect of temperature and fin-zone classification on *X. globicipitis* presence at each grid-cell. We did not include the fin plane and the leading edge in our model because of the complete absence of *X. globicipitis* attachments in these two locations.

## 2.2 | Geospatial distribution of *X. globicipitis* in Cetacea

To begin our literature review, we used “*Xenobalanus globicipitis*” as the keyword in Google Scholar searches. From these searches, we found 26 articles documenting *Xenobalanus globicipitis* host species, 24 of which were primary and 2 of which were major reviews (Kane et al., 2008 and Rajaguru & Shantha, 1992). Kane et al.'s 2008 review is counted both as a review and a primary source because they report four newly identified cetacean hosts: Bryde's whales (*Balaenoptera edeni*), long-beaked common dolphins (*Delphinus capensis*), humpback whales (*Megaptera novaeangliae*), and spinner dolphins (*Stenella longirostris*). We identified species without data from this first broad search and then searched for “*Xenobalanus globicipitis*” along with the scientific names of those missing species in Google Scholar. We did not find any additional primary sources from this step. Primary sources listed in Supplemental Data S1. Next, we collected a list of authors of long-term studies on cetacean species (>10 years) based on Mann and Karniski (2017), which has a supplement with a list of 67 studies and contacted them individually with a link to a survey, asking respondents to supply the following: Cetacean species, longitude and latitude of the study site, approximate number of animals photographed, duration of the study, and estimated percentage of individuals with *X. globicipitis* (Supplemental Data S3). By targeting authors of long-term studies, we hoped to obtain absence data, which is not reported in any publications.

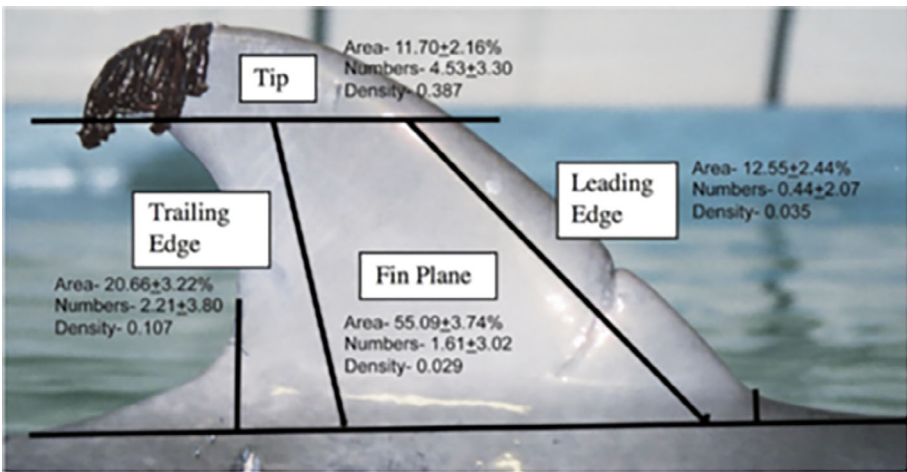
To test our hypothesis that attachment occurs in warmer waters but the barnacle hitchhikes on cetaceans to colder waters, we applied logistic regression, using the warmest sea surface temperature (SST) recorded for each species (extracted from <https://obis.org>) as the explanatory variable and presence-absence as the response variable (Supplemental Data S1). We simplify the *X. globicipitis* variable to just presence or absence for each species, rather than prevalence, to minimize bias due to variation in data collection for each species. Both temperature analyses were conducted in R version 4.0.5 (R Core Team, 2021).

## 3 | RESULTS

### 3.1 | Dorsal fin attachment location

#### 3.1.1 | Hydrodynamic distribution

Each of the four sections of the dorsal fins had distinct area percentages, with the largest, the fin plane, to the smallest, the fin tip ( $11.70 \pm 2.16\%$ ; Figure 3). When combined for all individual animals sampled, the fin tip had the



**FIGURE 3** Image of planar view of dorsal fin with the sections of the tip, leading edge, fin plane, and trailing edge indicated. The means  $\pm$  SD for the percent area of the section and number of attached barnacles, and the barnacle density are indicated.

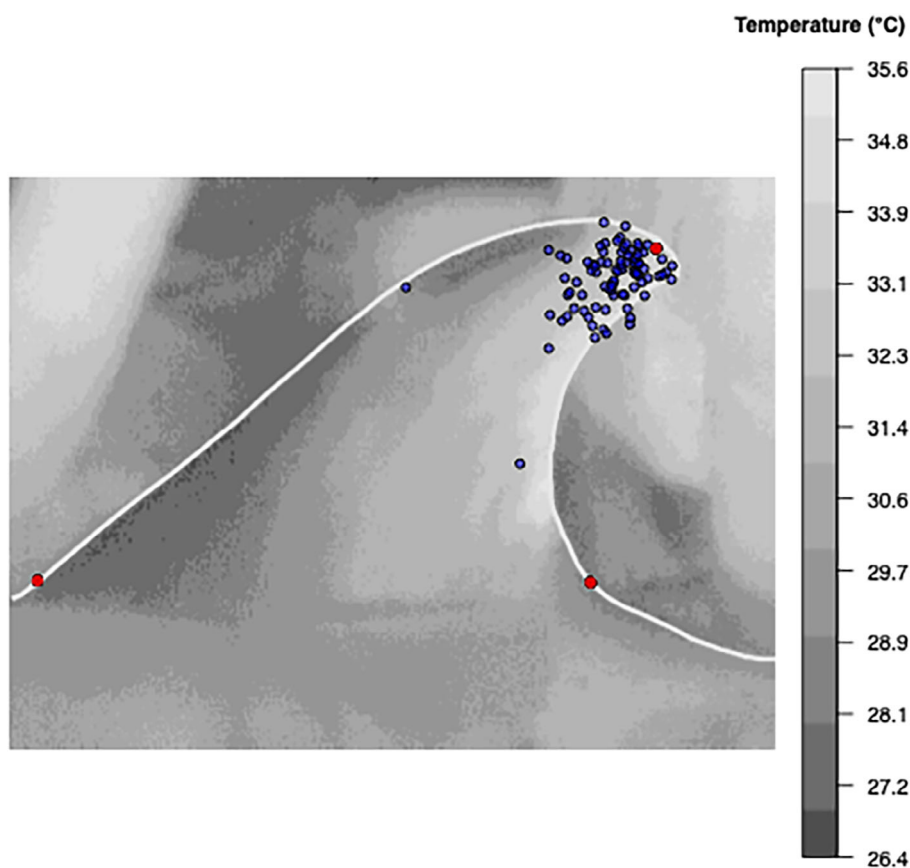
greatest mean number of *X. globicipitis* of  $4.53 \pm 4.30$  with a total number of attached barnacles of 684 (Figure 3), replicating the results with different dolphin populations. This number of barnacles was followed in decreasing order of numbers as 334, 243, and 67 for the trailing edge, fin plane, and leading edge, respectively. Despite having the second largest number of barnacles, the fin plane had the lowest density of barnacles, due to the area of the fin plane, which was 2.7–4.7 times larger than the other sections.

The results of the Friedman Test showed significant differences for the densities ( $p < .0001$ ,  $\chi^2 = 257.7$ ,  $df = 3$ ) and number of barnacles ( $p < .0001$ ,  $\chi^2 = 198.6$ ,  $df = 3$ ) among the four sections (Figure 3). The Wilcoxon paired sample test showed that all sections were significantly different from each other for the number of barnacles at  $p < .001$ , with the exception of the comparison of fin plane to trailing edge ( $p = .122$ ). Scarring of the dorsal fin had an impact. Fin planes with scars had 73.2% of barnacles attached on this section, whereas fin planes without scars accounted for 26.8% of the barnacles on this section. This differed from the other sections, where only 39.0% of the barnacles on the trailing edge occurred when scars were present. The leading edge and tip with scars accounted for 54.5% and 50.0%, respectively, for barnacles attached on those sections.

### 3.1.2 | Temperature-hydrodynamic attachment model

An affine transformation of the *X. globicipitis* attachment points on 53 bottlenose dolphins from the Potomac-Chesapeake onto the thermal fin raster revealed the top third of the trailing edge of the fin as the most common place of attachment (Figure 4). These dorsal fins had a range of one to four individual barnacles, but 24 had only one barnacle. The trailing edge of the dorsal fin has the warmest average temperature ( $M = 33.1^\circ\text{C}$ ). However, there is also little variation in temperature at this section of the fin (interquartile range =  $32.2^\circ\text{C}$ – $34.0^\circ\text{C}$ ). The generalized linear Poisson model indicated that both temperature and location are significant factors in explaining *X. globicipitis* presence at each grid cell ( $p < .0001$ ; Table 1.). One-degree Celsius increase in fin surface temperature corresponded to an expected 2.5-fold increase in *X. globicipitis* counts.





**FIGURE 4** *Xenobalanus globicipitis* attachment points on a thermal image shows the barnacle attaches to the warmest location on the fin ( $n = 53$ ,  $p < .0001$ ). Red points are reference points used in the affine transformation for the front insertion point, back insertion point, and tip of the fin. Each unique attachment point is indicated with black circles. Thermal image courtesy of Meagher et al. (2002).

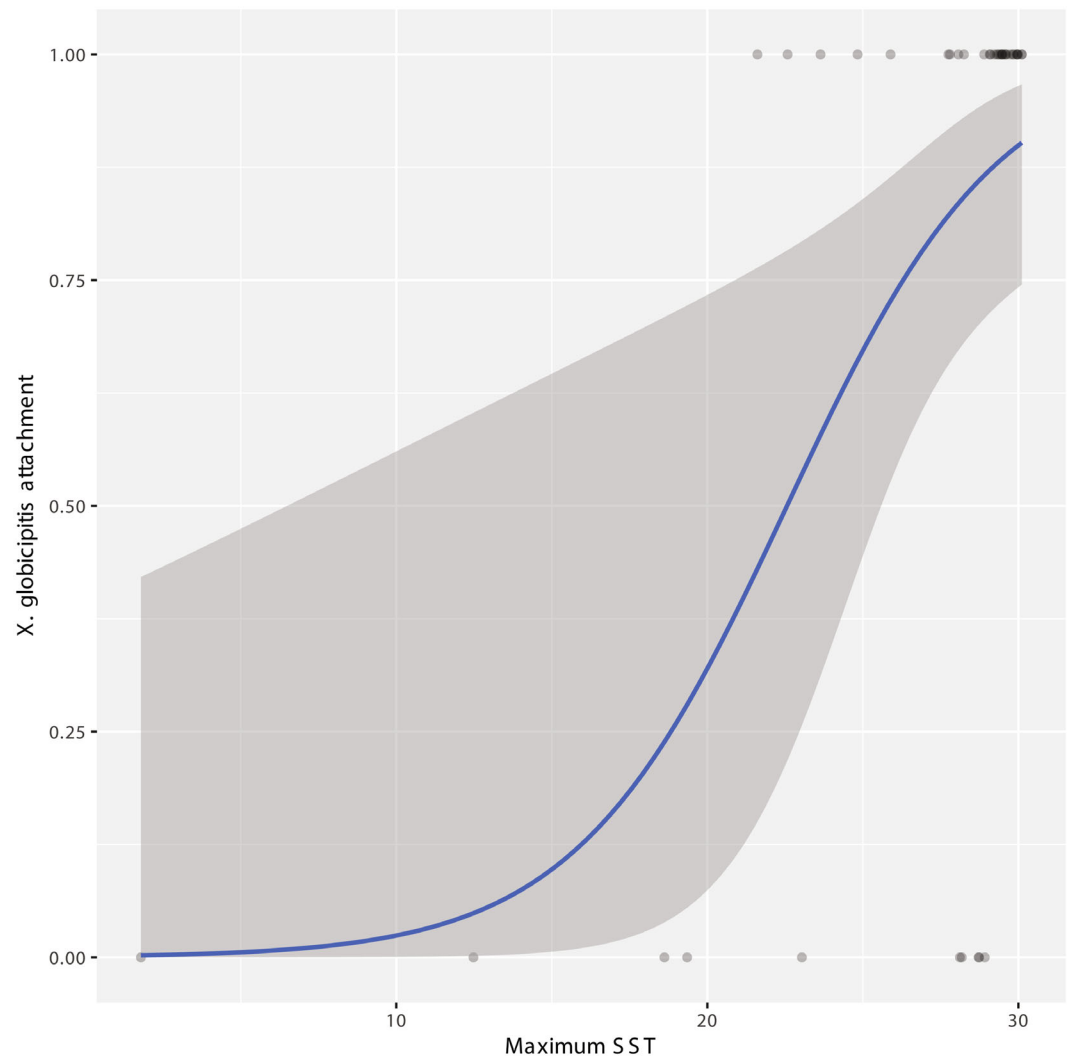
**TABLE 1** Poisson model of *Xenobalanus globicipitis* attachment with temperature and fin location variables.

	Model coefficient	SE	p
Intercept	−40.02	3.23	
Temperature (°C)	0.92	0.09	<.001
Location: tip	3.97	0.42	<.001

3.2 | Geographic distribution of *X. globicipitis*

Since Kane et al.'s 2008 review, presence of *X. globicipitis* has been documented in one additional species, the Atlantic spotted dolphin (*Stenella frontalis*; Siciliano et al., 2020). Responses from our survey yielded another species, the Guiana dolphin (*Sotalia guianensis*), bringing the total species count to 36 cetacean species with known *X. globicipitis* presence. The barnacle is present on cetaceans in every major ocean—as far south as Antarctica (fin whale, *Balaenoptera physalus*, 72°S) and as far north as the Faroe Islands (sei whale, *Balaenoptera borealis*, 61.8°N; see Supplemental Data S1).





**FIGURE 5** Logistic regression shows significant correlation between the warmest sea surface temperature (SST) in a species' range and documented *Xenobalanus globicipitis* presence ( $n = 42$ ,  $p < .05$ ). Species distribution and sea surface temperatures taken from <https://obis.org>.

From our survey of scientists conducting long-term studies, 55% (35) of responses reported *X. globicipitis* absence of the barnacle in a specific population. We were able to confirm the absence of *X. globicipitis* in nine species from these results (Supplemental Data S1). Notably, all four species that inhabit low SST waters year-round, belugas (*Delphinapterus leucas*), bowhead whales (*Balaena mysticetus*), narwhals (*Monodon monoceros*), and bottlenose whales (*Hyperoodon ampullatus*) do not have the barnacle. We did not have definitive data for two other populations which are thought to remain in low SST waters year round, Antarctic minke whales (*Balaenoptera bonaerensis*) and Antarctic killer whales (*Orcinus orca*), which have been observed in icy waters in the austral winter (Thiele & Gill, 1999). However, more recent research suggests that at least some Antarctic killer whales spend time in high SST waters (Pitman et al., 2020). Nevertheless, *X. globicipitis* has not been observed in these populations.

The logistic regression analysis reveals a pattern of host species spending at least some time (dependent on migratory patterns) in warmer waters based on average SST, as opposed to species that have not been documented

**TABLE 2** Binomial regression for species *Xenobalanus globicipitis* presence/absence and maximum sea surface temperature.

	Model coefficient	SE	p
Intercept	−6.64	3.17	
Maximum SST (°C)	0.29	0.12	<.05

with the barnacle (Figure 5, Table 2). The maximum SST of the presence points cluster around the warmest waters (~30°C), which are found near the equator. However, maximum SST varies greatly among cetaceans that have not been observed with the barnacle, ranging from 1.79°C (narwhals) to 28.92°C (Blainville's beaked whale; *Mesoplodon densirostris*).

## 4 | DISCUSSION

Our results show that both skin temperature and hydrodynamic factors predict *X. globicipitis* settlement location on the dolphin dorsal fin. The interaction of the morphology of the dorsal fin with its hydrodynamics can have a large effect on the settlement and distribution of barnacles. We extend the temperature-dependence hypothesis to ocean temperature and find a relationship between barnacle presence and SST. Migratory species likely acquire *X. globicipitis* in warmer waters before migrating to colder waters.

### 4.1 | Skin temperature and fin hydrodynamics influence *X. globicipitis* attachment location

Although water temperature has been proposed to influence infestation rates, we find new support for the influence of skin temperature. Our analysis of bottlenose dolphin dorsal fins in the Potomac River and Chesapeake Bay and an independent analysis of dolphins from other locations solicited through MARMAM shows that *X. globicipitis* congregates on the warmest part of the dolphin's dorsal fin. However, hydrodynamic factors, as previously proposed (e.g., Moreno-Colom et al., 2020; Pugliese et al., 2012), clearly play a role as well. We suggest that larvae can land and successfully attach near the tip and trailing edge due to hydrodynamic factors, but are able to survive there because the attachment site also has a favorable temperature environment. Here we summarize the hydrodynamic mechanisms that likely explain barnacle attachment. For a more detailed description, see Supplemental Data S5.

Barnacles are primarily located on the fin tip, followed by the trailing edge, the fin plane, and finally the leading edge. This pattern of attachment by *X. globicipitis* on the dorsal fin indicates a nonuniform distribution corresponding to differential flow patterns. Barnacle larvae fail to attach to a smooth surface in strong water flow (Crisp, 1955; Crisp & Stubbings, 1957; Fish & Battle, 1995; Lewis, 1978) so that the weak water flow at the fin's trailing edge would allow for easier attachment. In addition, an adverse pressure gradient is introduced across the fin plane from low pressure at the thick leading edge and high pressure at the thin trailing edge (Fox et al., 2009; Webb, 1975). An adverse pressure gradient will cause unsteady flow conditions (e.g., eddies, reversed flow) that reduces flow velocity near the trailing edge that can foster attachment of the barnacle larvae (Carrillo et al., 2015; Seilacher, 2005). The barnacles themselves and scars on the fin could change the flow structure to induce the attachments of clusters of barnacles (Kane et al., 2006).

The high density of *X. globicipitis* in the tip region of the dorsal fin can be associated with the formation of a tip vortex produced when the fin is oriented at an angle to the oncoming flow. *X. globicipitis* larvae could be drawn into the vortex core due to their small size and density similar to seawater (Cuthbertson & Irvine, 1999; Green, 1995;

Obst et al., 1996). The core of the vortex would have a low velocity, where the barnacle larvae could attach to the tip of the dorsal fin. In addition, the tip vortex could concentrate prey organisms for the developing barnacles making the fin tip a nutrient-rich environment.

While barnacles attach to hydrodynamically favorable locations, these locations were also the warmest locations on the fin (Figure 4). When we accounted for hydrodynamics in the model, fin skin temperature was still a significant factor (Table 1).

## 4.2 | *X. globicipitis* distribution suggests a preference for warmer waters

Ocean temperatures likely influence the global distribution of *X. globicipitis*. Given how expansive cetacean movements can be, we incorporated migration patterns into our analysis by identifying the warmest waters each species is found in (determined by SST) rather than the geographic location where *X. globicipitis* was observed. For example, the maximum SST recorded for fin whales is in tropical waters, even though this species routinely migrates to arctic waters. Our results suggest that animals which spend at least some time in warmer waters are more likely to become infested by *X. globicipitis* than those which do not, supporting our hypothesis that the presence of the barnacle in colder waters is the result of its host's migration from warmer waters. While we focus only on SST for this analysis, SST data do not represent the full variation of temperatures a species experiences. Future analyses could include diving depth and temperatures of deeper waters.

Some regions with a high density of data showed both presence of *X. globicipitis* on some cetacean species and absence for others within the same region, suggesting that both population membership and species characteristics play a role in attachment. For example, presence in the Guiana dolphin and absence in the La Plata dolphin (*Pontoporia blainvillei*) are reported in the same region off the coast of Brazil (Supplemental Data S1). La Plata dolphins are a slower moving species, potentially affecting the ability of *X. globicipitis* to attach (Wells et al., 2022). Future analyses might examine species-specific factors such as differences in skin sloughing rates, swimming speed and diving depth. If a cetacean species has high skin shedding, then *X. globicipitis* will have a difficult time attaching, regardless of temperature conditions. Environmental conditions such as water salinity, circulation, currents, pollution levels, and zooplankton abundance might also impact abundance.

## 4.3 | Preference for warmer fin attachment locations might increase *X. globicipitis* survival probability in migratory species

Our results suggest the presence of *X. globicipitis* in low SST populations may result from attachments that occur during migration to warmer waters. For example, humpback whales spend time in waters dipping to a SST of  $-1.79^{\circ}\text{C}$ , and yet we still found reports of infestations at this temperature. If *X. globicipitis* require warmer seas for larval attachment, then barnacles must have survival tactics for when their host moves to waters with extremely low temperatures. We suggest that the preference for attaching to warmer parts of the fins may be a life-sustaining tactic for *X. globicipitis* in colder waters. This is still consistent with our original hypothesis that posits temperature and hydrodynamics collaborate in the same moment to determine where the *X. globicipitis* larva makes its first settlement location. While fin hydrodynamics and temperature will encourage the larva to settle at a favorable location like the tip or trailing edge of the dorsal fin, as the host animal moves to colder waters, a warmer fin attachment location will increase the chances of barnacle survival. Our temperature-dependence hypothesis would predict that *X. globicipitis* would have to survive long enough on migratory species to reproduce near the original site of attachment, or in similarly warmer regions. Additionally, our temperature-dependence hypothesis predicts that other common attachment locations, such as the trailing edge of the flukes or on the edge of pectoral fins, are likely to be warmer than adjacent sites.

#### 4.4 | *X. globicipitis* as a bioindicator for warming waters

Previous research has suggested that *X. globicipitis* can act as a biosignature for cetaceans. For example, *Cryptolepas rhachianecti* barnacles serve as a biosignature for determining migratory patterns in gray whales (*Eschrichtius robustus*) (Killingley, 1980). Similarly, Urian et al. (2019) used *X. globicipitis* to discriminate between coastal and estuarine Atlantic common bottlenose dolphin stocks off the coast of North Carolina, as coastal stocks were found to have significantly greater *X. globicipitis* infestations than estuarine stocks. Others have hypothesized that animals with weakened immune systems may be more vulnerable to *X. globicipitis* infestation. Aznar et al. (2005) surveyed barnacle infestation on 136 stranded striped dolphins (*Stenella coeruleoalba*) that died during a 1990 morbillivirus outbreak in the Mediterranean and found increased *X. globicipitis* infestation in stranded dolphins during the epidemic. Whether compromised immunity or the slower swim-speed resulting from having a viral infection is responsible for higher rates of infestation is not resolved. Regardless, they established a link between *X. globicipitis* attachment and the health condition of the host.

Our work supports this biosignature hypothesis with additional implications. Although we still understand little about the biotic and abiotic factors influencing the *X. globicipitis* life cycle (e.g., salinity, plankton, water depth/pressure), their affinity for warm temperature can indicate probable movement or migration patterns in their host. This idea was recently suggested for killer whales observed in arctic waters (Matthews et al., 2020). Because *X. globicipitis* is easily identifiable, it could serve as a rapid indicator not just for the health and stock identity of the cetacean species, but also the waters they inhabit (Aznar et al., 2005, Urian et al., 2019). As such, changes in the prevalence of *X. globicipitis* in a population might indicate changes in space use, or significant changes to the average temperature of the waters they typically inhabit. This relationship with temperature is particularly relevant as global warming accelerates; the presence of *X. globicipitis* could be a useful indicator of how climate change impacts cetaceans. Barnacle prevalence and infestation rates will likely increase both within and between populations and species as sea temperatures rise.

#### 4.5 | Conclusion

Results from fin-temperature and geospatial analysis suggest an affinity of *X. globicipitis* for warmer temperatures—physiologically and globally. In addition, hydrodynamics plays an important role in barnacle attachment on the dorsal fin. Low flow regions on the dorsal fin due to the tip vortex and eddies would be advantageous for barnacle attachment and growth. While this analysis highlighted characteristics of *X. globicipitis*, previous biosignature work indicates that extending our knowledge about these barnacles will reveal more about the cetaceans they infest. For example, changes in the prevalence of *X. globicipitis* on cetaceans could indicate either geospatial shifts or altered temperature of existing habitat. With climate change, *X. globicipitis* is likely to become more widespread and present at higher latitudes; infestation rates are likely to increase and *X. globicipitis* is likely to be found in more cetacean populations and species.

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## AUTHOR CONTRIBUTIONS

**Milan Dolezal:** Conceptualization; formal analysis; investigation; methodology; visualization; writing – original draft; writing – review and editing. **Vivienne Foroughirad:** Conceptualization; formal analysis; investigation; methodology; supervision; visualization; writing – review and editing. **Frank Fish:** Conceptualization; data curation; formal analysis; investigation; methodology; visualization; writing – original draft; writing – review and editing. **Ann-Marie Jacoby:** Conceptualization; data curation; methodology; supervision; writing – review and editing. **Melissa Collier:** Conceptualization; data curation; methodology; supervision; writing – review and editing. **Colin Murphy:** Methodology; software. **Keith A. Rittmaster:** Data curation; formal analysis. **Janet Mann:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; resources; supervision; visualization; writing – review and editing.

## DATA ACCESSIBILITY

Data and code to reproduce the dorsal fin temperature and geographic range analyses are available at [https://github.com/GeorgetownMannLab/Xeno\\_analysis](https://github.com/GeorgetownMannLab/Xeno_analysis)

## ORCID

Milan M. Dolezal  <https://orcid.org/0000-0002-6215-7260>

Vivienne Foroughirad  <https://orcid.org/0000-0002-8656-7440>

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