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# Spatial distribution and habitat use patterns of humpback whales in Okinawa, Japan

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**Abstract.** Detailed knowledge of the population of humpback whales (*Megaptera novaeangliae*) in Okinawa is important for conservation management in this area; however, information on the spatial distribution of this population is limited. In this study, we investigated the distribution of whales using data on the sighting locations, water depth, and reproductive status of whales collected over 21 years in the area of Kerama and Ie Islands, Okinawa, Japan, one of the breeding grounds in the Western North Pacific. Of 1,402 whales that were photo-identified (856 males, 100 singers, 150 females, and 296 females with a calf), males, females, and singers were mainly distributed in deep offshore waters, while females with a calf were distributed in shallow interisland waters. The results suggest that certain reproductive activities, such as mating behavior or competition among males over females to mate, might occur in the offshore northern waters of Kerama Islands and western waters of Ie Island, while nurturing occurred in the interisland waters of Kerama and Ie Islands. Overall, these findings will contribute to the development of sustainable whale watching management plan in this area.

**Key words:** breeding ground, humpback whale, Okinawa, reproductive status, spatial distribution.

Humpback whales, *Megaptera novaeangliae*, are widely distributed in the world and migrate from higher latitudes (feeding grounds) in summer to lower latitudes (breeding grounds) in winter. In the North Pacific, there are at least three stocks of humpback whales that have been designated according to the breeding grounds: Mexico/Central America (Eastern North Pacific), Hawaii (Central North Pacific), and Asia (Western North Pacific) (Calambokidis et al. 2001).

The number of humpback whales in the North Pacific was drastically reduced in the 1960s, due to commercial whaling. Approximately 28,000 individuals were caught from 1905 to 1965 (Johnson and Wolman 1984), of which at least 644 individuals were caught from Okinawa (Nishiwaki 1959, 1960, 1961) which is one of the breeding grounds in the Western North Pacific. Rice (1978) inferred that the population in the North Pacific was reduced to as few as 1,000 individuals by the time of 1966 when the International Whaling Commission (IWC) pro-

hibited the commercial hunting of humpback whales. However, a recent evaluation showed that humpback whales in the North Pacific have an increasing tendency (Calambokidis et al. 2008), and thus its status has been down-listed from Vulnerable to Least Concern in 2008 in the Red List of Threatened Species produced by the International Union for Conservation of Nature and Natural Resources (IUCN). Meanwhile, whale watching tour to see humpback whales had begun in New England and Hawaii in 1975 and is expanding all over the world since then (Hoyt 2001). As the whale watching industry grows, the concern over negative impact on whales being watched also grows (Tilt 1987; Beach and Weinrich 1989; Corkeron 2004; Stamation et al. 2010). There are some reports suggesting that the behavioral changes of whales can be induced by close approach of tourist vessels (Williams et al. 2002; Lusseau 2003; Scheidat et al. 2004). These reports also indicate that females with a calf are more sensitive and susceptible to vessel disturbance

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than whales without a calf (Bauer 1986; Stamation et al. 2010). The Large Whale Ship Strike Database shows that approximately 14% of the collisions between ships and whales in the United States of America are associated with whale watching vessels (Jensen and Silber 2003).

In Okinawa, a sighting survey of humpback whales started in 1989 responding to the increase of humpback whale sightings around Okinawa Islands (Uchida 1997; Uchida et al. 2005), and whale watching tour of humpback whales has been expanded in Okinawa year by year. It is expected that both the expansion of the whale watching industry and the growth of the humpback whale population in this area might cause the increase of negative impacts on the whales in the near future, as reported in other areas. Therefore, understanding of the distribution patterns and habitat use of humpback whales in Okinawa, and reduction of the disturbance on whales and ship strikes are imperative for the development of sustainable whale watching management.

Some studies have been done on the distribution patterns and habitat use of humpback whales in the breeding grounds of the Central and the Eastern North Pacific such as in Hawaii, Mexico, and Central America. According to those studies, humpback whales tend to occur in nearshore waters shallower than 200 m in breeding areas, while females with a calf tend to occur in coastal shallow waters than whales without a calf (Herman and Antinaja 1977; Urban and Aguayo 1987; Rasmussen et al. 2011). However, the information on habitat use of humpback whales is lacking, especially in the Western North Pacific,

including Okinawan waters.

In this study, we analyzed the sighting data and the photo identification data of humpback whales collected over 21 years (1992–2012) to clarify the distribution pattern and habitat use of humpback whales in Okinawan waters depending on their status for the first time. The information will contribute to the development of sustainable whale watching management in this area.

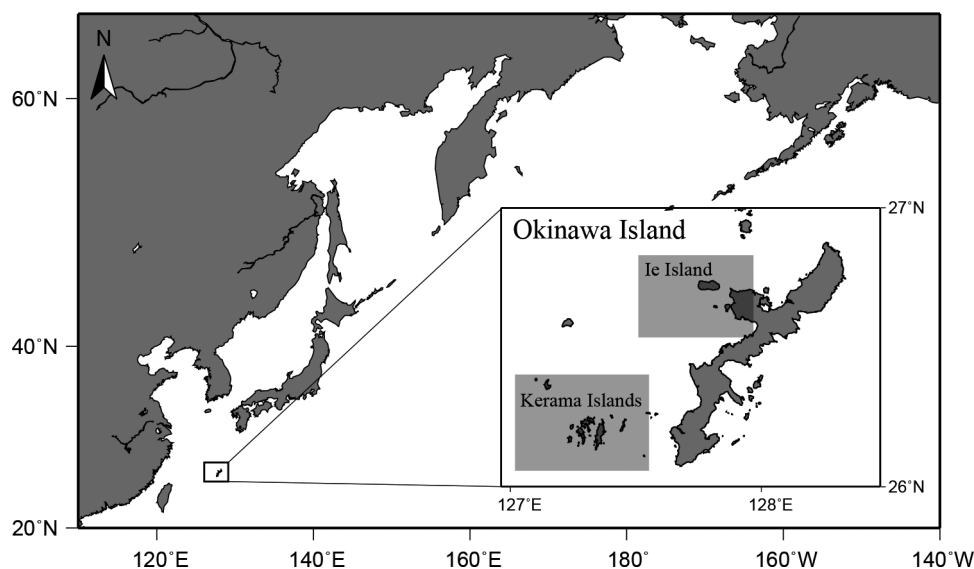
## Materials and methods

### Boat surveys

Using small vessels (3.2–4.9 t) with at least two observers on board, sighting surveys for humpback whales were conducted during the winter breeding season (January–March), off the coast of Kerama Islands (study area: 26° 03' 3832" N, 127° 06' 2505" E–26° 24' 14" N, 127° 31' 10"E) and Ie Island (study area: 26° 33' 12" N, 127° 34' 22" E–26° 48' 37" N, 127° 56' 11" E) in Okinawa, Japan (Fig. 1). The surveys were conducted from 1991 to 2012 in the area of Kerama Islands and from 2006 to 2012 in the area of Ie Island in water depths of up to 1,000 m. In this study, we only used the sighting data of whales found in the waters shallower than 200 m where we examined thoroughly.

### Data collection

When whales were sighted, photographs of their tail flukes were taken for photo-identification (Katona and Whitehead 1981), and the sighting location (latitude and



**Fig. 1.** The study area in Okinawa, Japan. The shaded parts represent the survey areas around Kerama and Ie Islands, respectively.

longitude) and time of sighting, group size, group composition, as well as the water depth of the exact sighting points, were recorded. Photographs were taken using single-lens reflex cameras; the location was recorded using portable global positioning system (GPS) receivers; and water depth data were collected using the underwater sonar equipment of vessels. The fluke photographs of individual whales were stored for individual identification (Katona and Whitehead 1981). All of these photographs were compared to catalogs of all whales previously identified in the both study areas. Photographed individuals identified in each year that did not match the whales identified in past years were assigned a new identification numbers and added to the catalogs. The sex of individual whales was determined by the social role of whales based on the definition described in Glockner (1983) and Payne and McVay (1971). In this study, a whale which has observed as a singer (an individual emitting song in breeding area) and/or as an escort (an individual accompanying a female with a calf) assigned as a male, and a whale which has observed swimming closely with a calf was assigned as a female. Furthermore, we categorized the status of the whales into four defined status as follows. Male ( $M_0$ ) was an individual which was observed as an escort at the moment of the surveys and/or in the previous surveys, or has a record of being a singer in the previous surveys but not at the moment of the surveys. Singer ( $M_s$ ) was an individual that was observed singing during the surveys. Female ( $F_0$ ) was an individual which has a record of being with a calf in the previous surveys but not at the moment of the surveys. Female with a calf ( $F_c$ ) was an individual with a calf during the surveys.

When we located singers (singing male individuals), we stopped the engine of the vessel and listened to the song through the hull of the boat without the aid of a hydrophone at the exact position where the whale dove in order to make sure the singing individual. Due to the relatively low density of whales in the study area, it was not difficult to identify which individual was singing. After we made sure the singing individual, we took fluke photographs of the singer and recorded the song with a hydrophone for more than 10 min, in order to identify repeat phrases and themes (Payne and McVay 1971) and confirm their behavior as a singer.

#### *Data analysis*

The sightings, which were associated with locational data and defined individuals for each status ( $M_0$ ,  $M_s$ ,  $F_0$ ,

and  $F_c$ ), were respectively plotted on the area maps of each status of Kerama and Ie Islands, in order to identify the geographical differences in their habitat use according to sex and status. The sightings were counted and plotted on the maps that include the resightings of same individuals. We counted and plotted sighting of the same individuals when the day of sightings were different. We used only the first sighting record in a day for each individual observed in the same status category in a same year. Also, the sightings of the same individuals categorized in different status were plotted respectively on each map of status even in a same day. Additionally, we compared the distribution of each status in association with the water depth. Since some sightings included both locational and water depth data, while others included either, one of these number of locational data sets was different from that of water depth data sets.

We plotted the sightings on the map using Generic Mapping Tools 5.1.1 (<http://gmt.soest.hawaii.edu>). Sea-floor data and water depths on the maps were obtained from the M7020 2.0 bathymetric topography digital data product of the Japan Hydrographic Association (<http://www.jha.or.jp/en/jha/>). All statistical analyses were conducted using Microsoft Excel (Microsoft Corp., Redmond, WA, USA). The comparison of representative values of the sighting water depth of each status category was tested within two groups using the Kolmogorov-Smirnov test.

## **Results**

### *Sightings and photo-identification*

We conducted a total of 912 days (6,575 hours) and 268 days (2,278 hours) of sighting surveys of humpback whales in the areas of Kerama and Ie, respectively.

1,268 whales were photo identified and 178 individuals of them were sexed. A total sighting number of photo identified and sex determined whales observed in the area of Kerama and Ie Islands were 1,402. The number includes resightings of the same individuals in different days and/or years and maximum resightings of the same individual were 50 times which observed for  $M_0$  (Tables 1 and 2).

### *Sighting locations*

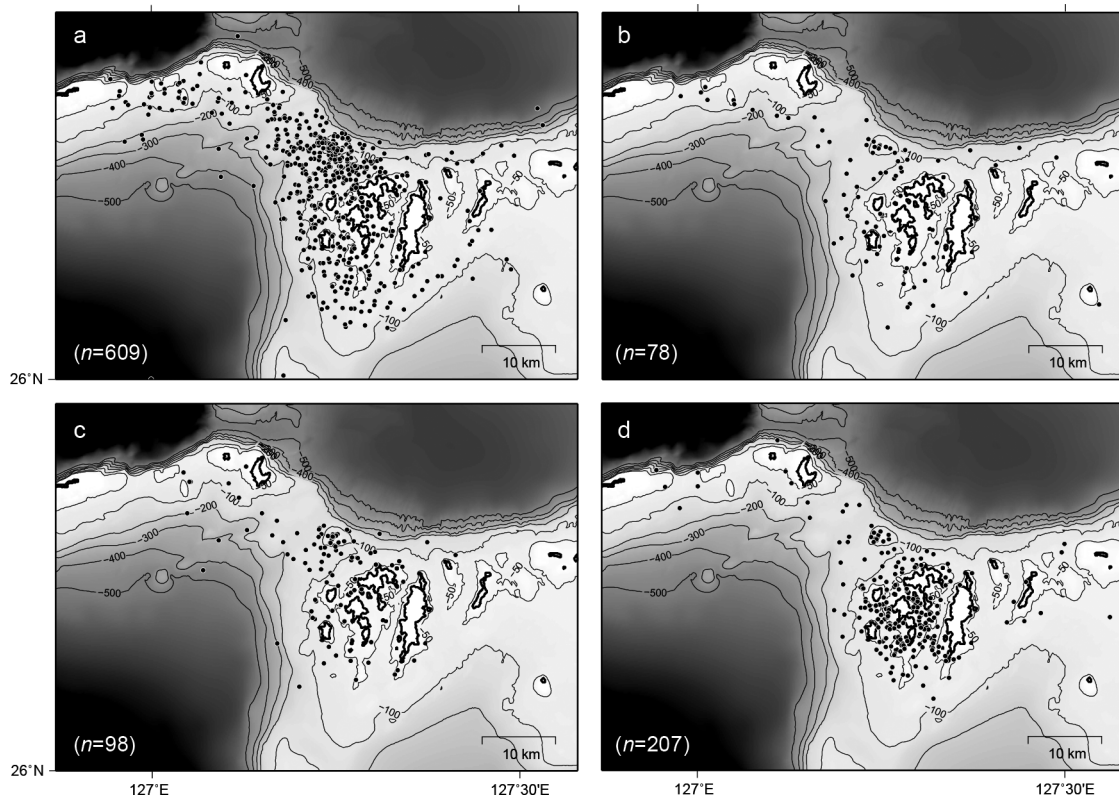
In the area of Kerama,  $M_0$ ,  $M_s$ , and  $F_0$  were mostly observed in the offshore area of the Kerama Islands, especially in the northwest areas which are called 'sone' areas and characterized by abyssal hills (Fig. 2a–c).  $F_c$  were more frequently observed in the interisland area than off-

**Table 1.** Number of individuals that were identified from photos (photo-identification) and the sex was determined

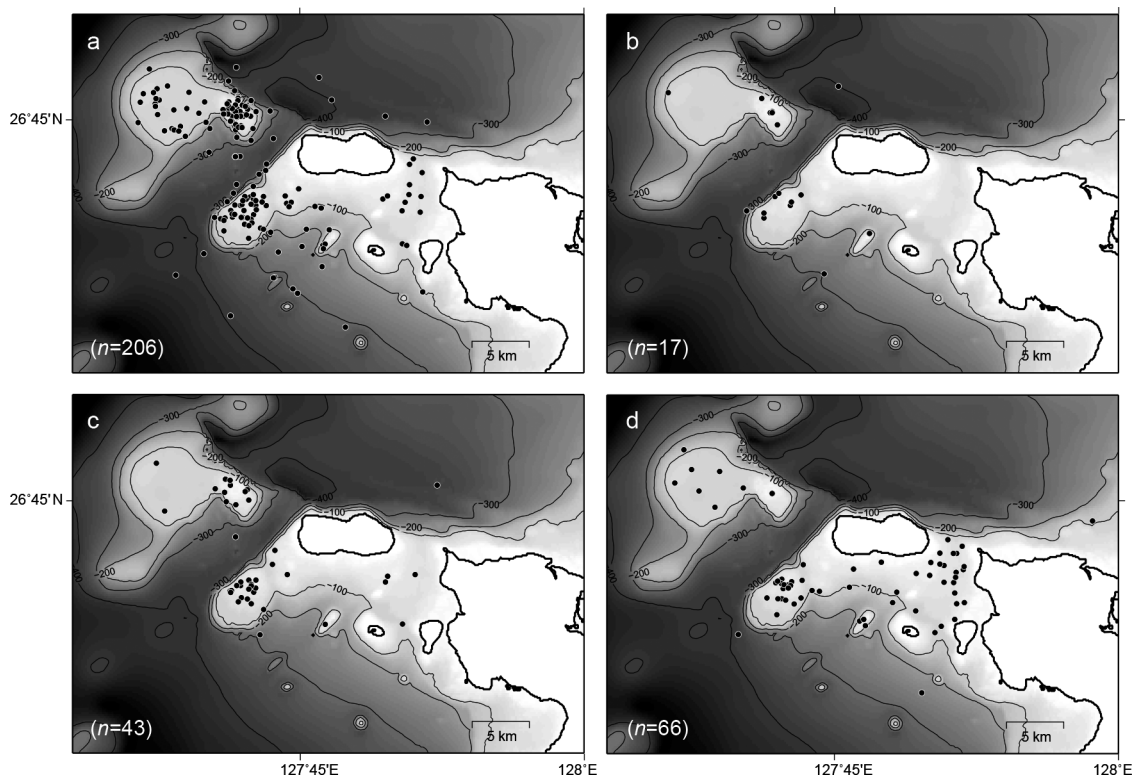
Sex	Number of IDs	Status of whale	Number of IDs	Number of sightings	Average number of sightings with the same individual within status	Maximum number of sightings with the same individual
Male	102	Male ( $M_0$ )	101	856	8.47	50
		Singer ( $M_s$ )	61	100	1.64	5
Female	76	Female ( $F_0$ )	39	150	3.84	20
		Female with a calf ( $F_c$ )	74	296	4	22
Total	178		275	1,402	—	—

**Table 2.** Number of sightings with available locational data and water depth data

Status of whale	Sighting with available locational data		Sighting with available water depth data	
	Kerama	Ie	Kerama	Ie
Male ( $M_0$ )	596	181	591	153
Singer ( $M_s$ )	78	14	77	15
Female ( $F_0$ )	94	41	96	36
Female with a calf ( $F_c$ )	206	64	204	64
Total	974	300	968	268
	1,274		1,236	

**Fig. 2.** Sighting and number of humpback whales in the area of Kerama Islands: (a) male:  $M_0$ , (b) singer:  $M_s$ , (c) female:  $F_0$ , and (d) female with calf:  $F_c$ . Black dots indicate the exact sighting position of each whale. Color strength reflects water depth from shallow (light) to deep (dark).





**Fig. 3.** Sighting and number of humpback whales in the area of Ie Islands: (a) male:  $M_0$ , (b) singer:  $M_s$ , (c) female:  $F_0$ , and (d) female with calf:  $F_c$ . Black dots indicate the exact sighting position of each whale. Color strength reflects water depth from shallow (light) to deep (dark).

shore area of the Kerama Islands (Fig. 2d). In the area of Ie,  $M_0$ ,  $M_s$ , and  $F_0$  were commonly observed in the 'sone' areas of the western waters of Ie Island (Fig. 3a–c), while  $F_c$  were more frequently observed in the interisland area of Ie Island and Motobu peninsula and also observed in the 'sone' area south-west of Ie Island (Fig. 3d).

#### Water depth

In the area of Kerama Islands,  $F_c$  were distributed in significantly shallower waters than  $M_0$ ,  $M_s$ , and  $F_0$  respectively (Kolmogorov-Smirnov test,  $M_0$ ,  $F_c$ :  $P < 0.01$ ;  $M_s$ ,  $F_c$ :  $P < 0.01$ ,  $F_0$ ,  $F_c$ :  $P < 0.01$ ), while no significant differences were detected in the distribution of  $M_0$ ,  $M_s$ , and  $F_0$  (Kolmogorov-Smirnov test;  $M_0$ ,  $M_s$ :  $P = 0.76$ ;  $M_0$ ,  $F_0$ :  $P = 0.94$ ;  $M_s$ ,  $F_0$ :  $P = 0.97$ ).

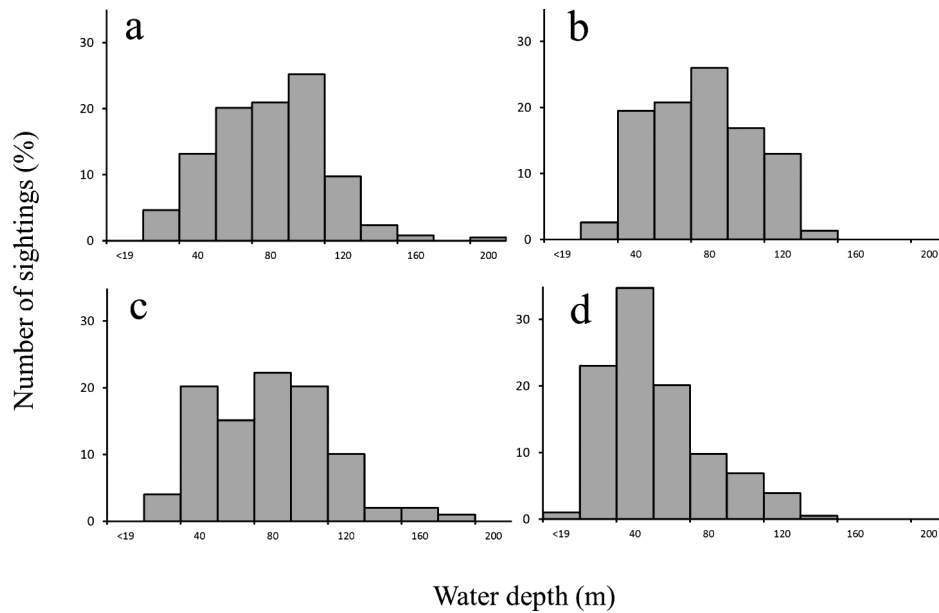
In the area of Ie Island, no significant differences were detected in the distribution of  $M_0$ ,  $M_s$ , and  $F_0$  (Kolmogorov-Smirnov test;  $M_0$ ,  $M_s$ :  $P = 0.26$ ;  $M_0$ ,  $F_0$ :  $P = 0.87$ ;  $M_s$ ,  $F_0$ :  $P = 0.70$ ), while  $F_c$  were distributed in significantly shallower waters than  $M_0$  (Kolmogorov-Smirnov test,  $P < 0.05$ ).

#### Discussion

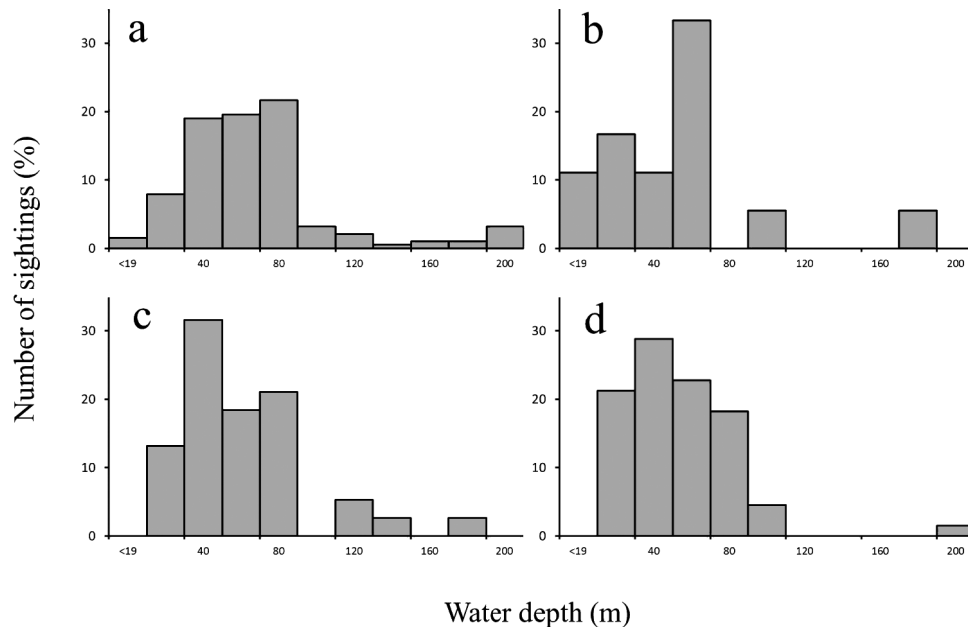
This 21-year study revealed the distribution patterns and habitat use patterns of humpback whales according to its sex and status of individuals in Okinawan waters. This study is also the first report providing detailed information on habitat use of humpback whales in the Western North Pacific.

In Okinawa,  $M_0$ ,  $M_s$ , and  $F_0$  were found in deeper offshore areas (Figs. 2, 3, 4, and 5), while  $F_c$  were mostly found in shallower interisland areas. Similar patterns in habitat use between the two sexes and among the different status categories have also been observed in other breeding areas of the Central and the Eastern North Pacific (Herman and Antinaja 1977; Urban and Aguayo 1987; Rasmussen et al. 2011). The similar results found in different breeding areas indicate that the habitat use pattern detected in this study is the universal trend of humpback whales commonly found in the breeding areas in the whole North Pacific.

Mating activities and aggression between male and female humpbacks tend to occur in deeper offshore waters (Smultea 1994; Ersts and Rosenbaum 2003; Felix



**Fig. 4.** Water depth distribution of humpback whales in the area of Kerama Islands: (a) male:  $M_0$  ( $n = 591$ ), (b) singer:  $M_s$  ( $n = 77$ ), (c) female:  $F_0$  ( $n = 96$ ), and (d) female with a calf:  $F_c$  ( $n = 204$ ).



**Fig. 5.** Water depth distribution of humpback whales in the area of Ie Islands: (a) male:  $M_0$  ( $n = 153$ ), (b) singer:  $M_s$  ( $n = 15$ ), (c) female:  $F_0$  ( $n = 36$ ), and (d) female with a calf:  $F_c$  ( $n = 64$ ).

and Botero-Acosta 2011). The singing behavior of male humpback whales is considered to be a part of the male's mating display and intrasexual competition among males (Winn et al. 1973; Winn and Winn 1978; Glockner 1983). In our study,  $M_0$ ,  $M_s$ , and  $F_0$  were mainly distributed in the offshore northern waters of Kerama Islands and the offshore western waters of Ie Island (Fig. 2). These results

also support the concept that mating activity occurs in offshore waters of breeding areas. In contrast,  $F_c$  were mainly observed in the nearshore shallow waters in Okinawan waters. Our results supported those from other humpback whale breeding rounds in the North Pacific, such as in Hawaii and Mexico (Herman and Antinoya 1977; Urban and Aguayo 1987; Rasmussen et al. 2011).

These previous studies suggested that females with a calf need to store their energy, because they must produce milk for a calf in the fasting situation in the wintering grounds (Chittleborough 1965; Dawbin 1966). Felix and Botero-Acosta (2011) and Craig (2014) reported that the number of males escorting a female with a calf increased significantly with increasing water depth, and that the swimming speed of females with a calf increased as a function of male presence. Therefore, authors suggested in the reports that females with a calf also incur energetic costs when escorted by males; consequently, these females position themselves in shallow waters to reduce the likelihood of unwanted male attention. Brodie (1977) and Whitehead and Moore (1982) suggested that the calm and warm environment of shallow nearshore waters between islands may minimize the energy expenditure of females nursing their calves when compared with more open offshore areas. In our study,  $M_0$  were more frequently found in offshore areas compared to nearshore areas, whereas  $F_c$  were more frequently found in nearshore areas. Therefore, our results also support the idea that females with a calf preferentially use shallow nearshore waters as nursing areas to avoid harassment from sexually active males and rough sea conditions, which might cause females to incur higher energetic costs.

This long-term study provided detailed information on the areas used by males and females with and without calves in Okinawan waters. The information is expected to contribute towards developing effective and sustainable whale watching tours, as well as preventing the incidence of ship strikes against whales by regulating vessel speed and access to these areas during the peak season of humpback whales in Okinawa. However, in the present study, only two places in Okinawa were surveyed, although humpback whales were observed and watching tours were conducted in other places of Okinawan waters. Therefore, additional sighting surveys in the wider areas in Okinawan waters are required to clarify the pattern of habitat use by humpback whales in this region. Furthermore better understanding on the movement patterns of humpback whales within the Okinawa area, including the movement between the areas of Kerama and Ie Islands, is important to know the specific habitat use pattern of humpback whales in Okinawan waters.

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## References

- Bauer, G. B. 1986. The Behavior of Humpback Whales in Hawaii and Modifications of Behavior Induced by Human Interventions. Ph. D. Dissertation, University of Hawaii, Honolulu, Hawaii, 314 pp.
- Beach, D. W. and Weinrich, M. T. 1989. Watching the whales: Is an educational adventure for humans turning out to be another threat to endangered species? *Oceanus* 32: 84–88.
- Brodie, P. F. 1977. Form, function and energetics of Cetacea: a discussion. In (Harrison, R. J., ed.) *Functional Anatomy of Marine Mammals*, Vol. 3, pp. 45–56. Academic Press, London.
- Calambokidis, J., Falcone, E. A., Quinn, T. J., Burdin, A. M., Clapham, P. J., Ford, J. K. B., Gabriele, C. M., LeDuc, R., Mattila, D., Rojas-Bracho, L., et al. 2008. SPLASH: Structure of Populations, Levels of Abundance and Status of Humpback Whales in the North Pacific. Final report for Contract AB133F-03-RP-00078, pp. 57. Cascadia Research for U. S. Department of Commerce, Olympia, WA.
- Calambokidis, J., Steiger, G. H., Straley, J. M., Cerchio, S., Salden, D. R., Urban, R. J., Jacobsen, J. K., Von Ziegeler, O., Balcomb, K. C., Gabriele, C. M., et al. 2001. Movements and population structure of humpback whales in the North Pacific. *Marine Mammal Science* 17: 769–794.
- Chittleborough, R. G. 1965. Dynamics of two populations of the humpback whale, *Megaptera novaeangliae* (Borowsk). *Australian Journal of Marine and Freshwater Research* 16: 33–128.
- Corkeron, P. J. 2004. Whale watching, iconography, and marine conservation. *Conservation Biology* 18: 847–849.
- Craig, A. S. 2014. Habitat segregation by female humpback whales in Hawaiian waters: avoidance of males? *Behaviour* 151: 613–631.
- Dawbin, W. H. 1966. The Seasonal Migratory Cycle of Humpback Whales. *Whales, Dolphins, and Porpoises*, pp. 145–169. University of California Press, Berkeley, CA.
- Ersts, P. J. and Rosenbaum, C. H. 2003. Habitat preference reflects social organization of humpback whales (*Megaptera novaeangliae*) on a wintering ground. *Journal of Zoology* 260: 337–345.
- Felix, F. and Botero-Acosta, N. 2011. Distribution and behavior of humpback whale mother-calf pairs during the breeding season off Ecuador. *Marine Ecology Progress Series* 426: 227–287.
- Glockner, D. A. 1983. Determining the sex of humpback whales (*Megaptera novaeangliae*) in their natural environment. In (Payne, R. S., ed.) *Behavior and Communication of Whales*, pp. 447–464. Westview Press, Boulder, CO.
- Herman, L. M. and Antinaja, R. C. 1977. Humpback whales in the Hawaiian breeding waters: Population and pod characteristics. *Scientific Reports of the Whales Research Institute, Tokyo* 29: 59–85.
- Hoyt, E. 2001. Whale Watching 2001: Worldwide Tourism Numbers, Expenditures, and Expanding Socioeconomic Benefits, pp. 1–158. International Fund for Animal Welfare, Yarmouth Port, MA, USA.
- Jensen, A. S. and Silber, G. K. 2003. Large Whale Ship Strike Database. U. S. Department of Commerce, NOAA Technical Memorandum. NMFS-OPR-25, 37 pp.
- Johnson, J. H. and Wolman, A. A. 1984. The humpback whale,



- Megaptera novaeangliae*. Marine Fisheries Review 46: 30–37.
- Katona, S. K. and Whitehead, H. P. 1981. Identifying humpback whales using their natural markings. Polar Record 20: 439–444.
- Lusseau, D. 2003. The effects of tour boats on the behavior of bottlenose dolphins: Using Markov chains to model anthropogenic impacts. Conservation Biology 17: 1785–1793.
- Nishiwaki, M. 1959. Humpback whales in Ryukyuan waters. Scientific Reports. Whales Research Institute 14: 49–87.
- Nishiwaki, M. 1960. Ryukyuan whaling in 1960. Scientific Reports. Whales Research Institute 15: 1–15.
- Nishiwaki, M. 1961. Ryukyuan whaling in 1961. Scientific Reports. Whales Research Institute 16: 19–28.
- Payne, R. S. and McVay, S. 1971. Songs of humpback whales. Science 173: 585–597.
- Rasmussen, K., Calambokidis, J. and Steiger, G. H. 2011. Distribution and migratory destinations of humpback whales off the Pacific coast of Central America during the boreal winters of 1996–2003. Marine Mammal Science 28: 267–279.
- Rice, D. W. 1978. The humpback whale in the North Pacific: Distribution, exploitation, and numbers. In (Norris, K. S. and Reeves, R. R., eds.) Report on a Workshop on Problems Related to Humpback Whales (*Megaptera novaeangliae*), pp. 29–44. U.S. Department of Commerce, National Technical Information Services, PB280794, Springfield, VA.
- Scheidat, M., Castro, C., Gonzalez, J. and Williams, R. 2004. Behavioural responses of humpback whales (*Megaptera novaeangliae*) to whale watching boats near Isla de la Plata, Machalilla National Park, Ecuador. Journal of Cetacean Research and Management 6: 63–68.
- Smultea, M. A. 1994. Segregation by humpback whale (*Megaptera novaeangliae*) cows with a calf in coastal habitat near the island of Hawaii. Canadian Journal of Zoology 72: 805–811.
- Stamaton, K. A., Croft, D. B., Shaughnessy, P. D., Waples, K. A. and Briggs, S. V. 2010. Behavioral responses of humpback whales (*Megaptera novaeangliae*) to whale-watching vessels on the southeastern coast of Australia. Marine Mammal Science 26: 98–122.
- Tilt, W. C. 1987. From whaling to whale watching. Transactions of the 52nd North American Wild and Natural Resources Conference 52: 567–585.
- Uchida, S. 1997. Surveys of cetaceans in the Japanese waters. In (Uchida, S., ed.) Kings of the Sea: Humpback Whales: A 1991–1995 Survey of Cetaceans in the Japanese Waters, pp. 18–25. The UFJ Environment Foundation.
- Uchida, S., Higashi, N., Maeda, H., Koido, T. and Takemura, A. 2005. What is humpback whale? In (Uchida, S., ed.) Kings of the Sea: Humpback Whales II: A 1999–2005 Survey of Cetaceans in the Japanese Waters, pp. 6–17. The UFJ Environment Foundation.
- Urban, R. J. and Aguayo, L. A. 1987. Spatial and seasonal distribution of the humpback whale, *Megaptera novaeangliae*, in the Mexican pacific. Marine Mammal Science 3: 333–344.
- Whitehead, H. and Moore, M. J. 1982. Distribution and movements of West Indian humpback whales in winter. Canadian Journal of Zoology 60: 2203–2211.
- Williams, R., Trites, A. W. and Bain, D. E. 2002. Behavioural responses of killer whales (*Orcinus orca*) to whale-watching boats: Opportunistic observations and experimental approaches. Journal of Zoology 256: 255–270.
- Winn, H. E. and Winn, L. K. 1978. The song of the humpback whale *Megaptera novaeangliae* in the West Indies. Marine Biology 47: 97–114.
- Winn, H. E., Bischoff, W. L. and Taruski, A. G. 1973. Cytological sexing of Cetacea. Marine Biology 23: 343–346.

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