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FIN WHALES (*BALAENOPTERA PHYSALUS*) FORAGING ON DAYTIME SURFACE SWARMS OF THE EUPHAUSIID *NYCTIPHANES SIMPLEX* IN BALLENAS CHANNEL, GULF OF CALIFORNIA, MEXICO

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We identified specific areas where fin whales (*Balaenoptera physalus*) forage on daytime surface swarms of euphausiids in Ballenas Channel, Gulf of California. During 2003 and 2004, 4 field trips per year were carried out (winter–spring, spring, summer, and autumn). Systematic line transects and random surveys for whales were conducted in small boats (6 m) and euphausiid swarms were sampled with a zooplankton net. Fin whales foraged mostly in shallow waters (10–100 m) off the west and south coast of Coronado Island and were observed feeding on 18 of 19 swarms of *Nyctiphanes simplex* (5 in 2003 and 14 in 2004). Swarms occurred from March to early August and were almost absent from October to November. Although fin whales were sighted throughout the study area, there was a characteristic distribution pattern of feeding activity, mainly during spring and summer seasons. Examination of our data shows that the adjacent waters off Coronado Island constitute a unique seasonal foraging habitat for fin whales in the Gulf of California.

Key words: *Balaenoptera physalus*, euphausiids, fin whale, Gulf of California, *Nyctiphanes simplex*, surface swarms

Fin whales (*Balaenoptera physalus*) have a worldwide distribution with less-predictable latitudinal seasonal migrations than most other baleen whales (Evans 1987). For many areas of the Northern Hemisphere the pattern of movements by fin whales is not clear (Aguilar 2002). Moreover, in some cases, fin whales may remain at lower latitudes year-round if food is available (Aguilar 2002), as seems to be the case for the populations of fin whales in the Mediterranean and the Gulf of California (Notarbartolo-di-Sciara et al. 2003; Urbán et al. 2005). Genetic evidence suggests fin whales from the Gulf of California constitute a unique population, isolated from fin whales in the eastern North Pacific (Bérubé et al. 2002). Seasonal movements by this population in the Gulf of California appear related to the patchy distribution of prey (Urbán et al. 2005), which highlights the importance of research on feeding and foraging behavior of fin whales.

Although large animals require large amounts of food and scan the environment at wide scales, they typically use specific areas of their home range because of patchiness of the environment (Stern 1998). In marine systems the base of the food chain for many large marine mammals is small, schooling fishes and crustaceans (such as ‘‘krill,’’ hereafter euphausiids). The distribution and abundance of euphausiids varies spatially and temporally, which is reflected by similar variation in the foraging behavior of whales that rely on euphausiids as prey (Bowen et al. 2002). Hence, seasonal studies are important to identify temporal patterns in use of these areas by whales, and assess how important an area is for a particular population (Stern 1998).

As with other baleen whales, fin whales capture their prey by lunge feeding (Croll et al. 2001). They engulf large volumes of water containing fishes and euphausiids (Kawamura 1980), principally at depth, in areas of dense prey aggregations (Croll et al. 2001). Off the coast of North America, fin whales have been reported foraging on euphausiids at 150–300 m depth during the day (Croll and Tershy 2002). In the southwestern Gulf of California, fin whales were observed foraging most often at around 100 m and rarely at the surface (Croll et al.

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2001). When surface feeding was observed, it occurred mainly in the Midriff Islands region (Gendron 1993; Rojas-Bracho 1984; Tershy et al. 1993), and in the southwestern Gulf of California (Gendron 1992; Rojas-Bracho 1984). The primary species of euphausiid prey consumed by fin whales in this region was reported as *Nyctiphanes simplex* (Gendron 1992; Tershy et al. 1993).

Nyctiphanes simplex is the most abundant and widespread euphausiid in the Gulf of California. Similar to other euphausiids, *N. simplex* reproduces year-round, occurs in large swarms, and undertakes diel vertical migrations (Brinton 1967; Lavaniegos et al. 1989). Although the typical pattern of vertical migration in euphausiids is to descend to deep waters during the day and ascend to the surface at night, occasionally these marine invertebrates aggregate on the surface during daytime (Ritz 1994). Surface feeding on *N. simplex* has been reported for both fin whales and blue whales in the Gulf of California (Gendron 1992; Tershy et al. 1993). However, little is known about potential seasonal patterns for this type of foraging behavior.

We studied foraging behavior of fin whales in Ballenas Channel in the Gulf of California in relation to the distribution of surface swarms of euphausiids. The Gulf of California area encompassing Ballenas Channel is a Biosphere Reserve (Diario Oficial de la Federación 2007), which experiences relatively low levels of human activity and provides an excellent area to study the distribution and abundance of whales. Our primary objective was to identify areas in Ballenas Channel where fin whales forage on surface swarms of euphausiids during daytime and to determine the seasonal occurrence of these types of foraging events. A 2nd focus of our research was to identify potential patterns in the seasonal and annual abundance of fin whales in Ballenas Channel.

Materials and Methods

Study area.—The Ballenas Channel region is located west of the Midriff Islands, in the Gulf of California (Fig. 1). Subsurface topography in Ballenas Channel is complex (depth ranges from 100 to more than 1,500 m) with strong currents and intense tidal mixing contributing to a circulation pattern of persistent upwelling (~5 m/day—López et al. 2006) with very high productivity (Alvarez-Borrego and Lara-Lara 1991; López et al. 2006). Southwest of Ballenas Channel is Bahia de los Angeles (Fig. 1). This relatively shallow bay (10–40 m depth, maximum depth 100 m) maintains a wide communication with the channel. The entrance to the bay is protected by an archipelago of 14 islands, of which Coronado Island, located at the north end of the bay, is the largest (8 km long).

Fieldwork.—We used data on whale sightings collected during linear transect surveys from a 6-m fiberglass boat in 2003 and 2004 to assess patterns in seasonal abundance of fin whales. Most of our sighting surveys for whales were done at a speed of 14–16 km/h by teams of 4 or 5 observers; at least 1 observer was stationed on each side of the boat searching for whales with the naked eye and 7× 50-mm binoculars. Sighting surveys were designed to cross depth contours at perpendicular angles (Fig. 1) and they were conducted systematically in at least 1 month during each season (Buckland et al. 2001). However, because of poor weather conditions during winter, we were unable to complete as many surveys during this season. It was not always possible to conduct sighting surveys for whales in a structured and systematic fashion at boat speeds of 14–16 km/h. For purposes of boat safety, sighting surveys ceased when wind exceeded 3 on the Beaufort scale (wind speed = 5.4 m/s and swell ≥ 1 m). In these cases we continued to search for whales as the boat moved at higher speeds (16–30 km/h) to protected locations. We also counted any whales that we observed when transiting to and from the start and end points of most systemic transects. Search effort was considered as the time spent searching for whales. When whales were sighted, timing of search effort ceased and resumed once all data on the sighting were recorded. We defined a sighting as 1 or more whales observed at the same time showing similar behavioral characteristics and at distances of <500 m from each other.

We also searched for euphausiid swarms on the ocean surface during transect surveys for whales. Surface swarms of euphausiids were located by the reddish color and turbulence of surface water, or by lunge-feeding activities of whales. When a euphausiid surface swarm or group of whales was sighted, it was approached to record the geographic position (Garmin 12XL global positioning system; Garmin, Olathe, Kansas). To identify euphausiid species from the swarms, a net tow was done (0–2 m depth) horizontally through the aggregation at a constant velocity of 5 km/h to collect a sample. The net tow had a diameter of 50 cm and mesh size of 200 μm; we used these data together with the duration of the tow to calculate the volume of water filtered during each tow. In several cases zooplankton concentration was very high, which required us to reduce the duration of the net tow by several minutes to avoid clogging the net. Samples were preserved in 4% formaldehyde buffered with sodium borate.

For all whale sightings we recorded the number of whales present and photographed dorsal fins of as many animals in the group as possible for individual identification using a reference catalog of known individuals (Agler et al. 1990). Photographs were taken with cameras fitted with a 70–300-mm telephoto lens. We used photo-identification to determine the number and duration in days that whales foraged on euphausiid surface swarms.

Behavioral data on foraging whales were recorded ad libitum using standard techniques (Altmann 1974). We considered fin whales as foraging when they broke the water surface (usually right side down) with mouths open and throat grooves expanded, or when they were observed swimming in circles in the area of a surface swarm (Gaskin 1982; Tershy et al. 1993). We respected and followed the bylaws regarding marine mammal research of the Department of Environment and Natural Resources of the Mexican government (Secretaría de Medio Ambiente y Recursos Naturales [SEMARNAT] permits SGPA/DGVS/00510 dated 24 January 2003, 1564 dated 13 March 2003, and SGPA/DGVS/01640 dated 25 February 2004), and we met guidelines recommended by the American Society of Mammalogists (Gannon et al. 2007).

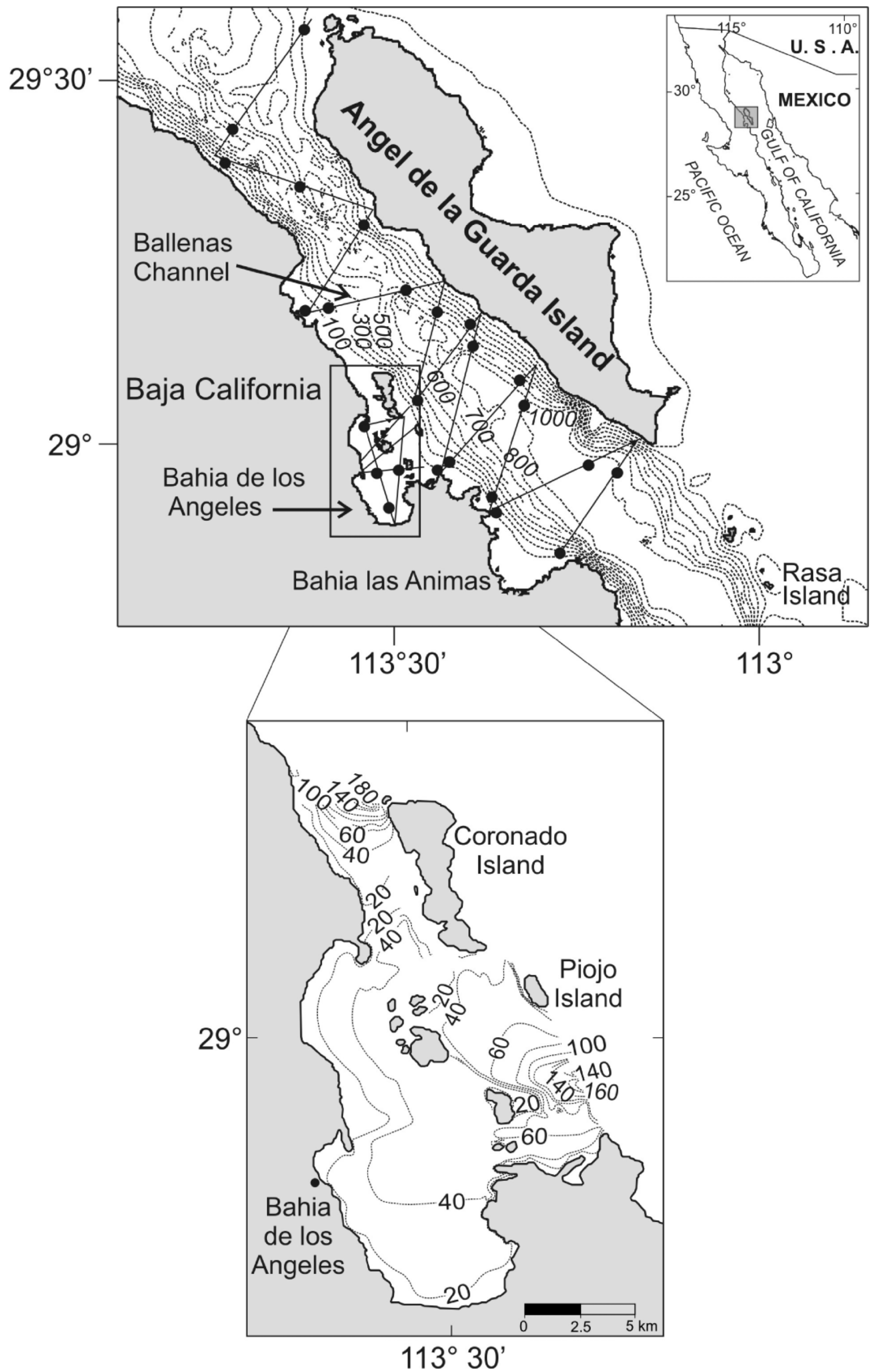

FIG. 1.—Study area in the Gulf of California, México, including Ballenas Channel and the main islands in the Bahia de los Angeles archipelago. Solid black lines represent transect lines used to survey for whales and euphausiid swarms (black points are positions where temperature of the sea surface was measured). Dashed lines describe bathymetry in meters.

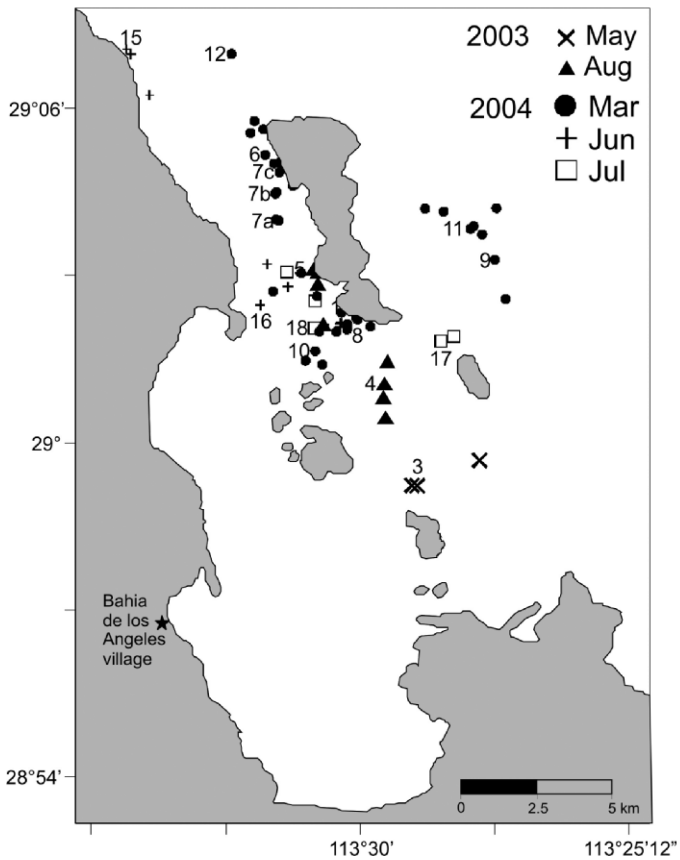

Fig. 2.—Geographic location of daytime surface swarms of *Nyctiphanes simplex* observed during 2003 and 2004 in Ballenas Channel. Numbers correspond to each swarm sample (Appendix I) and symbols to whale sightings for each month. Surface swarms 1, 2, 19, and 13 are not shown because they occurred to the south and east of the area included in the diagram.

Ocean temperatures at the surface exhibit pronounced seasonal variation (Wyrtki 1965), which influences productivity of krill and other organisms. Water temperature readings at the sea surface (30 cm depth) were recorded at positions of euphausiid swarms and at locations of fin whale sightings. We also recorded sea temperature at 2 predetermined stations along each survey transect, 1 station in waters over the continental shelf (100–200 m) and the other over deeper waters (300–1,000 m; Fig. 1).

Laboratory analyses.—We subsampled each euphausiid sample with a Folsom plankton splitter (Boltovskoy 1981) for laboratory analyses. Euphausiids in subsamples were identified (Brinton et al. 2000), counted, and adult organisms were measured for total length (± 0.1 mm) from the tip of the rostrum to the end of the telson. We used data on mean size of adults and a wet weight–length function (Gómez-Gutiérrez and Robinson 1997) to assess biomass of *N. simplex* in daytime surface swarms. Abundance of euphausiids was standardized to number of individuals per cubic meter.

Data analyses.—A digitized bathymetric map of Ballenas Channel (López et al. 2006) was used to associate ocean depth to each whale sighting and euphausiid swarm. We assessed the relationship between depth and number of whales foraging during spring and summer by Fisher's exact test (Zar 1996). Because this analysis requires data to be independent, we limited the test to photo-identified foraging whales.

We used an index of whale abundance (number of whales sighted per hour of search effort during days surveys were conducted) to assess potential seasonal and yearly variation in whale use of Ballenas Channel. Indices of fin whale abundance were compared among seasons and between years using Kruskal–Wallis 1-way analysis of variance (season) and a Mann–Whitney *U*-test (year). Significant differences in the abundance of whales among seasons were further analyzed by the a posteriori Student–Newman–Keuls test.

We used a Student's *t*-test to assess variation in weekly measurements of sea surface temperature between years. Unless otherwise noted, all means are reported ± 1 *SD*.

Results

Fin whales foraging on surface swarms of euphausiids.—Survey days varied between seasons (9–26 days) depending on weather conditions, with a total of 70 days for both years (mean effort and *SD* of 3.6 ± 1.4 h/day during 2003 and 3.2 ± 1.6 h/day during 2004). Fin whales were observed foraging within 18 of 19 surface swarms of euphausiids we detected during daytime surveys. *N. simplex* was the only euphausiid present in all the swarms. Most observations (84%) of foraging fin whales in Ballenas Channel were in relatively shallow waters (10–100 m) of the Bahia de los Angeles area, along the west coast of Coronado Island or south of Coronado Island (Appendix I; Fig. 2). Only 5 sightings of foraging fin whales were out of Bahia de los Angeles; 2 were near Rasa Island, 2 were in Bahia Las Animas, and 1 was on the east side of Ballenas Channel (Fig. 1).

Most (74%) surface swarms of euphausiids occurred during 2004 and all but 1 occurred during spring or summer (Appendix I). The number of fin whales foraging in shallow waters was similar during both spring and summer ($P = 0.08$).

The average duration of net tows for euphausiid sampling was 5 ± 1 min (mean ± *SD*), except for the late winter–early spring samples of 2003 (10.5 ± 0.7 min). The mean volume of filtered water was 172 ± 12 m^3 for samples collected in late winter–early spring of 2003 and 79 ± 19 m^3 for the rest of samples of 2003 and 2004. The abundance and biomass of *N. simplex* was highly variable. Abundance ranged from 8 to 9,394 individuals/m^3 (Table 1), whereas biomass ranged from 88 to 0.02 g wet weight/m^3 in swarms 18 and 13, respectively.

We observed 73 fin whales foraging during 19 sightings; 7 whales were photo-identified in 2003 and 57 in 2004. The mean group size for foraging fin whales was 3 ± 2.6 whales. A common pattern of foraging by fin whales on swarms of *N. simplex* was for 2–4 whales to initiate feeding whereupon several others would join them over a period of several minutes until 6–9 (maximum 13) whales were feeding. Lunge feeding typically involved 2 or 3 whales feeding from a lateral position right side down. Fin whales were generally observed foraging in a swarm area during 2 days and occasionally during 4–5 days.

TABLE 1.—Abundance of *Nyctiphanes simplex* and percentage of adults in daytime surface swarms. Mean length (±*SD*) of adults.

Sample	Total (individuals/m^3)	% of adults	Length (mm)
2003			
1	160	0	
2	176	0.03	9.1 ± 1.1
3	151		
4	15	0.9	8.8 ± 0.8
5	650	62.2	9.0 ± 1.0
2004			
6	47	31.5	8.2 ± 0.5
7	138	10	10.8 ± 1.4
8	9	70	11.9 ± 1.8
9	150	99	13.1 ± 2.0
10	28	31.9	13.8 ± 2.1
11	1,617	28	14.6 ± 1.0
12[a]		13.5	12.9 ± 1.8
13	451	0.3	10.7 ± 1.5
14	81	12.6	10.2 ± 1.4
15	8	18.6	11.0 ± 1.2
16	38	45.9	10.6 ± 1.6
17	44	16.9	12.5 ± 3.5
18	9,394	85.2	10.5 ± 1.4
19	20	0.0	

[a] Collected by hand with bucket device; abundance not estimated.

Seasonal and interannual differences.—The relative abundance of whales in Ballenas Channel was much higher in 2004 (1.51 whales/h) than in 2003 (0.29 whales/h; Table 2; $U = 912.0$, $P < 0.0001$). Whale abundance varied among season in both years (2003 $H = 13.47$, $d.f. = 3$, $P = 0.0037$; 2004 $H = 22.84$, $d.f. = 3$, $P < 0.0001$); maximum observed abundance in both years was during late winter–early spring and summer, whereas whales were relatively uncommon during fall (Table 2). Increased abundance of fin whales during spring and summer coincided with occurrences of daytime surface swarms of *N. simplex*. A posteriori contrasts failed to detect large differences in abundance of fin whales between seasons in 2003. However, if we removed the extreme value of 14.71 whales/h (9 April), the differences in abundance between seasons of 2003 varied in the same way as in 2004. In 2004 fin whales were similarly abundant in late winter–early spring and spring ($H = 22.84$, $P = 0.5930$), significantly increased in abundance between spring and summer ($H = 22.84$, $P = 0.0035$), and abundance declined from summer to fall ($H = 22.84$, $P = 0.0002$; Table 2).

Measurements of the temperature of the sea surface taken during sighting surveys (270 temperature readings for 2003 and 343 for 2004) indicated that water temperatures were warmer in 2003 ($\bar{X} = 25.2°C \pm 3.3°C$) than in 2004 ($\bar{X} = 23°C \pm 4.1°C$; $t = 6.44$, $d.f. = 548$, $P < 0.0001$). Particularly large differentials in water temperature between years were measured in March and October (Fig. 3).

DISCUSSION

Foraging activity of whales.—We identified a characteristic distribution pattern of surface foraging of fin whales in Ballenas Channel. Whales were feeding on swarms of *N. simplex* mainly off Coronado Island during spring and summer seasons. Although some periodicity has been documented for the occurrence of marine predators feeding at the surface on euphausiid swarms during the daytime (Brown et al. 1979; Gill 2002), in general, foraging by baleen whales on this type of euphausiid swarm has been reported as sporadic and opportunistic events.

The greatest biomass of *N. simplex* in daytime surface swarms in our study was 88 g wet weight/m^3, which is higher than the maximum (32.6 g wet weight/m^3) reported by Gendron (1992) for the Gulf of California. However, in our study the range of biomass was much greater than that reported by Gendron (1992—0.7–32.6 g wet weight/m^3). This difference might be accounted for by the variation in density of adult euphausiids in our samples. For example, in contrast to the 88 g wet weight/m^3 composed of adults in swarm 18, in swarm 11 adults comprised 13 g wet weight/m^3, or in swarm 13 adults comprised only 0.02 g wet weight/m^3. Despite the large range in biomass of euphausiids, our estimate agrees with the minimum prey concentrations of 17.5 g/m^3 that fin whales need

TABLE 2.—Comparison between seasons and years of the relative abundance index (RAI) of fin whales (number of whales per hour of search effort).

Survey date	Season	Survey days	RAI of whales per season	RAI of whales per year
2003				0.29
12 March–10 April	Late winter–early spring	9	0.61	
27 May–26 June	Spring	18	0.13	
11 July–4 August	Summer	17	0.90	
16 October–2 December	Autumn	26	0.09	
2004				1.51
6–31 March	Late winter–early spring	20	1.69	
3 Juny–30 June	Spring	22	1.47	
1–30 July	Summer	15	2.83	
7–31 October	Autumn	13	0.31	

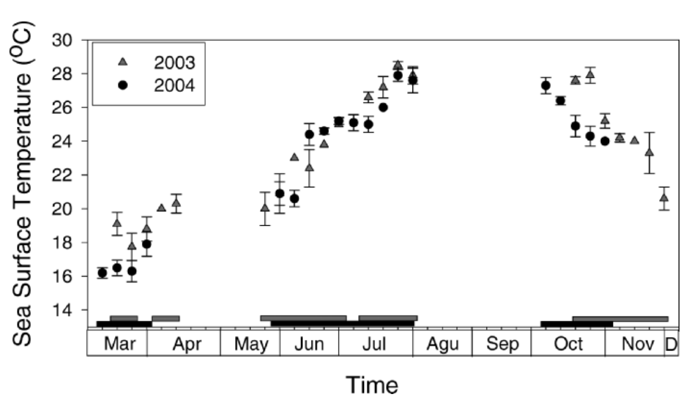

FIG. 3.—Weekly mean sea surface temperature (± 0.95 confidence interval) during 2003 and 2004 in Ballenas Channel. D = December. Gray and black bars indicate search effort during 2003 and 2004, respectively.

to meet their daily energy requirements (Brodie et al. 1978). Additionally, the presence of fin whales foraging in most of the surface swarms indicated that abundance of euphausiids was sufficient to serve as an attractive food resource.

With the exception of humpback whales (*Megaptera novaeangliae*), cooperative feeding in other species of baleen whales has rarely been described (Evans 1987). Our study provides detailed, corroborative evidence of cooperative feeding among fin whales along the west coast of Coronado Island in the Gulf of California. Previous observations by Tershy et al. (1993) had suggested the occurrence of cooperative feeding among fin whales in Ballenas Channel. These observations and those by Canese et al. (2006) in the Mediterranean Sea suggest that cooperative lunge feeding by fin whales may be common and an important part of foraging behavior in the species.

Seasonal and interannual differences.—Feeding activity by fin whales was observed in both cold and warm periods of the year in Ballenas Channel, indicating that fin whales will remain at lower latitudes year-round when food is available (Aguilar 2002; Urbán et al. 2005). In addition, seasonal movements and lunge feeding by fin whales were closely linked to the patchy distribution of daytime surface swarms of the euphausiid *N. simplex*. Previous observations of fin whales moving throughout the Gulf of California had failed to identify that seasonal movements by the animals were associated with the patchy and ephemeral occurrence of high concentrations of their prey (Urbán et al. 2005). Notably, Urbán et al. (2005) were able to affix satellite transmitter devices to 11 fin whales in spring 2001 in the southern Gulf of California. Three of the 11 fin whales localized their movements during summer 2001 in the Midriff Islands region where chlorophyll values were the highest in the Gulf of California (Urbán et al. 2005). These data and information from our study indicate that fin whales in the Gulf of California regularly move distances up to 400 km (Urbán et al. 2005) to locate euphausiid swarms and forage in localized areas with relatively high densities of prey. Based on these types of observations, we suggest that the seasonal patterns in abundance of fin whales may provide an important indication of biological productivity in Ballenas Channel and the Gulf of California in general.

Even though euphausiid swarms and fin whales occurred in the Ballenas Channel area during both study years, they were more abundant in 2004 than in 2003. The differences in sea surface temperature between the 2 years indicated a light warming during 2003, which may have influenced the productivity of euphausiids, and therefore a reduction in the availability of forage for whales. This apparent anomalous warming in the Gulf of California may have been related to the weak 2002–2003 El Niño (Lagerloef et al. 2003; McPhaden 2004). Clearly, movements and feeding behavior of fin whales in a given year vary according to environmental factors. We recommend long-term research and monitoring to examine interannual changes in the foraging ecology of fin whales in Ballenas Channel. Examination of these data will provide important insight into how environmental variations and regular cycles in sea surface temperature contribute to the productivity of populations of fin whales in the southern area of their range, while also providing important insight into factors promoting the evolution of cooperative feeding among baleen whales in general.

Resumen

El objetivo de este estudio fue identificar áreas específicas de forrajeo del rorcual común asociadas a la presencia de enjambres superficiales diurnos de eufáusidos en el Canal de Ballenas, Golfo de California. Durante 2003 y 2004 se llevaron a cabo 4 visitas por año a la zona de estudio (invierno–primavera, primavera, verano y otoño). Se realizaron transectos lineales y recorridos aleatorios en embarcaciones menores (6 m) desde las cuales se muestrearon los enjambres de eufáusidos con una red de zooplancton. El rorcual común se observó forrajeando principalmente en aguas someras (10–100 m) adyacentes a la costa oeste y sur de la Isla Coronado. Se registraron alimentándose en 18 de los 19 enjambres de *Nyctiphanes simplex* registrados (5 en 2003 y 14 en 2004). Los enjambres ocurrieron de marzo a agosto y estuvieron casi ausentes de octubre a noviembre. Aun cuando el rorcual común se observó en toda el área de estudio, se identificó un patrón único de distribución de la actividad de forrajeo, principalmente durante la primavera y el verano. Nuestros datos muestran que las aguas adyacente a la Isla Coronado constituyen un hábitat estacional de forrajeo para el rorcual común en el Golfo de California.

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Appendix I

Sampling dates and data from samples of surface swarms of *Nyctiphanes simplex*.

Season	Sample no.	Date (h)	Swarm location	Bottom depth (m)
2003				
Late winter−early spring	1	9 April (1025)	28°51′N, 113°05′W	600
	2	9 April (1232)	28°51′N, 113°02′W	100
Spring	3	29 May (1017)	28°59′N, 113°28′W	60
Summer	4	1 August (0950)	29°01′N, 113°29′W	50
	5	3 August (0950)	29°03′N, 113°30′W	20
Autumn	—	—	—	
2004				
Late winter−early spring	6	11 March (0959)	29°05′N, 113°33′W	40
	7	12 March (0743)	29°04′N, 113°31′W	20
	8	16 March (0735)	29°02′N, 113°30′W	20
	9	20 March (1012)	29°03′N, 113°27′W	300
	10	21 March (0811)	29°01′N, 113°30′W	30
	11	26 March (1126)	29°03′N, 113°28′W	300
	12	30 March (1501)	29°07′N, 113°32′W	100
Spring	13	15 June (1605)	29°10′N, 113°23′W	100
	14	20 June (0655)	29°02′N, 113°30′W	20
	15	20 June (1643)	29°07′N, 113°35′W	20
Summer	16	23 June (1352)	29°02′N, 113°31′W	20
	17	26 July (0720)	29°01′N, 113°28′W	100
	18	30 July (0844)	29°01′N, 113°30′W	40
Autumn	19	28 October (1117)	28°51′N, 113°20′W	100