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Feeding behavior of gray whales in relation to patch dynamics of their benthic prey

Jo A. Guerrero
San Jose State University

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their benthic prey**

Guerrero, Jo Ann, M.Sc.
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**FEEDING BEHAVIOR OF GRAY WHALES
IN RELATION TO
PATCH DYNAMICS OF THEIR BENTHIC PREY**

A Thesis

Presented to

**The Faculty of the Department of Moss Landing Marine Laboratories
San Jose State University**

In Partial Fulfillment

of the Requirements for the Degree

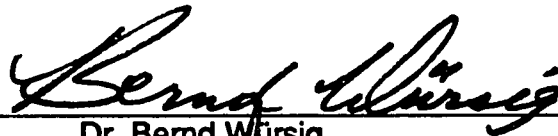
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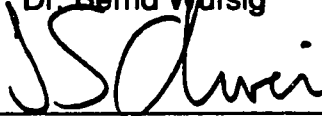
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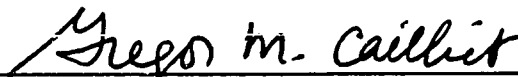
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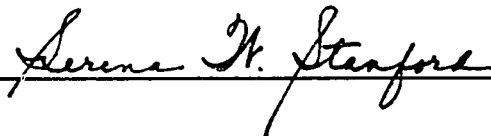


Dr. John S. Oliver



Dr. Gregor M. Cailliet

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FEEDING BEHAVIOR OF GRAY WHALES IN RELATION TO PATCH DYNAMICS OF THEIR BENTHIC PREY

Jo A. Guerrero

ABSTRACT

Significantly different patterns in the feeding behavior of gray whales (*Eschrichtius robustus*) were related to the patchiness and mobility of two benthic prey assemblages at Vancouver Island, Canada. Whales feeding on highly localized hyperbenthic swarms of mysid crustaceans (*Neomysis rayii* and *Holmesimysis sculpta*) dove and surfaced for shorter periods, and respired fewer times during surfacings, than whales feeding on an extensive, relatively homogeneous infaunal amphipod community dominated by *Ampelisca agassizi*. Mysid-feeding individuals moved more quickly at the surface and made more frequent changes in direction than those feeding on infaunal amphipods. These differences in feeding behavior were consistent over time and geographic areas.

The unique accessibility of gray whale benthic prey has made possible this first quantitative correlation between the feeding behavior of a baleen whale and the natural histories of two different prey. Diel, seasonal and annual changes in prey availability, as well as risk of predation, may further impact gray whale feeding behavior.

INTRODUCTION

The feeding behavior and food of many terrestrial mammals can be directly observed and quantified. As a result, their basic feeding ecology is often well-described (e.g. Jarman and Sinclair 1979, Duncan 1983, Danell 1985, McNaughton 1985). In contrast, neither behavior nor prey of most marine mammals is readily observed: feeding typically occurs at depth on pelagic, elusive prey (Ridgway and Harrison 1981a, 1981b, 1985, Gaskin 1982). Feeding studies of large whales are particularly problematic, as the sheer size of these animals limits information available from captive studies (but see Ray and Schevill 1974). Thus, the strategies that whales use to capture and consume prey must be largely deduced from whale morphology and very limited observations of whale and prey behavior. An accurate description of this basic natural history is fundamental to an evaluation of whale predator-prey interactions and their role in the marine ecosystem.

The stomach contents of whales killed during commercial whaling have established that the large baleen whales generally feed on aggregating crustaceans or fish (Scammon 1874, Nemoto 1959, 1970). Numerous studies have further linked whale occurrence to high densities of these prey (e.g. Berzin and Rovnin 1966, Whitehead and Carscadden 1985, Schoenherr 1988, Wishner et al. 1988; and see review in Gaskin 1982). The ventilations and surface movements of feeding whales have been quantified from direct observations (Würsig et al. 1984, 1986) and radio tracks (Watkins et al. 1981, 1984). However, only recently have studies also quantified depth and density of prey patches in relation to whale behavior (Hamner et al. 1988, Goodyear 1988). Surface observations of whales combined with underwater photographs

to assess prey density and sonar records of whale and prey depth provide the strongest link between whales and prey to date (Dolphin 1987a, 1988).

Surface observations reveal that baleen whales use a variety of feeding modes. They may skim prey (Watkins and Schevill 1979) or gulp prey (Jurasz and Jurasz 1979, Watkins et al. 1979; and see reviews in Nemoto 1970, Gaskin 1982), sometimes in combination with bubble nets or clouds created to contain the prey (Jurasz and Jurasz 1979, Hain et al. 1982). Recent radio tracking and sonar studies suggest that some species may be able to vary their feeding behavior with different prey species (Watkins et al. 1984) and densities (Hamner et al. 1988). However, quantifiable differences between these prey have not yet been linked to different whale feeding strategies.

Gray whales (*Eschrichtius robustus*) are an excellent subject for a quantitative study matching feeding behavior and prey. Unlike other baleen whales, they feed primarily on benthic invertebrates (Rice and Wolman 1971, Bogoslovskaya et al. 1981, Nerini 1984, Yablokov and Bogoslovskaya 1984, Kim and Oliver in press). Most gray whales migrate annually along a narrow coastal corridor from calving grounds in Baja California to primary feeding grounds in the northern Bering and southern Chukchi Seas (Pike 1962, Rice and Wolman 1971, Braham 1984, Herzing and Mate 1984, Poole 1984). They excavate infauna inhabiting soft substrates in water depths of less than 50 meters. Secondly, they consume nearshore hyperbenthic swarming prey (Kim and Oliver in press). Thus, gray whales and their prey can be readily observed and quantified. The accessibility of benthic prey has already improved our understanding of the feeding ecology of gray whales (Johnson and Nelson 1984, Nerini and Oliver 1983, Oliver et al. 1984, Oliver and Slattery

1985, Nelson et al. 1987), walrus (*Odobenus rosmarus*; Oliver et al. 1983a,1985) and sea otters (*Enhydra lutris*; VanBlaricom and Estes 1988).

A small number of gray whales summer annually along the west coast of Vancouver Island (Darling 1978, 1984). They feed near shore on two distinct crustacean prey communities which occur in soft substrate and over rocky reefs (Darling 1984, Murison et al. 1984, Oliver et al. 1984, Oliver and Slattery 1985, Kvitek and Oliver 1986). The soft-bottom prey are dominated by tube-dwelling amphipods, and are ecologically similar to the benthic prey communities in the primary feeding grounds. The prey in rocky reefs are mysids, which swarm just above the rock substrate in kelp forests (Murison et al. 1984, Oliver et al. 1984).

This study quantifies the surface behavior of feeding gray whales and the patchiness of amphipod and mysid prey. Respiration and movement patterns of feeding whales are related to differences in the spatial and temporal patchiness of amphipod infauna and mysid swarms.

METHODS

Gray whale behavior and benthic communities were quantified in the soft-bottom habitats of Ahous Bay and the rocky reefs of Pachena Bay along the southwest coast of Vancouver Island, British Columbia (Figure 1). Field observations were made at Pachena Bay from 21 July to 15 August 1983 and 10 August to 8 September 1984, and at Ahous Bay between 23 August and 2 September 1984.

Study Sites

Ahous Bay (Figure 2) encompasses approximately 8 km² of fine sand substrate which is protected from oceanic swell by surrounding islands and submerged reefs. The bottom slopes gradually to a water depth of 22 meters, where the substrate changes to coarse sand and gravel. The protected fine sand bottom inside Ahous Bay is similar to Pachena Bay; both harbor dense communities of tube-dwelling ampeliscid amphipods (Oliver et al. 1984, Kvitek and Oliver 1986). The mouth of Pachena Bay (Figure 3) is surrounded by rocky bottom extending to a water depth of at least 20 meters within 0.5 km of shore. This zone is covered with a dense canopy of bull kelp, *Nereocystis luetkeana*. The rocky outcrops in deeper water have a lower vertical relief and are less continuous than the shallower kelp forest reefs.

Behavioral Observations

Gray whales were located and observed from small boats (4-5 meters length) fitted with 15-35 horsepower outboard engines. Many extended observations of localized behaviors were conducted with the engine off in calm water (e.g. in kelp beds). Observers resumed motoring, at a constant speed and avoiding sudden movements toward whales, when a focal animal moved

beyond the range it could be visually re-identified, generally about 200 meters. Under these conditions, no change in whale behavior was detected. Observers occasionally motored too close to whales (this distance varied with behavior state and individual), which clearly disturbed them; these observations were omitted from analyses.

Individual whales were identified and visually tracked as long as possible by means of unique pigment patterns, scars and other markings (as in Darling 1984). A four-person boat team described and recorded all respiratory and dive behavior, and determined locations using nearby landmarks, site maps, and compass bearings. A sketch of easily-observed markings was made for each animal for later re-identification.

Behaviors systematically recorded included all exhalations (or "blows") and all postures preceding dives (e.g. raising flukes from the water). Five respiratory parameters were quantified: blow interval, length of surfacing, length of dive, number of blows per surfacing, and blow rate. Blow rate was calculated as the total number of blows from complete surface-dive cycles divided by the total duration of the surface-dive cycles, as in Würsig et al. (1986).

Additional observations recorded included those which revealed underwater activity, such as vertical flukes moving just below the surface indicating a vertical, head-down feeding position. Relative surfacing speed was estimated when possible as slow (no white water around body or insignificant bow wave), fast (easily visible white water and surface agitation or bow wave), or medium. Most whale behavior was visible with the naked eye, but

observations were aided by binoculars, and, on one occasion, by the use of a Javelin night-vision scope (Model NVD 221).

Individual behavior was categorized during each observation period as feeding, traveling, resting or socializing. Whales were considered feeding when repeatedly diving over a restricted area. Fecal slicks and foul-smelling breath provided additional indirect evidence of feeding at both sites. Comparable evidence has been used by others to identify feeding (Darling 1978, Oliver et al. 1983b, 1984; Nerini 1984, Dolphin 1987b) Results confirmed that this behavior occurred only when prey were present. Traveling was defined as medium to fast movement along a relatively straight course through several surface-dive cycles. Resting was identified by very slow surfacing speeds, with little or no forward rolling and flukes rarely exposed. Socializing was defined as two whales making physical contact or swimming within 1/2 body length of each other in coordinated fashion (e.g. side by side). Behavioral data in 1984 were obtained more systematically than in 1983. Therefore, unless specifically noted, statistical behavioral comparisons were made using only 1984 data. Differences between respiratory parameters at the two feeding areas, and the relative impact of variability between and within individuals (discussed further in Results) were statistically analyzed using standard procedures in Zar (1984) and Sokal and Rohlf (1969).

Benthic Prey Communities

Scuba divers working from small boats sampled benthic communities at Ahous Bay and Pachena Bay. Previously reported diver and side scan sonar surveys conducted in 1983 and 1984 (Oliver and Kvitek 1984, Kvitek and Oliver 1986) determined where ampeliscid amphipods were present at Ahous Bay

and Pachena Bay. Those surveys mapped the geographic extent of the amphipod tube mats, and included quantitative sampling of the densest portions of the tube mats. In the present study, infaunal communities were further examined only at Ahous Bay, as this was the only local soft-bottom habitat where gray whales were present. Divers expanded the earlier qualitative surveys and quantitative sampling in Ahous Bay by mapping the relative density of amphipods along additional transects extending from the surf zone to the offshore edge of the tube mat. The relative density of amphipods was assessed by gently suspending surface sediments by hand and exposing the tubes. Since tubes quickly break up without regular maintenance, intact tubes generally signified a living occupant. These observations of tube density were combined with previously reported diver and side scan sonar observations (Kvitek and Oliver 1986) to map the general cover of amphipod tube mats in Ahous Bay.

Previous studies have identified mysid crustacean prey over rocky bottoms (Murison et al. 1984, Oliver et al. 1984). However, these qualitative surveys were much less extensive than the previous work in local soft-bottom habitats (Oliver et al. 1984, Oliver and Kvitek 1984, Kvitek and Oliver 1986). Side scan sonar cannot survey rocky-bottom prey as it can soft-bottom prey; therefore mysids were sampled by diving. Divers swam weekly transects through and outside the kelp forests surrounding Pachena Bay in the summers of 1983 and 1984, making qualitative notes on the locations of swarms, their thickness and relative density, and their spatial scale. These observations were used to map the occurrence of mysid swarms in the study area. The aerial

cover and vertical thickness of swarms were not quantified, due to their highly irregular dimensions over complex bottom topography in the kelp forests.

Biomass, reproductive status and size frequency of mysids were quantified from several specific sites frequented by feeding whales. Biomass and average individual weights were calculated from wet weight measurements of cylinder trap samples (see below). Sex and life stages were recorded from 1-mm mesh diver-held net samples. Size frequency patterns were measured from two of the net samples. Individual lengths of fully extended specimens were measured from the eyes to the end of the telson. A subsample of *Neomysis rayii* individuals (n=85) was also measured in bent postures approximating those observed in underwater photographs. This average bent length was used to estimate actual distances between individuals in the field (see below). All samples were preserved in a 4% solution of formaldehyde and individuals were identified to species and counted.

Two different sampling techniques were used to quantify densities of the two mysid species from the Pachena Bay study area. Although mysids often occurred in large mixed-species shoals, within a shoal they were usually segregated by species and size into smaller swarms. Divers sampled the smaller and less active mysid, *Holmesimysis sculpta*, with an aluminum cylinder trap (0.03 m³ volume) attached to a pole spear. The cylinder was shot with stretched rubber tubing into a swarm from a distance of 1-3 meters. When the pole was extended, nets were closed over both ends of the cylinder by a trip cord in the diver's hand. The force of the ejected spear rapidly closed the nets with minimum mysid escapement. Three replicate cylinder samples were taken in August 1984 at two sites where *H. sculpta* was abundant (Table 2).

The larger species, *Neomysis rayii*, is very active and easily avoided the most rapid sampling efforts by divers. Its abundance was instead estimated from underwater photographs. Fortunately, the relatively narrow range in the size of *N. rayii* individuals, allowed estimates of individual lengths in photographs. Distance between neighboring individuals of equal size was measured under a 10 power dissecting microscope whenever both individuals were fully broadside and in focus. All pairs were measured in all photographs when the measurement criteria were met (i.e. both in focus, same size, and broadside). The ratio between the average length of each pair on the photo to the average true length of a *N. rayii* individual was used to determine the average distance between the pairs in the photos. These distances were converted to number of animals per 0.5 m³.

Quantitative mysid samples were converted to 0.5 m³ to most accurately compare them to the infaunal samples standardized to a 1 m² substrate area. Qualitative diver observations indicated that mysid swarms averaged 0.5 m thick. Therefore, a feeding whale was most likely to encounter a 0.5 m-thick swarm over a standard 1 m² substrate area, resulting in a 0.5 m³ standard mysid sample volume. Statistical comparisons of prey biomasses and sizes of mysid sexes and life stages used tests in Zar (1984) and Sokal and Rohlf (1969).

RESULTS

Gray Whale Behavior

Gray whales were encountered every day observer teams looked for them in 1983 (7 days) and 1984 (20 days, Pachena Bay; 4 days, Ahous Bay). Uninterrupted observation periods on individual whales ranged from 0.3 to 15.8 hours. In 1983 at Pachena Bay, nine gray whales were observed for a total of 16 hours. In 1984, thirteen individuals were observed for a total of 100 hours at Pachena Bay; four individuals were observed for a total of 22 hours at Ahous Bay. Average size range of these individuals was visually estimated as 10-13 meters (juvenile to adult size; Rice and Wolman 1971). No calves were observed.

Feeding Behavior

Feeding whales displayed distinct surface behaviors and movement patterns over known prey. Whales dived repeatedly over concentrations of mysid and amphipod prey, and restricted their feeding activities to these areas by turning at the boundaries of prey patches. Edges of mysid shoals were particularly distinct and were repeatedly verified by divers.

Gray whale ventilation patterns differed dramatically over amphipod and mysid prey (Figure 4; Table 1). At Ahous Bay, whales feeding on infaunal amphipods dove for an average of 3.7 minutes, then spent 0.9 minutes at the surface respiring at intervals of 14.9 seconds. In contrast, whales feeding on mysids at Pachena Bay dove and surfaced for much shorter periods of time, in both cases less than half the duration of amphipod feeding whales (average dive time = 1.6 min., average surface time = 0.4 min.). Blow intervals were also shorter than in amphipod-feeding whales. The differences between dive times,

surface times, and blow intervals over mysid and amphipod feeding grounds were highly significant (t prime test or Mann-Whitney U test as appropriate, $p < 0.01$).

The most conspicuous difference between whales feeding on amphipods and mysids was in the number of blows per surfacing (Figure 5). Mysid-feeding whales respired only once in almost half (43%) of the 1494 total surfacings observed. In contrast, 1-blow surfacings comprised less than 5% of the total surfacings observed in amphipod-feeding whales. The difference in the distributions of blows per surfacings over mysids and amphipods was highly significant (Kolmogorov-Smirnov test, $p < 0.001$).

Only 5 of 17 total individuals observed in 1984 provided 78% of the total observation hours used in analyses. Thus, it seemed possible that the significant differences found in the respiration patterns of mysid- and amphipod-feeding whales might be due to one or two easily-tracked but aberrant individuals. The relative impact of variability between and within individuals for one representative feeding parameter, dive duration, was assessed 1) within one individual in one day, 2) within one individual on different days, and 3) between individuals. Variation between individuals accounted for only 5 % of the total variability in feeding dive duration and was not statistically significant (nested ANOVA, $p > 0.10$).

Qualitative observations of differences in gray whale surface behavior over different prey were as striking as the quantified respiratory characteristics. Amphipod-feeding whales moved at the surface at slow to medium speeds along predictable, relatively straight courses. Dives were generally initiated by raising both flukes evenly out of the water. In contrast, mysid-feeding whales

moved at the surface at relatively fast speeds; direction and location at surfacings were unpredictable compared to those of amphipod-feeding whales. Dives were commonly initiated by rolling onto the side and exposing only one fluke. During mysid-feeding dives, vertical flukes were occasionally observed moving at or just below the water surface, creating a circular, stationary water disturbance. Fluke orientation and the duration of these events (at times 5 seconds or more) indicated that whales were assuming a head-down, vertical position in the water column. This behavior was only observed at Clutus Point, Fin Rock and Cormorant Rock, where divers documented the densest patches of mysid prey (see Kelp Forest Prey).

The trends in whale feeding behavior over different prey were consistent over different years and geographic locations (Figure 4). Mysid-feeding whales at Pachena Bay in different years exhibited similar respiratory characteristics. The respiratory characteristics of amphipod-feeding gray whales at Ahous Bay and Saint Lawrence Island, Alaska (Würsig et al. 1986) were remarkably similar in duration of dives and surfacings, and number of blows per surfacings. Comparison of these characteristics showed no significant difference (t or t prime test for unequal variances as appropriate, $p > 0.05$). Comparative data used from Würsig et al. (1986) included observations from all whales observed in the month of July, when feeding was the most common behavior.

Non-Feeding Behavior

Traveling and resting behaviors were observed only at Pachena Bay. Respiratory characteristics during travel (except for blow interval) did not differ greatly from those of mysid-feeding whales (Table 1), though generally these two behaviors were readily distinguished by the movement patterns of

individuals within or between areas of the study site. Traveling whales typically moved along a direct path from one mysid-feeding area to another, often over areas without prey. Unlike feeding whales, they were never observed turning onto one side before a dive or assuming a head-down vertical position during a dive. Resting whales were readily identifiable by respiratory patterns distinct from any other behavior (Table 1).

Socializing as defined occurred rarely: the 6.8 total hours observed include 1.5 hours each from two socializing individuals. In the field, socializing could generally not be differentiated from whatever behavior the animal was engaged in prior to the association with another whale. Therefore, the respirations which occurred during social behavior were not statistically analyzed.

Individual Activity Patterns

Feeding was the dominant activity of virtually all individuals, comprising 62 % of the total observation hours over mysids and 87% of total observation hours at Ahous Bay (Figure 6). Traveling and resting at Pachena Bay comprised 20 % and 6 % of total observation hours, respectively. Remaining observation hours were of social and unidentified behavior, combined as "other."

The activity patterns of individuals were clearly associated with the location of prey patches. Tracks of two whales typify the sequences and geographic locations of behaviors observed at Ahous Bay (Whale 15; Figure 2) and Pachena Bay (Whale 17; Figure 3). Whale 15 fed for the entire observation period (7.1 hours), primarily over the densest parts of the amphipod tube mat (Figure 2). The whale moved along relatively straight paths, especially

during the first 4 hours when it fed in a 2 km-long swath parallel to the mouth of the bay. However, even when feeding over a smaller, roughly circular area at the bay mouth, the whale moved in a series of fairly straight sweeps through the area (too concentrated to reproduce legibly on Figure 2). Whale 15 moved at a constant medium-slow speed throughout the bay.

Whale 17 was observed for 28.9 hours over a 34-hour period. It fed for 63 % of the observation period, primarily at Clutus Point (Figure 3). Feeding behavior was highly localized over dense mysid swarms. Surface activity included all qualitative characteristics of mysid-feeding behavior described earlier. Travelling and resting comprised 12% and 13 % of total observation hours, respectively; both behaviors generally occurred outside regions with prey communities.

Night observations of whale 17 were made possible by the combination of a full moon and a Javelin night-vision scope. At 2300 hours (i.e 2.5 hours after sunset, 0.5 hours after moonrise), the individual changed from feeding to resting behavior, simultaneously moving from Clutus Point to the mouth of Pachena Bay, over a sandy bottom (with no prey). Resting continued until the animal was lost at 0257 hours. At 0449 hours, whale 17 was relocated at mid-bay and followed to the south end of the bay. Pre-dawn light enabled unaided observation of the whale by 0520. It resumed feeding at 0527; sunrise was at 0550 hours.

Behavior with Killer Whales

On 16 August 1984, gray whales apparently left the Pachena Bay area. This unusual absence of gray whales coincided with the arrival of a pod of four killer whales (*Orcinus orca*). No feeding gray whales were located throughout

the study area and in a much larger area to the north and south. Observations from local residents and other researchers at nearby Bamfield Marine Station indicated that the killer whales were only present around the study area for one day and then moved north across Barkley Sound (Figure 1). The usual pattern of four locally-feeding whales prevailed until the killer whales arrived and was re-established the day after they moved through the region. As the killer whales passed through the area, three gray whales were discovered very near the Clutus Point shore. None appeared to be feeding. One individual was observed motionless, except for occasional respirations, in very shallow water between two large rocks within 10 meters of shore. No other inactive individuals were ever encountered in a comparable highly protected, shallow habitat.

Prey Occurrence

Soft-Bottom Prey

Gray whales fed over an extensive infaunal tube mat of amphipod crustaceans at Ahaus Bay. Infauna was dominated by the tube-dwelling amphipod, *Ampelisca agassizi*, which occurred within the top 5 cm of the sediment surface. The tube mat extended from the outer edge of the surf zone to about 20 m of water (Figure 2), where the substrate changed to a coarse sandy gravel forming large ripple marks (Kvitek and Oliver 1986; this study). Divers observed the densest amphipod tube mats at a water depth of approximately 12 m. Most observations of feeding gray whales also occurred along this 12 m depth contour, inside the mouth and parallel to the long axis of the bay (e.g. Figure 2 whale track). Gray whale feeding excavations 10-20 cm deep were located visually and by side-scan sonar (Kvitek and Oliver 1986)

throughout the *Ampelisca* tube mat, but were found most frequently at about 12 m depth. Infaunal amphipods and feeding excavations were located only in the areas where whales were observed feeding. Divers reported no changes in the boundaries or relative densities of the *Ampelisca* mat during the 1984 season. No mysid swarms were located in or around Ahous Bay.

Kelp Forest Prey

Divers found dense mysid swarms only where whales were observed feeding at the mouth of Pachena Bay in 1983 and 1984. Swarms were always overlying rocky reefs, with lower boundaries usually 1-10 cm from the rocky substrate, and covering areas less than 100 m². Swarm thickness varied from 20 to over 200 cm, but averaged about 50 cm. Swarms were most common at 5-13 m depth where kelp forests were well developed, and averaged approximately 10 m depth. Swimming into dense swarms at times decreased visibility from 8 m to 1 m.

In both years, mysid aggregations were formed by two species, *Holmesimysis sculpta* (formerly *Acanthomysis sculpta*) and *Neomysis rayii* (both species referred to by genus only in remaining text). Large shoals contained both species which were segregated into distinct swarms of each species and into large and small individuals. At sites where both species were collected, densities were similar. Density estimates within swarms of both species varied substantially, as indicated by high standard deviations of swarm samples (Table 2).

Locations and relative densities of mysid swarms remained constant within each summer, but varied significantly between years. Since swarms usually ended abruptly at the kelp forest edge, divers were able to accurately

map the boundaries of swarm edges. In 1983, divers consistently located the densest swarms along the east side of Seabird Island (Figure 3 inset). They were present throughout a month of field observations. No other dense swarms were located by divers throughout the study area, except for a small and less dense swarm at South Bed. In 1984, mysid swarms were much more widespread, but were not well developed at Seabird Island. Divers consistently identified densest swarms (>4500 individuals per 0.5 m^3 ; Table 2) where conspicuous geographic features marked local underwater habitats at Clutus Point, Cormorant Rock and Fin Rock (Figure 3). Less dense swarms (<3500 individuals per 0.5 m^3 ; Table 2) occurred consistently at South Bed. These spatial patterns persisted during a month of field observations. Diver categorization of less dense swarms at South Bed were only partially supported by statistical analyses. Swarms at the west end of South Bed were significantly less dense than those located at Clutus Point, Fin and Cormorant Rocks, but those at the north end were not (Table 2; Kruskal-Wallis test, multiple comparison by ranks, $p=0.05$), perhaps reflecting low sample size at the north end and high standard deviations at all sites.

Rockfish, as well as gray whales, consumed mysids at Pashena Bay. In 1983, five black rockfish (*Sebastes melanops*) were caught by hook and line at Seabird Island, where gray whales fed consistently. Examination of the gut contents revealed large quantities of mysids and no other visible prey. Schooling rockfish were frequently observed in and around mysid swarms by divers.

Prey Biomass

Biomass estimates reflected different individual sizes of the two mysid species and the proportions of different life stages present. *Neomysis* biomass was consistently greater than *Holmesimysis* biomass (Table 2), due to the larger size of *Neomysis* individuals (Table 3; Figure 7). Ovigerous females often accounted for over 50 % of the individuals in both mysid species (Table 4). They were significantly larger and weighed more than other life stages (Kruskal-Wallis test, $p < 0.001$, multiple comparison by ranks, $p < 0.001$; Table 3), and thus contributed significantly to total biomass. Males were not significantly larger than non-ovigerous females (multiple comparison by ranks, $p > 0.05$; Table 3), and were similar in general abundance (Table 4). Although immature mysids were virtually absent in samples, they were occasionally observed by divers in small swarms within larger shoals.

Mysid and amphipod biomass estimates were intermediate between infaunal biomasses reported in the northern Bering Sea primary feeding grounds and Baja California calving lagoons (Table 5). Maximum mysid biomass (211 g/0.5m³) was higher than infaunal biomass (160 g/m²), but this difference was not significant (t prime test, $p > 0.05$). Mysid biomass was equal to the lower range of infaunal biomass estimates documented in the primary feeding grounds. The infaunal biomass at Ahous Bay was comparable to that found inside Pachena Bay during documented whale feeding in previous years (Table 5).

Prey Patchiness and Gray Whale Sightings

The geographic cover and relative densities of prey patches corresponded to the occurrence of feeding whales at Pachena Bay. In 1983,

Pachena Bay was scanned daily for whales. Feeding whales were consistently observed only along the east side of Seabird Island, where divers located the densest mysid swarms. Whales occurred occasionally at South Bed, where less dense swarms were located. Whales were rarely observed in any other part of the study area.

In 1984, more extensive observations and quantitative prey sampling allowed better correlation of the occurrence of whales and prey. An average of 3-4 gray whales (range=1-5, n=20 days) were observed daily in the Clutus Point-Cormorant Rock-Fin Rock area (Figure 3). This area also contained the densest mysid swarms (>4500 individuals per 0.5 m³; Table 2). One or two whales occasionally fed at South Bed on swarms which were less dense (<3500 individuals per 0.5 m³). No whales were observed feeding at Seabird Island; no swarms were found here in 1984. Only one whale was typically observed at Ahous Bay. However, observer effort was also much lower at Ahous Bay than Pachena Bay (22 hours vs. 100 hours).

DISCUSSION

Gray whale feeding behavior differed significantly over infaunal amphipod and swarming mysid prey. Differences in behavior matched differences in prey patch size and mobility. At Ahous Bay, whales made long-duration dives to consume infauna which was relatively evenly dispersed over an 8 km² area. Gray whales can apparently make six or more feeding excavations during a single dive (Oliver et al. 1984, Nerini 1984). Long dives may have maximized the number of excavations possible per dive. In addition, by feeding over an extensive, homogeneously dispersed infaunal community along a relatively straight path (thus minimizing the chance of reworking a previous excavation), an amphipod-feeding whale making multiple excavations in a dive would be likely to consume prey at each excavation. Long dives alternated with long surfacings, when animals respired several times and swam at fairly slow, constant speeds along predictable paths. A correlation between the duration of dives and surfacings has been noted for gray whales feeding in the Bering Sea (Würsig et al. 1986) and bowhead whales (*Balaena mysticetus*) in the Beaufort Sea (Würsig et al. 1984).

Mysid prey were extremely patchy in comparison to infaunal prey, occurring in distinct, isolated swarms interspersed with large areas void of mysids. Whale feeding strategy varied accordingly. Gray whales fed in highly restricted areas over dense, discrete mysid swarms. Swarms maintained their positions over specific sites despite frequent disturbances by feeding whales. Other researchers have confirmed that mysid swarms actively maintain home sites (Clutter 1969, McFarland and Kotchian 1982, Hahn and Itzkowitz 1986). Individual mysid size varied from 7-25 mm, comparable to the size range of

infaunal amphipods (Mills 1967, Oliver et al. 1983b) and greater than the minimum prey size (3 mm) previously documented in gray whale stomachs (Nerini 1984). Mysid biomass was comparable to the lower biomass estimates reported from the primary feeding grounds (Thomson 1984). Mysid calorie content per gram may have been higher than that for infaunal prey. Ovigerous female mysids have a higher calorific value than males or other life stages (Mauchline 1980), and a large proportion were consistently found in the shoals sampled. In contrast, *Ampelisca* ovigerous females are found mainly during winter (Kannevorff 1965).

Whales moved quickly and frequently changed directions and body orientations over these localized prey patches. Unlike infaunal feeding, fast speeds may be necessary to capture mobile prey. Varying surface speeds of a feeding southern right whale (*Eubalaena australis*; Hamner et al. 1988) and fin whale (*Balaenoptera physalus*; Watkins et al. 1984) have been correlated to the mobility of different prey. Unpredictable orientations at successive surfacings indicated that whales were changing direction underwater. By rolling onto one side upon descent, individuals may have increased usefulness of the pectoral fins in maneuvering over restricted areas underwater (Watkins and Schevill 1979). Whales made short-duration dives; surfacings were also short, with only one or two respirations per surfacing. The combination of short-duration surfacings and frequent direction changes minimized time spent and, perhaps more importantly, distance traveled away from a highly localized, mobile prey source.

These data are the first to establish clear, measurable differences in whale activity over two very different prey communities. Though not well-

quantified, behavior changes in response to different prey have also been proposed for bowhead (Würsig et al. 1985), right (*Eubalaena glacialis*, Watkins et al. 1984; *E. australis*, Hamner et al. 1988), and humpback whales (*Megaptera novaeangliae*; Jurasz and Jurasz 1979, Hain et al. 1982, Watkins and Schevill 1979). In this study, observations of mysid-feeding gray whales further suggest that feeding behavior also varies measurably and consistently with different prey densities. Head-down, vertically-oriented whales occurred only over the densest mysid swarms identified by divers. Feeding individuals also appeared to move faster at the surface and be more restrictive in horizontal distance covered than whales feeding over less dense swarms. Recent observations of a southern right whale altering behavior in response to different euphausiid densities (Hamner et al. 1988) lend additional support to Norberg's (1977) prediction that foraging behavior changes with prey density.

Feeding was the most common behavior at both study sites, though travel and resting behaviors were also occasionally observed at Pachena Bay between and outside mysid swarms. A comparison of blow rates of feeding and non-feeding behaviors revealed unexpected trends. Not surprisingly, mysid-feeding whales had a higher blow rate than amphipod-feeding whales, presumably indicating a higher oxygen demand due to higher energy expenditure. However, the blow rate of traveling whales was higher than that for either feeding mode, and the rest blow rate was highest of all. Apparently, blow rate alone cannot be used as an indication of physiological stress. Other variables, such as adjustments in lung capacity suggested by Dolphin (1987c), may also influence breathing rates.

Differences in whale feeding behavior cannot be attributed to different prey depths. The average depths of mysids (10 m) and amphipods (12 m) were very similar. However, prey depths differing by 20 m or more have been correlated to changes in the surface behavior of whales (Würsig et al. 1986, Dolphin 1987a, 1987b, 1987c) and pinnipeds (Croxall et al. 1985, Kooyman and Goebel 1986).

Though the infaunal amphipod community utilized by Vancouver Island gray whales is much less extensive than the primary feeding grounds to the north, it is ecologically very similar (Oliver et al. 1984). In both areas, recruitment and reproductive patterns of *Ampelisca* maintain a relatively stable, resilient prey resource year-round (Kannevorff 1965, Mills 1967, Oliver et al. 1984, Oliver and Slattery 1985). Infaunal biomass is higher during summer months due to peaks in individual growth and release of young (Kannevorff 1965, Mills 1967). Some individuals from the *Ampelisca* infaunal community disperse into the water column at night as reproductive adults or newly released young (Kannevorff 1965, Oliver and Slattery 1985). However, these temporarily mobile individuals generally account for less than 10 % of the total infaunal biomass (Oliver and Slattery 1985, P. Slattery pers. comm.).

The *Ampelisca* community in the primary feeding grounds is several orders of magnitude larger than that at Vancouver Island, covering about 22,000 km² (Nelson et al. 1987), compared to only 16 km² total *Ampelisca* infauna occurring in three different bays along the Vancouver Island coast (Kvitek and Oliver 1986). Of these three isolated pockets of infaunal prey, Ahous Bay is the largest and most heavily used. The respiratory patterns of whales feeding on infaunal amphipods at Ahous Bay do not differ significantly

from those in the Bering Sea (Würsig et al. 1986). Feeding behavior over amphipod prey is apparently not influenced by the size of infaunal area or its geographic location.

Prey biomass at both study sites was intermediate between the high biomass available in the primary feeding grounds of the northern Bering Sea (Stoker 1978, Thomson 1984) and the extremely low biomass documented in the calving lagoons of Baja California (Oliver et al. 1983b). The annual occurrence of about 50 feeding whales along the Vancouver Island coast (Darling 1984) is similarly intermediate between the hundreds of feeding whales observed annually in the primary feeding grounds (Moore and Ljungblad 1984) and the very rare reports of presumably feeding whales in the calving lagoons (Nerini 1984).

Mysid swarms occurred in much smaller patches than infaunal amphipods. However, their extensive distribution along the Vancouver Island coast and heavy utilization at Pachena Bay suggest that mysids are the major prey of Vancouver Island gray whales. A previous survey of potential whale feeding areas along the open coast revealed a predominance of kelp forest habitats harboring mysid swarms (Kvitek and Oliver 1986). In this study, more whales consistently fed on mysid prey than ever observed over known infaunal communities at Ahous or Pachena Bay.

Though mysids appear to be the primary prey resource available to whales summering at Vancouver Island, their occurrence is highly variable. Within dense swarms, patchiness is evidenced by high variability in swarm samples. Larger scale changes in swarm abundance and location may reflect annual and seasonal population fluctuations, as well as changes in weather

and light levels. In successive summers, the occurrence of dense mysid swarms varied greatly in the Pachena Bay-Barkley Sound region. Abundant mysids and feeding whales were documented in 1981 (Murison et al. 1984) in a nearshore region of Barkley Sound. Though the same easily located sites were dived in 1982 and 1983, no dense patches were observed (Oliver et al. 1984). The dense mysid patches observed at Seabird Island in 1983 were absent in 1984. Conversely, the dense aggregations observed at the mouth of Pachena Bay in 1984 were not located in 1982 (Oliver et al. 1984) or 1983.

The seasonal population dynamics of *Neomysis* and *Holmesimysis* are not well known. However, marked seasonal fluctuations in abundance are common in many species (Mauchline 1971, 1980). In addition, the proportion of ovigerous females often varies seasonally in temperate regions (Mauchline 1980), and Tyler (1973) noted that calorific values of temperate mysid species were likely to show seasonal variation. Within each summer, mysid swarms occurred at the same specific sites and in the same relative densities. However, immediately following a summer storm, mysids were not present at their usual nearshore sites, but occurred in a thin dispersed layer over sandy substrate outside the rocky reefs. No feeding whales were observed. Offshore movement in response to increased wave action has been noted in other species (Mauchline 1980). Swarm formation is no doubt even more strongly inhibited during the stormy winter season.

Diel changes in mysid behavior significantly affect their availability as prey. *Holmesimysis* disperses up into the water column at night (Hobson and Chess 1976, Murison et al. 1984). Though no comparable observations exist for *Neomysis*, they probably either disperse or settle onto the algae-covered

reefs, typical night behaviors noted in many other species (Mauchline 1980). Murison et al. (1984) observed that gray whales feeding on mysids near Pachena Bay during the day were absent at night. Subsurface, mid-water and epibenthic tows caught virtually no mysids at night, though many were caught in epibenthic tows during the day. In the present study, a whale tracked over a 24-hour period changed from feeding before dark to resting behavior further offshore, and resumed feeding at sunrise the following day. These observations suggest that prey dispersal, perhaps combined with a decrease in prey locating ability, makes mysid feeding inefficient at night. The sensory cues baleen whales use to detect prey are unknown, but it has been suggested that they rely to a large extent on vision (Jansen and Jansen 1969, Madsen and Herman 1980). If so, a gray whale's ability to locate and capture prey within a feeding area would be more likely to succeed during daylight hours, particularly for mobile, swarming prey.

The high resilience of an infaunal *Ampelisca* community to intensive feeding pressure is clearly reflected in the long-established annual use of this prey resource in the northern Bering Sea, and further supported by results from quantitative sampling of infaunal recruitment into feeding excavations over time (Oliver and Slattery 1985). Though mysid swarms maintained the same consistent locations and relative densities during one month of whale feeding at Pachena Bay, long-term impacts of whale feeding are unknown. Assessment of this long-term influence on local mysid populations is complicated by the high variability in mysid occurrence noted here and in other species (Mauchline 1980), and the concurrent utilization of mysids by other local predators such as Black Rockfish.

Gray whale feeding on both swarming and infaunal prey exemplifies the behavioral flexibility which allows them to exploit a wide range of prey types (see review in Nerini 1984). At Vancouver Island, they have also been observed feeding on highly seasonal runs of schooling herring (J. Oliver pers. comm.) as well as on an infaunal polychaete bed (Darling 1978); the latter was apparently depleted beyond recovery (Kvitek and Oliver 1986). Their highly opportunistic feeding strategies may have been crucial to survival of the population when lower sea levels made the shallow primary feeding grounds inaccessible (Kim and Oliver in press).

Several factors other than those related to prey availability may influence gray whale foraging patterns. It may be that young, inexperienced whales are more likely to utilize habitats and associated prey outside the richest northern feeding grounds. Darling (1978, 1984) noted a number of small gray whales in the summering Vancouver Island population, and small whales have been noted feeding on a variety of prey in peripheral feeding areas (Carl 1968, Wellington and Anderson 1978, Plewes et al. 1985, Oliver et al. 1984). Within the primary feeding grounds, several Soviet researchers (Zenkovich 1934, 1937, Bogoslovskaya et al. 1981, Yablokov and Bogoslovskaya 1984) have noted concentrations of juvenile whales nearshore and adults further offshore over the richest feeding areas. Unfortunately, these impressions of young whales occurring more often over peripheral feeding areas are largely unsubstantiated by actual size measurements. Better data may reveal age-specific trends in prey utilization.

The threat of predation may influence an individual's behavior as much as food availability (Krebs 1981). Killer whales are the primary marine predator

on gray whales, as substantiated by direct observations of attacks on gray whales (Andrews 1914, Morejohn 1968, Baldrige 1972, Lowry et al. 1987), and evidence of attacks deduced from wounds on beached carcasses (Fay et al. 1978). Killer whales were observed only once during this study, but at that time appeared to dramatically reduce local gray whale numbers and cause one whale to seek shelter near shore. The extensive overlap of gray whale and killer whale population distributions (Jones et al. 1984, Rice 1977, Braham and Dahlheim 1982, Lowry et al. 1987) suggests that encounters are not uncommon. Poole (1984) proposed that a nearshore migratory route may afford protection from killer whales. Gray whales may take advantage of visual or acoustic screens provided by kelp beds and rocky reefs, and may gain further advantage from distracting surf noise. The remarkably near shore migration of adult females with young calves may reflect an attempt to utilize these coastal predator avoidance features. Thus, gray whales may be attracted to nearshore kelp beds for predator protection as well as food. Compromises between feeding success and predation risk have been documented in birds (e.g. Barnard 1980) and fish (e.g. Milinski and Heller 1979).

Gray whale respiration and movement patterns reflect differences in the spatial and temporal patchiness of their prey. Prey patchiness and biomass also influence general whale distribution and abundance. Annual, seasonal and diel changes in prey availability probably significantly impact whale feeding. Feeding strategy may also be influenced by a number of factors unrelated to prey availability, including the risk of predation by killer whales. Thus, a suite of ecologic pressures affecting feeding individuals may maintain the behavioral and geographic patterns of gray whale feeding.

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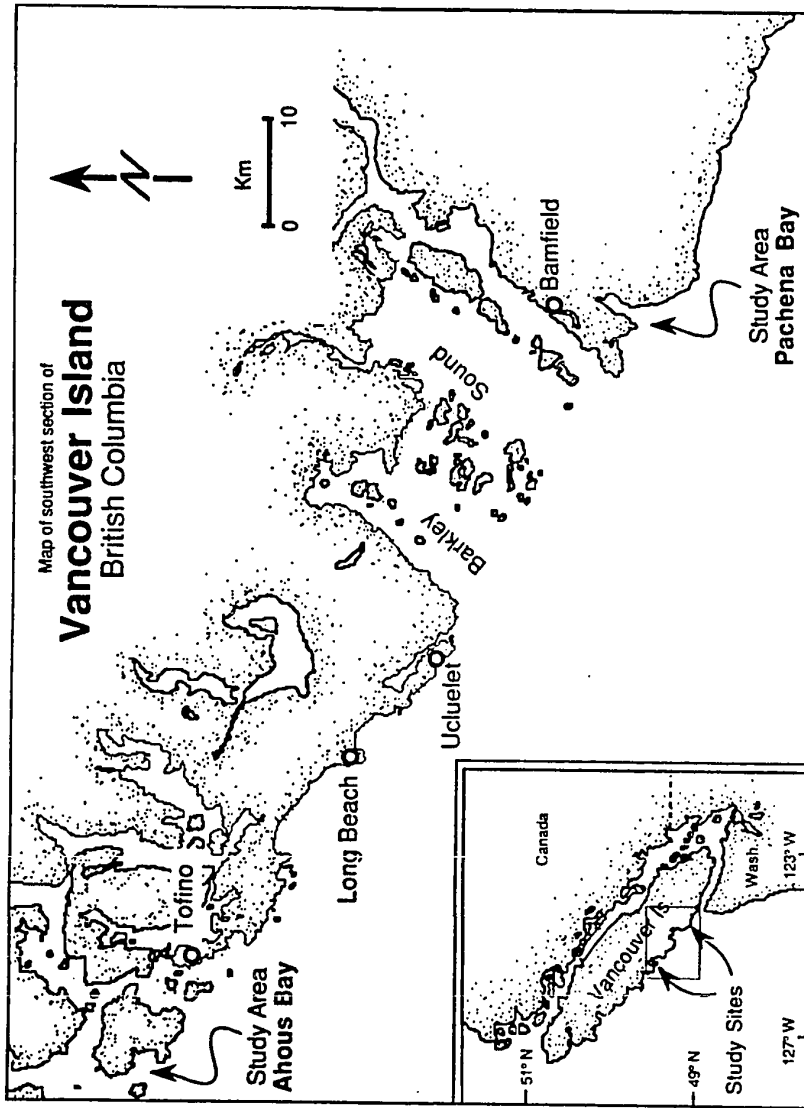


Figure 1. Pachena and Ahous Bay study sites, Vancouver Island, British Columbia, Canada.

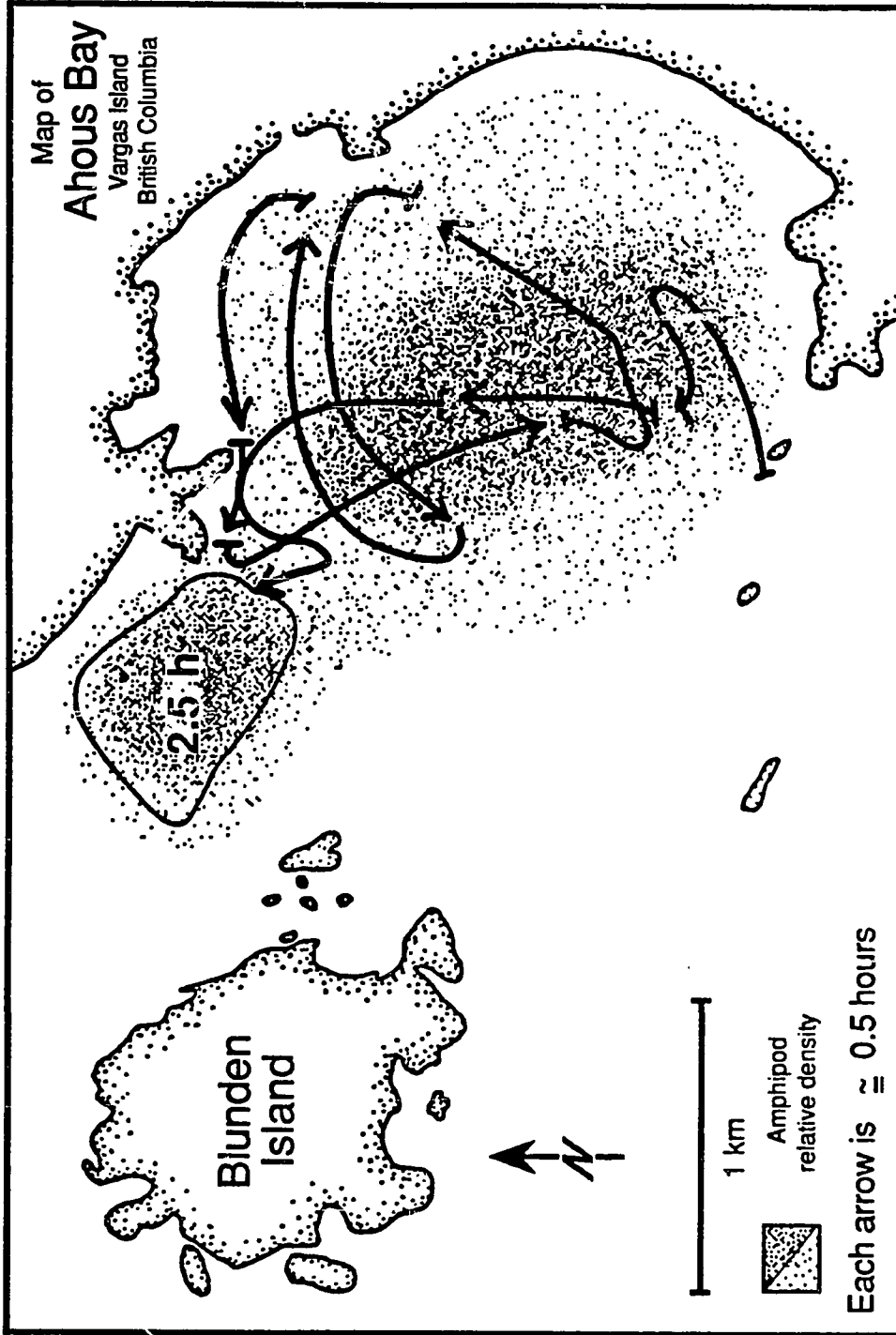


Figure 2. Location and relative density of amphipod tube mat and track of Whale 15 at Ahous Bay. Whale 15 fed continuously for 7.1 hours, 23 August 1984. Maximum amphipod density was at 12 m depth; tube mat depth range = 5-20 m.

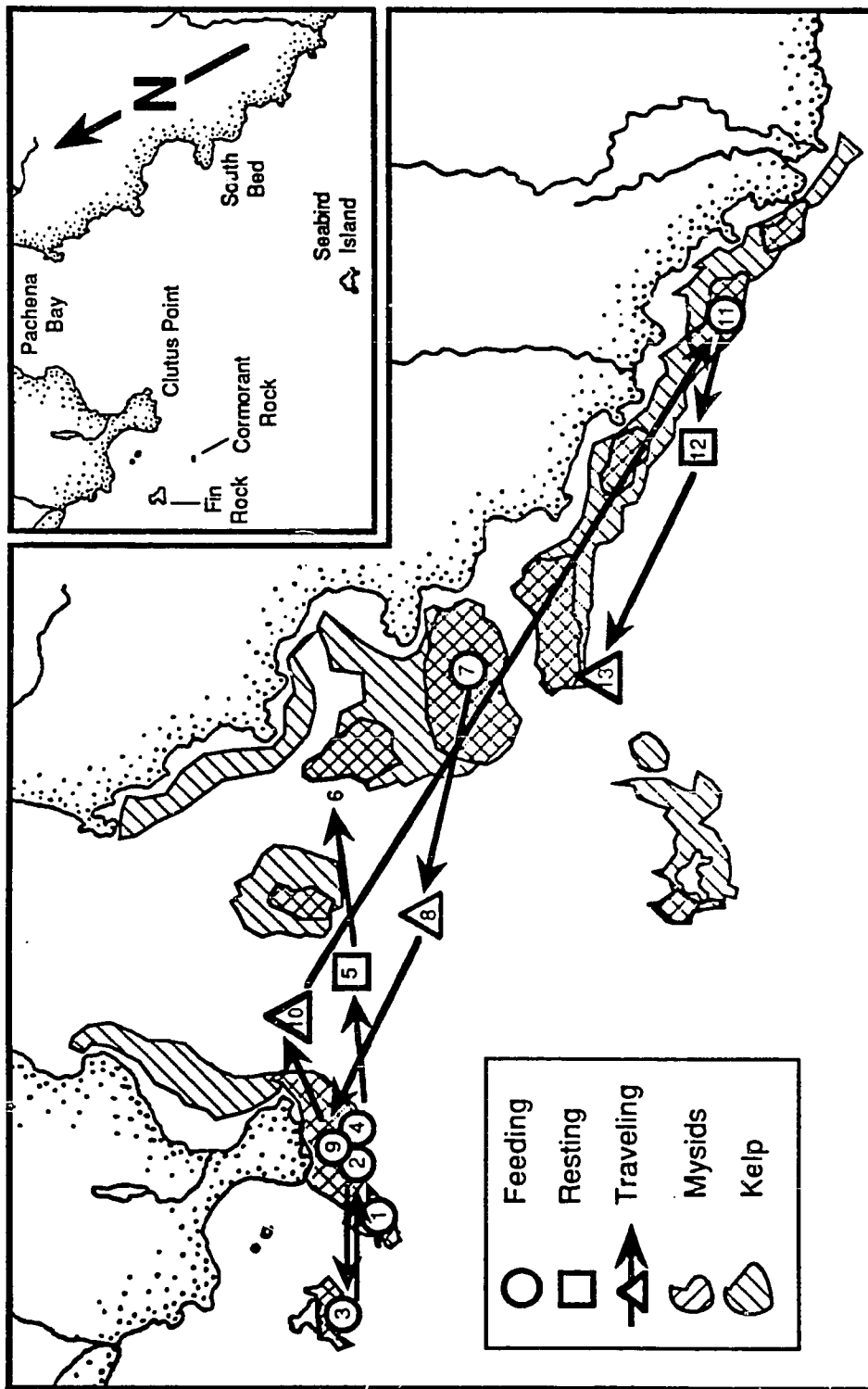


Figure 3. Location of mysid swarms and track of whale 17 at Pachena Bay. Whale 17 was observed for 28.9 hours, 13-14 August 1984 (see text for details). Mysid swarms occurred at average 10 m depth; swarm depth range = 5-13 m.

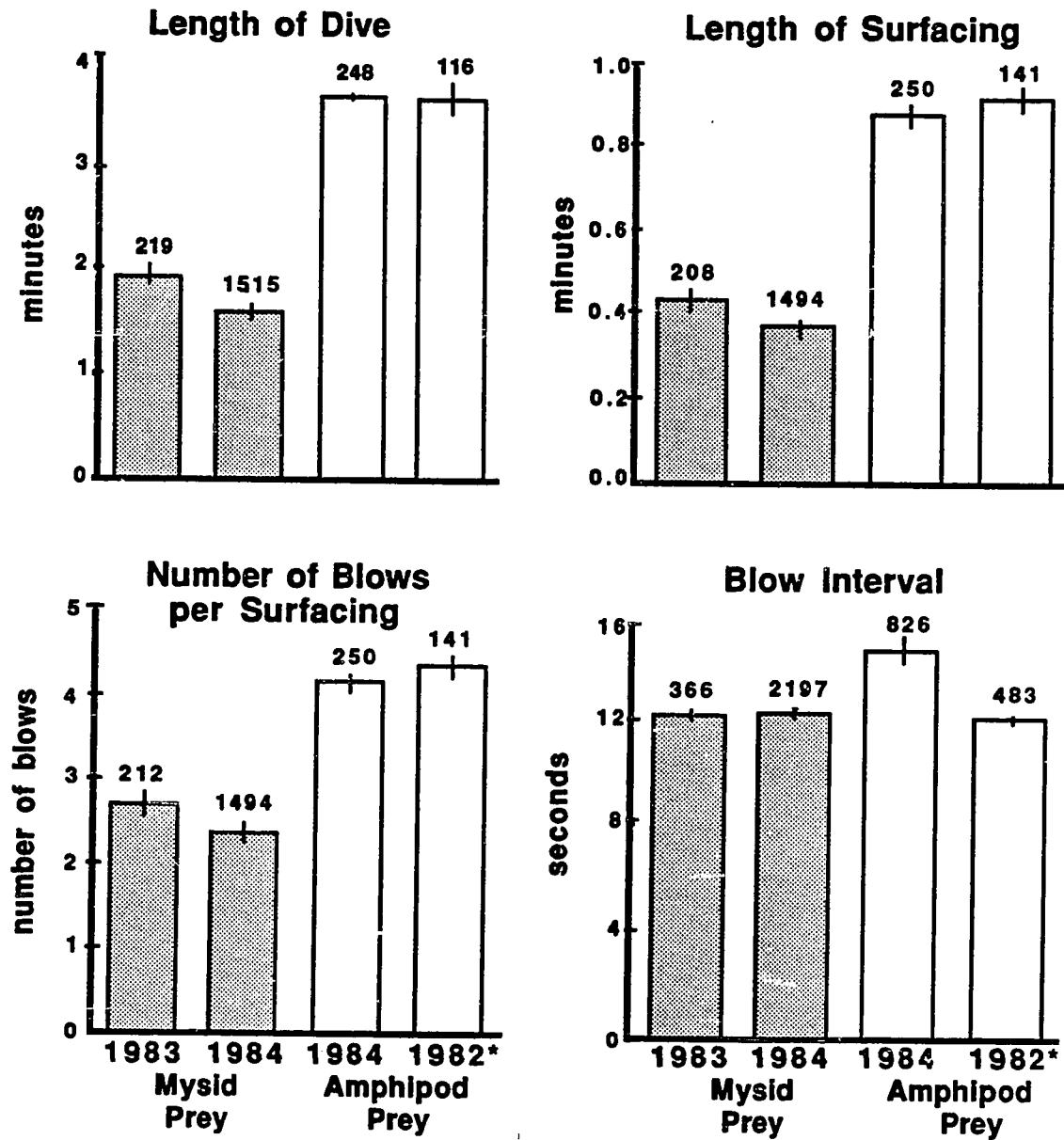


Figure 4. Respiratory characteristics of gray whales feeding over mysid and amphipod prey.

*data from Würsig et al. 1986

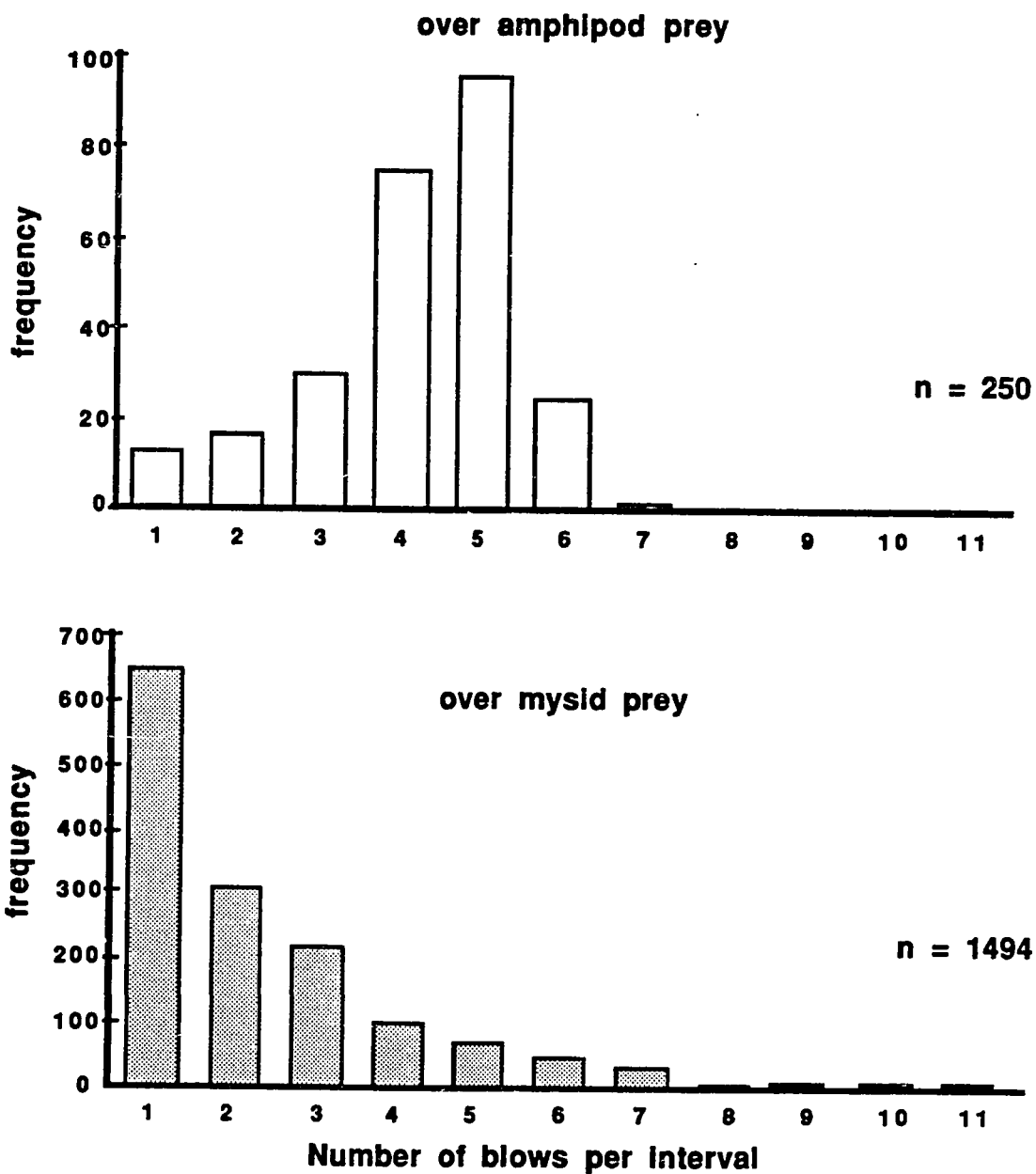


Figure 5. Number of blows per surfacing for gray whales feeding over amphipod amphipod prey, 1984.

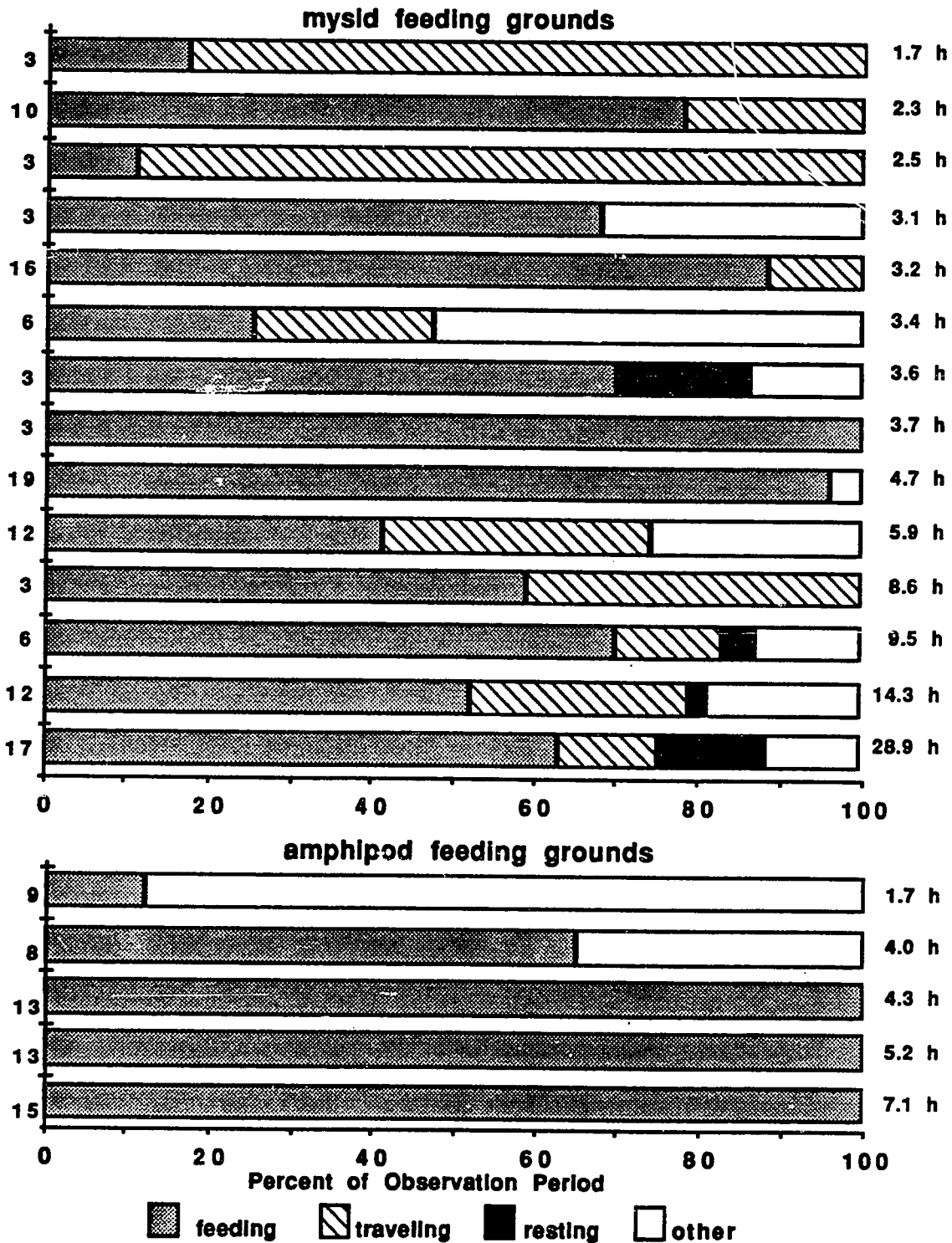


Figure 6. Percent time spent feeding, traveling and resting by individual gray whales. Numbers at left = individual whale codes; numbers at right = total observation hours.

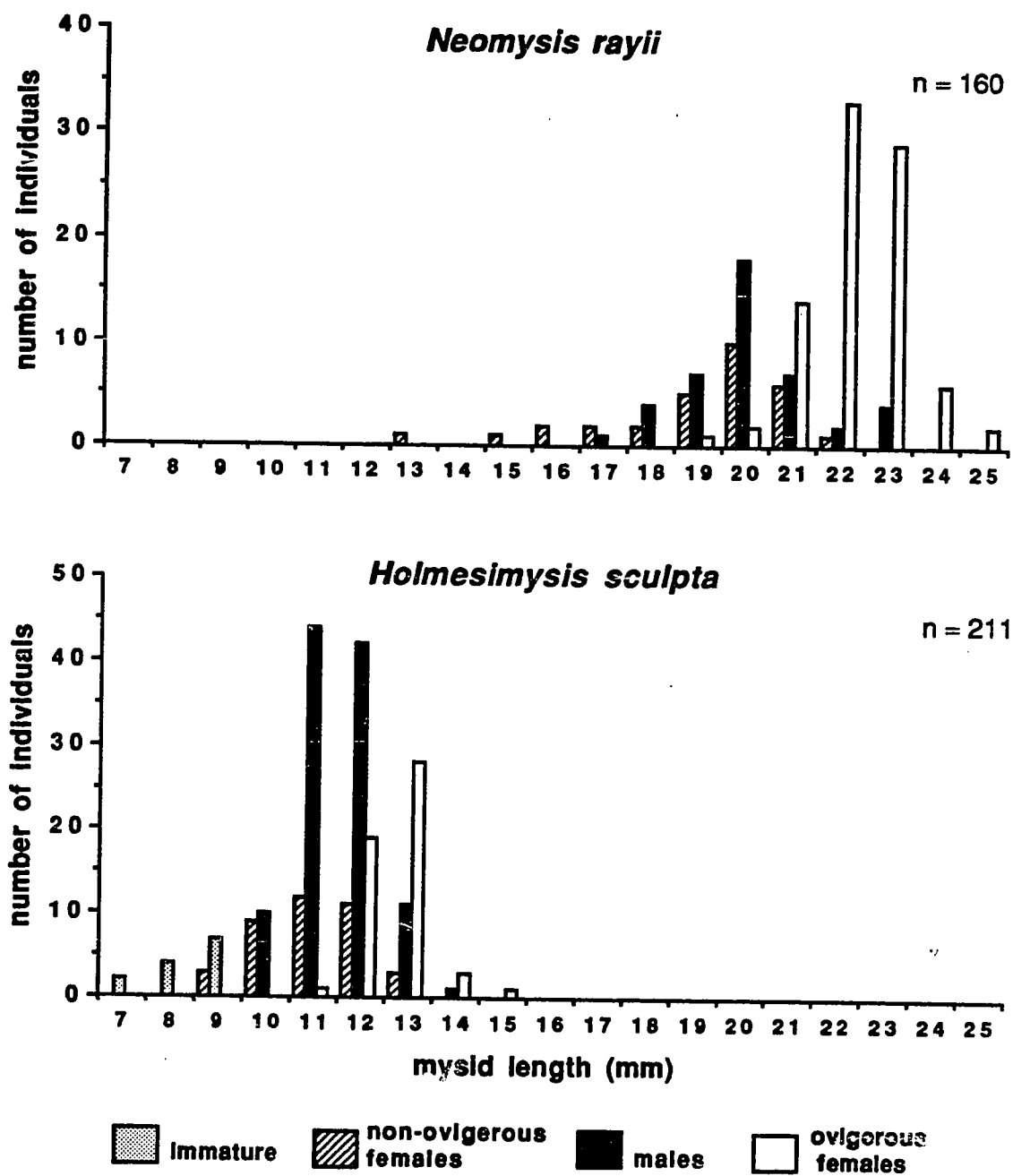


Figure 7. Length frequency of two mysid species at Pachena Bay.

Table 1. Respiratory characteristics of feeding, traveling and resting gray whales.

Behavior	Length of Dive (minutes) mean (± 1 s.d.)	Length of Surfacing (minutes) mean (± 1 s.d.)	Blow Interval (seconds) mean (± 1 s.d.)	Number of Blows per Surfacing mean (± 1 s.d.)	Blow Rate (# sfc-dive cycles) $\frac{n}{n = \text{total minutes}}$
Amphipod Feeding* n	3.7 (1.04) 248	0.9 (0.33) 250	14.9 (3.26) 826	4.2 (1.29) 250	0.92 (244) 1135
Mysid Feeding** n	1.6 (1.08) 1515	0.4 (0.39) 1494	12.4 (8.32) 2197	2.4 (1.78) 1494	1.21 (1379) 2738
Traveling** n	1.4 (0.98) 458	0.6 (0.27) 455	14.7 (4.52) 539	2.1 (1.91) 455	1.33 (305) 573
Resting ** n	1.1 (0.82) 199	0.3 (0.45) 199	14.5 (3.76) 216	2.0 (1.94) 199	1.49 (162) 235

* Ahous Bay, 1984.

** Pachena Bay, 1984.

Table 2. Abundance and biomass of two mysid species at Pachena Bay, 1984.
Neomysis rayii data are from photographs.
Holmesimysis sculpta data are from cylinder trap samples

Location	Number of individuals (per 0.5 m ³)			Biomass (grams/0.5 m ³)		
	mean	s.d.	n	mean	s.d.	n
<i>Neomysis rayii</i>						
Cormorant Rock	5577.1	4890.26	16	251.0	220.06	16
Clutus Point	5535.9	2133.22	14	249.1	95.99	14
Fin Rock	4869.1	7326.63	7	219.1	329.70	7
South Bed (north end)	3225.6	2105.69	5	145.2	94.76	5
South Bed (west end)	3022.2	3743.55	12	136.0	168.46	12
<i>Holmesimysis sculpta</i>						
Cormorant Rock	5290.0	3960.36	3	112.5	85.01	3
Fin Rock	4962.1	1464.81	3	75.5	31.26	3

Table 3. Individual length and weight of two mysid species at Clutus Point, Pachena Bay.

	Sex / Life stage	Length ^t (mm)		Average weight ____(grams)____	n
		mean	(±1 s.d.)		
<i>Neomysis rayii</i> (10 m station)	Female, ovigerous	22.3	(1.0)	0.052	87
	Female	19.1	(2.1)	0.031	30
	Male	20.1	(1.4)	0.037	43
<i>Holmesimysis sculpta</i> (7 m station)	Female, ovigerous	12.7	(0.70)	0.018	52
	Female	11.0	(1.09)	0.010	38
	Male	11.5	(0.84)	0.012	108
	Immature	8.4	(0.77)	0.004	13

Table 4. Sex and life stage composition of two mysid species at Pachena Bay.

Swarm Location	% females ovigerous	% females non-ovigerous	% males	% immatures	n
<i>Neomysis rayii</i>					
Clutus Point (10 m)	61	26	13	0	68
Clutus Point (10 m)	54	19	27	0	160
Fin Rock (10 m)	56	34	10	0	105
<i>Holmesimysis sculpta</i>					
Clutus Point (7 m)	25	18	51	6	211
Clutus Point (7 m)	30	37	33	0	132
Fin Rock (10 m)	60	0	40	0	53

Table 5. Biomass of gray whale prey in the Bering Sea, Baja and Vancouver Island. Infaunal prey biomass is in grams/m²; hyperbenthic prey biomass is in grams/0.5m³.

	Total Biomass mean ± s.d. (n)	Primary Prey Species	References
INFAUNAL PREY			
Northern Bering Sea	211 ± 167 (75) 482 ± 286 (140)	<i>Ampelisca macrocephala</i> <i>A. macrocephala</i>	Thomson 1984 Stoker 1978
Vancouver Island			
-Pachena Bay	110 ± 42 (6) 197 ± 71 (6)	<i>Ampelisca agassizi</i> <i>A. agassizi</i>	Kvitek and Oliver 1986 Oliver et al. 1984
-Ahous Bay	160 ± 39 (6)	<i>A. agassizi</i>	Kvitek and Oliver 1986
Baja calving lagoons	24 ± 1 (45)	<i>A. agassizi</i>	Oliver et al. 1983
HYPERBENTHIC PREY			
Vancouver Island			
-Pachena Bay	211 ± 188 (54) 94 ± 61 (6)	<i>Neomysis rayii</i> <i>Holmesimysis sculpta</i>	Total mean biomass, this study Total mean biomass, this study