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Feeding ecology of gray whales in Agate Bay, California, Summers 1990 and 1991

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summers 1990 and 1991**

Hawkinson, Craig Allen, M.S.

San Jose State University, 1992

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FEEDING ECOLOGY OF GRAY WHALES IN AGATE BAY,
CALIFORNIA, SUMMERS 1990 AND 1991

A Thesis

Presented to

The Faculty of Moss Landing Marine Laboratories
San Jose State University

In Partial Fulfillment
of the Requirements for the Degree
Master of Science

By

Craig Allen Hawkinson

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ABSTRACT

FEEDING ECOLOGY OF GRAY WHALES IN AGATE BAY, CALIFORNIA, SUMMERS 1990 AND 1991

by Craig Allen Hawkinson

During the summers of 1990 and 1991, gray whales (*Eschrichtius robustus*) fed on the infaunal cumacean *Diastylopsis dawsoni* in Agate Bay, just offshore of Patrick's Point State Park in Humboldt County, California. With the exception of surface interval, the respiratory characteristics of feeding gray whales in Agate Bay were similar to gray whales feeding elsewhere. Gray whales sighted along the coast of northern California between 15 June and 15 October probably spent most of the summer there.

The benthic community in Agate Bay was comprised of a dense aggregation of the cumacean *Diastylopsis dawsoni*, with lesser numbers of clams, polychaete worms, isopods and amphipods. The greatest mean biomass estimate of 131 grams/m² from Agate Bay was intermediate between values from the primary feeding grounds in the Bering and Chukchi Seas, and the winter calving lagoons of Baja California Sur, Mexico.

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INTRODUCTION

The route and timing of the annual migration of the gray whale (*Eschrichtius robustus*) has been well documented (Pike 1962; Rice and Wolman 1971; Poole 1984). However, far less information is available on the use of localized areas along the migratory pathway during non-migratory times, particularly summer (Sund 1975; Wellington and Anderson 1978). Although census information indicates that most gray whales spend the summer feeding in the primary feeding grounds of the Bering and Chukchi Seas (Hall et al. 1977; Rugh and Braham 1979), some animals spend summer south of this area (Hatler and Darling 1974; Sullivan et al. 1983), occupying what have been termed the tertiary feeding grounds (Kim and Oliver 1989).

Numerous gray whales have been observed during summer along the coasts of British Columbia, Washington, Oregon, and California (Gilmore 1960; Rice and Wolman 1971; Darling 1978; Dohl et al. 1981; Sumich 1984). Dohl et al. (1983) reported the presence of small "resident" groups of gray whales during the summer in four locations in central and northern California. Mallonee (1991) further documented the activities of gray whales during summer at three of these same locations (Big Lagoon-Patrick's Point area, mouth of

the Klamath River, and St. Georges Reef area off Crescent City).

Evidence from early reports of whaling along the coast of California indicate that gray whales were usually taken only during the northern and southern migrations (Sayers 1984). Records of the whaling station at Trinidad from the 1920's (Trinidad Station Logbook, 1922) also indicate that gray whales were rare in the waters off northern California during summer. Recent observations of the distribution of gray whales during summer suggest that these animals may be expanding their summer range into previously unoccupied areas (J. Oliver, pers. comm.).

Most reports of gray whales seen during the summer include observations of apparent feeding behavior (Sumich 1984; Mallonee 1991). Feeding increases from Baja California Sur, Mexico, to British Columbia, with evidence of a distinct north-south gradient in the use of tertiary feeding grounds during summer (Kim and Oliver 1989). This trend is probably related to an increase in the amount of accessible food northward along the migratory pathway. The presence of gray whales in any one location during the summer is most likely limited by the availability of prey (Kim and Oliver 1989).

Extensive work has been conducted during summer on the feeding ecology of gray whales along the west coast of

Vancouver Island (Hatler and Darling 1974; Oliver et al. 1984; Guerrero 1989), where they feed on tube-dwelling amphipods and swarming mysids, yet very little is known about their summer feeding activities south of this area. The recent discovery of gray whales consuming ghost shrimp (*Callinassa* sp.) in Puget Sound represents the first documentation of infaunal feeding by gray whales south of British Columbia (Earth Almanac, National Geographic, February, 1992).

The Patrick's Point-Agate Bay area appears to be a principal feeding site for those gray whales that spend summer along the coast of northern California because observations of apparent bottom feeding are reported in almost all previous work from this area (Dohl et al. 1983; Mallonee 1991). Gray whales were observed milling in the center part of Agate Bay during the past three summers and mud plumes seen around surfacing animals on a regular basis (Hawkinson, pers. obs.), but the food of these gray whales was not determined.

My objectives were to document the feeding behavior of gray whales in Agate Bay during the summer, and to determine the prey organism(s) consumed. I also attempted to relate the feeding efforts of gray whales to the distribution and abundance of their prey.

The first northward migrating gray whales usually pass through the Patrick's Point area in mid- to late March and by the early part of June, the bulk of the migration is finished. Based on the timing sequence of the northward migration as reported by Dohl et al. (1983), I defined summering whales as those sighted between 15 June and 15 October.

I predicted the dominant food items available to feeding gray whales in Agate Bay were densely aggregated infaunal crustaceans whose abundance was greatest in the center part of the bay. I predicted that general feeding behavior and respiratory characteristics for gray whales in Agate Bay would be similar to those reported for gray whales feeding on benthic infauna in other locations.

I also predicted that the number of gray whales and the level of available benthic resources in Agate Bay during summer were intermediate between the calving lagoons of Baja California Sur, Mexico, and the primary feeding grounds of the Bering and Chukchi Seas.

STUDY AREA

The feeding activities of gray whales and the relative distribution and abundance of their benthic prey were documented in Agate Bay (41 08' N latitude, 124 09' W longitude), situated along the northwest coast of Humboldt

County, California (Fig. 1). Located approximately 9 km north of Trinidad, Agate Bay encompasses approximately 4 km² of the inshore waters along the northern boundary of Patrick's Point State Park. It is exposed to the open ocean and receives a great deal of direct wave energy from the predominant northwestern swell. Days of strong winds, moderate to high swell, and dense fog are common.

The topography of the coastline and the longshore currents create a circular movement of water within Agate Bay. This causes deposition of fine sand sediments (mean grain size of 0.105 mm) in the center of the Bay and slightly coarser sediments (mean grain size of 0.125 mm) to dominate the outer periphery. This transition appears to be fairly gradual and is first detected in about 13 meters of water (Hawkinson, pers. obs.).

METHODS

All field observations were conducted from 15 June to 29 October 1991, with preliminary behavioral observations and benthic sampling done the previous summer between 14 June and 1 August, 1990. Due to improvements in methods and the early termination of observations in 1990, the only information from that summer used in the statistical analyses were behavioral observations and respiration data

of gray whales. Information on whale movement patterns in 1990 were not included in the statistical analysis.

Observations of gray whale movements and behavior, both from boats and from shore, were made opportunistically throughout the study period, depending on the presence of whales and the weather. To monitor temporal changes in the relative abundance and distribution of the benthic prey community, benthic sampling was conducted every 3 or 4 weeks, weather permitting.

Preliminary Sampling

To conduct the preliminary sampling, a Texas Instruments 9000-A Loran unit was used to define a 100 X 100 meter study area in early June of 1990. This study area was situated in the central portion of Agate Bay where gray whale feeding behavior had been observed the previous two summers. Ten sample sites were selected using random numbers applied to the Loran grid. On 16 June and 9 July, at each site I collected one bottom-grab sample and a vertical tow with a plankton net (254 μ mesh) to detect the presence of any potential epi-benthic prey (i.e. mysids).

The preliminary samples revealed a very dense aggregation of the infaunal cumacean *Diastylopsis dawsoni* (Crustacea: Cumacea), with the highest densities in the center of Agate Bay diminishing toward the outer edges. To

determine the extent of the offshore distribution of *Diastylopsis*, a reduced number of bottom samples (4 sites, 2 replicates) were collected in a haphazard manner beyond the offshore edges of the study area on 8 July, 1990 (Fig. 2).

In response to information provided by this preliminary work, a diamond-shaped study area was established in the nearshore waters of Agate Bay on 20 June, 1991, to encompass the area of highest *Diastylopsis* density and most concentrated gray whale feeding efforts (Fig. 2). The study area was 125 meters on each side and extended approximately 200 meters offshore. Water depths in the study area ranged from 10 to 14 meters, and the bottom was gently sloped.

The corners and centerpoint of the study area were designated using anchored buoys at pre-determined positions, which were verified with a theodolite (or surveyors transit) from a cliff-top observation station. These buoys were used only during benthic sampling and were not present when whales were in the bay. Unless otherwise noted, use of the term "study area" hereafter will refer to the diamond-shaped area established in 1991.

Gray Whale Behavior

Small boats (4-5 meters in length) with outboard motors were launched from Trinidad, and used during benthic

sampling, recording of behavioral and respiration data, and photographing animals for identification purposes. I also collected samples of mud plumes with a plankton net on 18 July 1990 and on 21 September 1991. Larger boats (6-7 meters) were used to conduct the side-scan sonar surveys and to support the diving work.

A large proportion of the behavioral observations used in the analyses were gathered from a cliff-top observation station (height of 27 meters) using a Pentax TH-20D analog theodolite or a pair of 7X35 binoculars. Supplemental behavioral observations were made from a boat and from the shoreline without the use of the theodolite. I used a voice-actuated cassette recorder to record all observations and theodolite positions and later transcribed the tapes into a field notebook. Individual whales were identified by pigment patterns and natural markings (Darling 1984) on their sides and backs, usually on successive days.

Movements of individual whales were documented using the theodolite, and each record was considered a continuous "track" when the same animal was identifiable. Observation time, horizontal and vertical angles, whale identification number, and behavioral notes were recorded for each surfacing. Tracks of whales using the theodolite were most often interrupted either by the onset of dense fog or when

the whale under observation could not be distinguished from other whales.

Whale behavior was classified as feeding, traveling, or other. The presence of mud plumes or repetitive diving in a confined area was considered evidence of feeding. Whales were scored as traveling when they moved in a relatively straight-line through several surface-dive cycles. I grouped socializing and resting behaviors into the category "other" because previous observations suggested that both of these behaviors occurred far less frequently than did feeding or traveling. Also, it was difficult to differentiate between socializing whales and whales feeding in close proximity to one another, which was very common.

For focal animals, the following respiration characteristics were quantified. Dive duration was defined as the period of time a whale was below the surface on a dive lasting greater than 60 seconds. Surface interval was defined as the period of time a whale was visible at or near the surface including all short dives of 60 seconds or less. Exhalation interval was the time interval between successive exhalations that occurred during any one surface interval, and number of exhalations per surface interval. These variables were only quantified when the same whale was observed through several surface-dive cycles.

Benthic Sampling

During the summer of 1991, the benthic community of Agate Bay was quantitatively sampled on five occasions, at roughly 3- to 4-week intervals. On two of these sampling days (11 July and 15 August) 20 benthic samples were collected within the study area. On two of the other days (24 July and 12 September) only 10 samples were obtained due to the onset of poor weather.

In response to observed changes in the distribution of gray whale feeding, on 21 September three transect lines were established originating in the study area and projecting outward into deeper water (Fig. 3). I collected samples at 30-meter intervals along the lines in an attempt to detect changes in the relative distribution of the cumaceans.

With the exception of samples gathered in a gray whale feeding pit (see below), all benthic samples were collected using a small Ekman bottom-grab (15x15 cm, area= 0.0225 m²) with a surface activated release mechanism. The position of each sample was generated using a random numbers table and converting these numbers into headings from the center of the diamond and travel times for the boat.

On 28 September, a gray whale feeding excavation was located using SCUBA approximately 75 meters north of the

study area in 16 meters of water (feeding excavation #1, Fig. 2). Due to poor visibility, the feeding excavation was located by conducting a standard search pattern on the bottom in an area where whales had been observed actively feeding during the previous three days. The pit was elliptical in shape, approximately 6 square meters in area and 28 cm deep in the center. Using hand-held corers (diameter= 5 cm, area= 0.003 m²) haphazardly placed samples were collected inside (n=3) and directly outside (n=3) of the pit.

All samples were washed over a 0.5 mm mesh screen, fixed in a buffered 5% formalin solution, and later transferred into 70% ethanol. Invertebrates were then identified and counted. Wet weights were determined using a Mettler PC 440 analytical balance. In those samples containing clams, weight of shell was subtracted from total weight before calculating biomass.

To detect and document feeding excavations produced by gray whales, I used an Edo Corporation Model 606-D 100 kHz side-scan sonar unit and a wet paper recorder. Both 50 and 100 meter channel widths (width of sonar signal produced on both sides of the transducer measured along the sea floor) were used to obtain the best resolution. A boat speed of between 2.5 and 3.0 knots was used during side-scan operations.

A sediment grain size analysis was performed on samples of bottom sediments from the center of Agate Bay (n=2) and from the periphery of the bay (n=2). Standard dry grain sieve techniques were employed following Ingram (1971) to determine the mean grain size of the sediments.

All statistical analyses followed either Sokal and Rohlf (1969) or Zar (1984), and were performed using a Stat-View 512 statistical program or on a Hewlett-Packard 97 calculator.

RESULTS

Gray Whale Behavior

Although observations during summer of 1990 ended in early August, more gray whales were sighted in Agate Bay during that summer than during summer of 1991; 13 whales were observed in 1990 and only 8 in 1991. With the exception of one calf sighted on 17 June 1990, which was seen in the area (with its presumed mother) on only one day, all whales observed during the summer in Agate Bay were an estimated 9 to 14 meters in length and were considered either juveniles or adults.

Between 11 June and 1 August 1990, 13 whales (AB1-AB13) were observed on 18 separate days (26.5 hours). In 1991, three gray whales (AB14-AB16) were observed in Agate Bay between 18 June and 21 July (26 hours) and six more animals

(AB17-AB21), including one whale (AB15) that had been sighted earlier in the summer, were observed between 5 September and 23 October (141 hours). Although gray whales were seen north of Big Lagoon between 21 July and 5 September, no whales were observed in the Agate Bay area during that time.

Three of the six whales sighted during the latter part of the summer (AB19, AB20, and AB21) were seen together regularly. These three whales were usually observed in the immediate vicinity of Agate Bay, although on several occasions they were sighted in the Freshwater Lagoon-Redwood Creek area, 3.5 km to the north. Observations of these three individuals in Agate Bay between 5 September and 23 October accounted for 63% of my observation hours. The other three whales, AB15, AB17 and AB18, were each observed for less than three days before leaving the area.

During 1990 and 1991, gray whales in Agate Bay spent a large proportion of their time feeding, with less time spent traveling and in other behaviors. When all observations in 1990 are combined, gray whales were observed feeding 63% (SD $\pm 18.4\%$) of the time, traveling 21.5% (± 6.3) and in other behaviors 15% (± 4.5). In summer of 1991, gray whales fed an average 78% (± 21.9) of the time, 13% (± 3.1) was spent traveling, and only 9% (± 4.8) was spent in other behaviors.

The theodolite enabled me to correlate observed behaviors with the respiratory characteristics of individual gray whales. Feeding whales spent an average of 3.1 (± 1.13) minutes on each dive and then remained at or near the surface for 1.2 (± 0.89) minutes (Table 1). During this surface interval, they respired an average of 4.5 (± 1.94) times with an average of 17.6 (± 13.49) seconds between each blow. Whales engaged in traveling and other behaviors had shorter dive durations and surface intervals, fewer exhalations at the surface, and less time between successive exhalations than when they were feeding.

In 1991, the time spent traveling relative to feeding was greater during early summer and less at the end of summer. Between 18 June and 21 July, the whales fed 58% (± 22.3) of the time and were observed traveling 36% (± 12.0) of the time. From 5 September to 23 October, however, they were observed traveling only 10% (± 3.4) of the time compared with 82% (± 26.7) for feeding.

During the last six weeks of summer 1991 (5 September - 23 October), there was a shift of gray whale feeding effort in and around the Agate Bay study area. In early September, feeding behavior was observed primarily along the northeastern edge of the study area (Fig. 4), and by early October, most feeding occurred just offshore of the western edge of the study area (Fig. 5).

To examine this change, I compared all observations of gray whale feeding for this period relative to an arbitrary line bisecting the study area along its north-south axis. During the first three weeks, 61% (± 26.4) of observed feeding occurred east of this line and during the last three weeks 74% (± 24.5) of feeding took place west of this line. These differences in the location of feeding behaviors were highly significant ($X^2 = 14.74$, $df = 1$, $p < 0.001$).

Stomach contents of three dead gray whales, found stranded along the coast of Humboldt County, were examined for evidence of feeding. A 13-meter long female came ashore at Moonstone Beach on 10 June, 1989. The stomach contained only approximately 30 liters of partially digested brown algae, possibly *Alaria* or *Laminaria*. The stomach of a juvenile male (9.5 meters length) found along the Lost Coast on 1 April, 1990, was empty. The third animal was a 10-meter long female discovered on the Samoa spit on 25 May, 1990, whose stomach was also empty. These animals were considered northbound migrants, and there was no evidence of localized feeding.

Benthic Community

Diastylopsis dawsoni was present in all preliminary samples collected on three occasions in 1990, and was clearly a dominant member of the infaunal community. These

samples revealed significantly greater densities ($t= 2.863$, $n=28$, $p< 0.005$) within the center of Agate Bay and lesser densities on the periphery (Table 2). This transition in densities was abrupt and did not follow any depth contour. Other organisms collected in lesser densities were small razor clams (*Siliqua sp.*), polychaete worms (*Glycinde sp.*), isopods (*Synidotea sp.*) and amphipods (including *Mandibulophoxus sp.*, *Eohaustorius sp.*, and *Ishyrocerus sp.*). The plankton tows contained typical plankton (e.g. copepods, ctenophores, and crab zoea), but yielded no mysids.

Densities of *Diastylopsis* were highly variable both between sampling dates and among replicates, whereas the relative densities of the rest of the fauna remained more consistent throughout summer (Table 3). The cumaceans ranged in size from very small individuals (2.0 mm) of undetermined sex to large ovigerous females of 13.5 mm length. When all 1991 samples were considered, *Diastylopsis* represented from 41% (± 18.3) to 86% (± 31.6) of total infaunal individuals and accounted for 28% (± 13.1) to 79% (± 38.5) of total available biomass.

Observations beginning in early July 1991 within the study area indicated that mean densities of *Diastylopsis* and mean infaunal biomass estimates increased through the summer, peaked in August and declined in September (Table 2). The density of *Diastylopsis* in the samples ranged from

119,288 individuals/m² in August to 88 individuals/m² in September. Estimates of biomass in the samples ranged from a high of 244.0 g/m² in August to a low of 3.1 g/m² in September.

The mean density of *Diastylopsis* from the 15 August samples was significantly greater ($F = 7.31$, $N = 50$, $p < 0.0025$) than both the 11 July sample mean ($q = 15.72$, $p < 0.001$) and the 12 September sample mean ($q = 12.55$, $p < 0.001$). Similarly, the mean biomass estimate from the 15 August samples was significantly greater ($F = 5.84$, $N = 50$, $p < 0.01$) than both the 11 July sample mean ($q = 7.91$, $p < 0.001$) and the 12 September sample mean ($q = 5.80$, $p < 0.001$).

Samples collected along the transect lines on 21 September (Table 4) indicated greater densities and biomass levels offshore of the study area than were found inside the study area on 12 September (Table 2). Estimates of biomass and density of *Diastylopsis* were both positively correlated with distance offshore for all three transect lines. For lines 1 and 2, both of these correlations were significant ($t_1 = 2.481$, $t_2 = 2.955$, $n = 5$, $p < 0.05$).

The sediments in the center of Agate Bay had a smaller mean grain size (0.105 mm) than the sediments found on the periphery of the bay (0.125 mm). This difference, however, was not significant ($t = 0.714$, $n = 4$, $p > 0.25$).

On 18 October, 1991, a large gray whale feeding excavation was located using side-scan sonar due west of the study area in 15 meters depth (feeding excavation #2, Fig. 2). Two large whales had been actively feeding there for at least 20 minutes before we entered the area and began our sonar tows. Measurements of the sonar record indicated the excavation was approximately 9.5 m by 13.5 m and fairly elliptical in shape. No evidence of feeding excavations was found using sonar scans conducted in adjacent areas where whales had been observed feeding on both of the previous two days. Samples collected using SCUBA from a smaller feeding excavation (#1, Fig. 2) on 28 September, 1991, indicated a greater mean density of *Diastylopsis* on the outside of the pit (6,444 individuals/ m²) than on the inside (1,778 individuals/m²). This difference in densities was highly significant ($t= 3.340$, $n=6$, $p< 0.025$).

On 18 July 1990 and 21 September 1991, plankton net (254 μ mesh) samples were collected in mud plumes generated by feeding whales and on both occasions at least four adult *Diastylopsis* were captured. No *Diastylopsis* were visible in the water from the boat, and identical tows in adjacent areas with no mud plumes contained no *Diastylopsis*.

DISCUSSION

During the summers of 1990 and 1991, gray whales fed on the infaunal cumacean *Diastylopsis dawsoni* in Agate Bay, California, just offshore of Patrick's Point State Park in Humboldt County. Other sites along the coast where gray whales have been observed during summer include Redwood Creek, off the Klamath River, and near St. Georges Reef off Crescent City. Gray whale feeding behavior has been observed frequently in the Patrick's Point-Agate Bay area, indicating this area may be a principal feeding site for gray whales along the coast of northern California during summer (Dohl et al., 1983; Mallonee 1991).

Sampling Variability

Density of *Diastylopsis* and estimates of total infaunal biomass among all benthic samples from Agate Bay showed a high degree of variability, both temporally among sampling dates and spatially among samples and replicates. Taken alone, this information suggests a very patchy distribution of *Diastylopsis* in Agate Bay. However, the use of an unweighted bottom grab to sample these highly mobile crustaceans in a hard sand environment undoubtedly introduced additional sources of variation.

Information on the impacts of this type of benthic grab on the cumaceans and its ability to obtain a consistent sample is unclear. Other important potential sources of sampling variability include sea state at the time of sampling, direction and strength of the surface currents, and presence of surge along the bottom.

Overall, these sources of variability would most likely prevent the sampler from capturing all the cumaceans present (J. Oliver, pers. comm.), so densities and biomass estimates probably underestimated the actual densities of *Diastylopsis* and biomass of total infauna. The role of this sampling variability needs to be considered when evaluating the biological significance of observed spatial and temporal trends in the *Diastylopsis* assemblage in Agate Bay.

Benthic Community

The benthic community in Agate Bay was comprised of a dense aggregation of the cumacean *Diastylopsis dawsoni* and lesser numbers of clams, polychaete worms, isopods, and amphipods. *Diastylopsis* is a year-round member of the bottom fauna, usually is found superficially burrowed into the sediments (J. Oliver, pers. comm.), and is an important food source for several genera (e.g. *Liparis*) of marine fishes (Johnson 1969). The highest mean density of 63,860 individuals/m² for the 15 August samples was significantly

greater ($t = 10.76$, $n = 20$, $p < 0.0005$) than the highest mean density of *Diastylopsis* (29.7 individuals/m²) reported by Lesley (1974) in her work along the Samoa spit near Eureka.

Lesley (1974) observed two periods of peak abundance of *Diastylopsis*, one in mid-March and another in late August. Based on her observation that ovigerous females were present in all samples, she suggested that *Diastylopsis* was capable of producing offspring throughout the year.

My data from Agate Bay indicated only a single peak in abundance in mid-August, possibly because no sampling was conducted before the beginning of summer. Although ovigerous females were present in all samples throughout the summer, the data indicated that the density of *Diastylopsis* reached its greatest level in late summer (Table 2).

The greatest mean biomass level of 131 grams/m² from Agate Bay (Table 5) is intermediate between values from the primary feeding grounds in the Bering Sea and from the winter calving lagoons of Baja California Sur, Mexico (Oliver et al. 1983). It is also less than biomass estimates reported by Guerrero (1989) for infaunal prey at Vancouver Island. These trends appear to agree with the observations of Kim and Oliver (1989), who concluded that gray whale prey availability decreased from Canada to Baja California Sur, Mexico.

Gray Whale Presence During Summer

The presence of gray whales in the Patrick's Point-Agate Bay area during summer has been previously described (Dohl et al. 1983; Mallonee 1991), yet information on the numbers of individual whales, the tenure of their residency, and extent of their use of the coast as summer habitat has remained incomplete. A comparison of data from Agate Bay and information from previous reports indicates the number of gray whales that spend summer along the coast of northern California may be increasing.

During their three years (1981-1983) of semimonthly aerial surveys along the coast of California, Dohl et al. (1983) sighted an average 6 to 8 whales during summer at each of four locations, including the Patrick's Point area. Mallonee (1991) reported sighting thirty-one gray whales, probably representing a fewer number of resighted individuals, at Patrick's Point during his 12 months of work over the three summers of 1986 (1 September to 31 October), 1987 (1 May to 31 October) and 1988 (1 May to 31 August). During my six months of observations at Agate Bay during the summers of 1990 and 1991, I recorded a total of 21 gray whales, all of which were identified as different individuals, not resightings.

Due to limitations inherent in aerial survey techniques, Dohl et al. (1983) could not confirm whether their observations were of the same individuals and had no information on movements of the animals during summer. Mallonee (1991) did not exclude resighted individuals from his total count, and his definition of summer was six weeks longer than used in the present study, so it is possible that his total may be an overestimate of the actual number of gray whales using the area during his study period.

To assess the extent of summer habitat used by gray whales in northern California requires knowledge of movement patterns of identified animals and reliable information on the resightings of individuals. During summers of 1990 and 1991, several whales were observed in Agate Bay and then resighted in other areas along the coast. On 23 July, 1990, one identified individual from Agate Bay (AB7) was observed at the mouth of the Klamath River, approximately 8 km north of Patrick's Point. During September 1991 another gray whale (AB19) originally seen at Agate Bay was sighted on at least three occasions over a two-week period at Moonstone Beach near Trinidad, nearly 10 km south of the study area.

These data agree with the conclusions of Mallonee (1991) and indicate some gray whales that spend summer along northern California might use a relatively large portion of the coast as summer habitat. The estimates of available

biomass in Agate Bay were less than values reported for other known feeding areas, so it is possible that gray whales in northern California, like summer gray whales in other areas, may move regularly between adjacent feeding areas. Based on models of optimal foraging theory, if density of prey in one location drops to a critical low level, gray whales might terminate foraging in that location and move to another, possibly more profitable area (Norberg 1977).

Gray whales sighted along the coast of northern California between 15 June and 15 October probably spent most if not all of the summer there. During the summer of 1990, the longest uninterrupted tenure of any individual whale was 24 days. In 1991, three of five whales seen after 5 September were last sighted on 29 October, or 54 consecutive days. It seems highly unlikely that these whales would remain in the Agate Bay area for such extended periods of time, exhibiting a high degree of individual site fidelity, if they were migrating through the area on their way to their actual summer destinations.

Further evidence of summer residency comes from observations of a juvenile gray whale feeding on tube-dwelling amphipods (*Corophium spinicorne*) inside the mouth of the Klamath River (Avery and Hawkinson, in press). This whale was first seen in early July of 1989, observed

throughout the summer and fall, and was reportedly seen in the river as late as mid-February of 1990 (L. Berner, pers. comm.).

Gray Whale Behavior

With the exception of surface interval, respiration patterns of feeding gray whales in Agate Bay were very similar to those reported for feeding gray whales in the Bering Sea (Wursig et al. 1986), at Vancouver Island (Guerrero 1989), and along the coast of northern California (Mallonee 1991). They were also similar to the values obtained by Dolphin (1987a) in his work on humpback whales (*Megaptera novaeangliae*) in southeast Alaska.

Average dive duration of feeding gray whales in Agate Bay was nearly identical to that reported by Wursig et al. (1986) for gray whales near St. Lawrence Island, and is slightly less than values reported by Guerrero (1989) for gray whales feeding on amphipods near Vancouver Island. Gray whales in Agate Bay also had similar numbers of exhalations per surface interval and only slightly longer exhalation intervals than gray whales in these other studies.

Respiration patterns of feeding whales have been correlated with water depth (Wursig et al. 1984; Wursig et al. 1986) and prey type (Guerrero 1989). Wursig et al.

(1986) reported an increase in the surface interval of feeding gray whales with increasing water depth. Similarly, Guerrero (1989) described longer surface intervals in gray whales feeding on infaunal amphipods when compared with whales feeding on epi-benthic mysids.

However, water depths in Agate Bay were less than those reported by Wursig et al. (1986) at St. Lawrence Island. Likewise, the infaunal cumaceans at Agate Bay are probably ecologically similar to the infaunal amphipod prey reported by Guerrero (1989). Yet, while probably not statistically significant, the average surface interval of gray whales in Agate Bay (1.2 ± 0.89 min.) was slightly greater than values reported by Guerrero (0.9 ± 0.33 min.) for amphipod-feeding whales near Vancouver Island and by Wursig et al. (0.90 ± 0.87 min.) at St. Lawrence Island.

Respiration trends exhibited by whales can be an excellent indicator of physiological state (Dolphin 1987b), so another possible explanation of the longer surface interval at Agate Bay might be related to the amount of energy expended during feeding on infaunal cumaceans. *Diastylopsis* are considerably smaller than ampeliscid amphipods consumed at Vancouver Island and in the Bering Sea (Oliver et al. 1983; Nerini 1984), and the level of available biomass is less. Newly-released *Diastylopsis* young can be as small as 2-3 mm in length, which coincides

with the reported minimum prey size of gray whales (Nerini 1984). Such small prey items might require the whales to invest more "handling" time to manipulate their food.

The *Diastylopsis* bed also appeared to exhibit a high degree of spatial patchiness, perhaps complicating the process by which the whales locate and feed on areas of greatest prey densities. However, Guerrero (1989) reported shorter surface intervals in gray whales feeding on extremely patchy epi-benthic mysids than in whales feeding on homogenous infaunal amphipods. Given the high standard deviations associated with these respiratory characteristics, it is also possible that observed differences in surface intervals were artifacts of the sampling methods used at Agate Bay.

Although my respiration data were of 18 different whales over the two summer period, a large proportion (63%) of the observations were from three whales seen regularly during the latter part of summer, 1991. Hence, it is also possible that observed differences in ventilation patterns could result from limited observations of a few highly visible, yet aberrant individuals.

In an attempt to maximize their food intake and minimize their energy expenditure, gray whales feeding on a stationary and structured amphipod tube mat near Vancouver Island produce large feeding excavations using a tactic

known as edge feeding, returning to the same excavation rather than creating numerous small ones (Kvitek and Oliver 1986). The cumaceans in Agate Bay are highly mobile, superficial burrowers, and gray whales can probably capture them more effectively by skimming along the bottom. However, the detection of a large excavation with side-scan sonar directly beneath actively feeding whales in Agate Bay provides evidence that gray whales might also produce large feeding excavations when consuming infaunal cumaceans. Significant differences in the density of *Diastylopsis* on the inside and outside of another feeding excavation also indicated that gray whales may be very effective at removing cumaceans from the sediments.

In the summers of 1990 and 1991, feeding was the dominant daytime activity of gray whales in Agate Bay. Very little resting or socializing behavior was observed, and traveling appeared limited mostly to moving from one feeding area to another. In addition to mud plumes and distinctive respiration patterns, there were other characteristic observations that were useful as indicators of feeding. Repetitive diving in a localized area with relatively little forward movement on successive surfacings, and 180-degree turns made by whales after long dives were highly suggestive of feeding.

An association between feeding gray whales and numerous marine birds has been described by several authors (Wilke and Fiscus 1961; Harrison 1979; Wursig et al. 1986). Most of these reports were from Alaskan waters, and information on this association along the coast of northern California is largely anecdotal. During summers of 1990 and 1991, gray whale feeding episodes in Agate Bay were often accompanied by large mixed aggregations of seabirds, including brown pelicans (*Pelecanus occidentalis*), double-crested cormorants (*Phalacrocorax penicillatus*), western gulls (*Larus occidentalis*), pigeon guillemots (*Cepphus columba*), and common murrelets (*Uria lomvia*). Observations of birds moving to remain in close association with whales at the surface were common, but I did not observe any evidence of bird feeding.

During the latter part of summer 1991, gray whales spent less time traveling relative to time feeding than was observed earlier in the summer. This change may have been related to observed variations in the density of *Diastylopsis* and estimates of available biomass between early and late summer. Even with the degree of sampling variability mentioned earlier, it seems likely that the significant differences in density and biomass estimates between early and late summer are biologically significant. Hence, higher densities of prey and concomitant higher levels of available biomass might enable gray whales to

reduce their searching time and increase the amount of time spent actually feeding.

There was a detectable shift in the distribution of gray whale feeding behavior during the last six weeks of the 1991 study period. Theodolite-generated tracks of gray whales gathered during this period confirmed the location of feeding behavior gradually moved to an area directly west and slightly offshore of the study area (Figs. 4 and 5). The biomass estimates and density of *Diastylopsis* were both positively correlated with distance offshore along the transect lines of 21 September, suggesting a similar trend in the distribution and relative abundance of prey.

This apparent match between location of gray whale feeding and increased density and biomass of prey is interesting, but its biological significance is unclear. The observed trends in prey distribution and abundance could merely have been artifacts of the sampling methods used. It is possible, however, that concentrated gray whale feeding within the study area depleted the levels of *Diastylopsis* and whales shifted their feeding effort to this offshore area where food was perhaps more abundant.

Previous observations on the distribution patterns of gray whales indicate the number of whales using the tertiary feeding grounds during summer is increasing (Dohl et al. 1983; Kim and Oliver 1989). Increased competition for food

resources, resulting from continued population growth, may be forcing individuals to use alternative summer foraging areas. The results from my study at Agate Bay support these conclusions, and provide further documentation of the feeding activities of gray whales in these ancillary feeding areas.

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Figure 1. Agate Bay study area, Humboldt County, California.

Figure 2. Agate Bay study area and positions of the preliminary samples collected outside of the study area in 1990.

Figure 3. Positions of transect line samples collected in Agate Bay, California, on 21 September, 1991.

Figure 4. Theodolite-generated tracks of feeding gray whales in Agate Bay, California, from 5 September to 29 September, 1991.

Figure 5. Theodolite-generated tracks of feeding gray whales in Agate Bay, California, from 30 September to 23 October, 1991.

Table 1. Respiratory variables (n= number of observations) of gray whales engaged in feeding, traveling, and other behaviors in Agate Bay, California, for all whales combined during summers 1990 and 1991.

Behavior	Surface Interval (minutes) mean (± 1 SD)	Dive Duration (minutes) mean (± 1 SD)	Number of Exhalations per Surface Interval mean (± 1 SD)	Exhalation Interval (seconds) mean (± 1 SD)
Feeding n	1.2 (0.89) 2455	3.1 (1.13) 2443	4.5 (1.94) 2439	17.6 (13.49) 3816
Traveling n	0.5 (0.35) 436	0.7 (0.57) 427	1.8 (1.52) 431	13.2 (12.91) 1107
Other n	0.5 (0.45) 172	0.6 (0.57) 184	1.6 (1.43) 180	13.7 (11.31) 572

Table 2. Density of Diastylopsis dawsoni and biomass of total infauna for preliminary and primary benthic samples and feeding pit samples collected in Agate Bay, California, during summers 1990 and 1991. Values given are the mean $\pm$ 1 standard deviation, and n is the number of samples. The area of the benthic sampler was 0.0225 square meters.

Sample Date	Density (Individuals / square meter)			Biomass (grams / square meter)		
	mean (± 1 SD)		[n]	mean (± 1 SD)		[n]
Preliminary Samples						
Inside Study Area						
16-Jun-90	10250	(9936.72)	[10]	37.8	(34.47)	[10]
9-Jul-90	26333	(23589.47)	[10]	70.4	(63.55)	[10]
Outside Study Area						
8-Jul-90						
Site 1	1857	(1656.21)	[2]	12.9	(11.22)	[2]
Site 2	689	(621.11)	[2]	5.9	(4.86)	[2]
Site 3	2354	(2286.55)	[2]	14.3	(13.22)	[2]
Site 4	1678	(1453.38)	[2]	9.3	(8.23)	[2]
Primary Samples						
11-Jul-91	3600	(3893.44)	[20]	17	(8.49)	[20]
24-Jul-91	9280	(10924.80)	[10]	26.3	(16.45)	[10]
15-Aug-91	63860	(26516.97)	[20]	131	(48.70)	[20]
12-Sep-91	4933	(4240.53)	[10]	23.7	(18.63)	[10]
Feeding Pit Samples						
28-Sep-91						
Inside Pit	1778	(1071.63)	[3]	6.3	(3.41)	[3]
Outside Pit	6444	(2169.14)	[3]	16.8	(5.51)	[3]

Table 3. Numbers of individuals (No.), wet weights (Wt.) in grams, and sample size (n) for all preliminary and primary benthic samples collected inside and outside (periphery) of the Agate Bay study area during summers 1990 and 1991. Values given are the means with the standard deviations in parentheses. Biomass is of total infauna. Area of the benthic sampler was 0.0225 square meters.

Infauna	1990						1991							
	Inside Study Area			Outside Study Area			Inside Study Area							
	16 June n=10	9 July n=10	8 July n=8	11 July n=20	24 July n=10	15 August n=20	12 September n=10							
	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.		
Cumaceans	231.2 (192.3)	0.31 (.21)	593.6 (427.4)	0.85 (.66)	37.4 (22.1)	0.06 (.03)	81.6 (57.4)	0.08 (.05)	209.8 (163.0)	0.29 (.16)	1436.1 (1265.8)	2.23 (1.87)	111.5 (93.2)	0.18 (.12)
Clams	53.1 (23.4)	0.20 (.12)	42.5 (26.2)	0.24 (.11)	38.1 (21.5)	0.09 (.04)	37.1 (19.7)	0.10 (.04)	43.1 (24.5)	0.15 (.09)	51.0 (26.3)	0.25 (.15)	41.2 (26.3)	0.16 (.10)
Polychaetes	103.8 (67.3)	0.14 (.06)	96.1 (68.3)	0.18 (.12)	83.2 (54.2)	0.06 (.03)	81.4 (59.7)	0.09 (.04)	109.4 (69.9)	0.06 (.02)	92.4 (53.6)	0.16 (.07)	90.4 (48.3)	0.12 (.05)
Isopods	23.7 (16.3)	0.10 (.05)	26.0 (17.9)	0.16 (.08)	26.5 (13.6)	0.02 (.01)	16.0 (7.3)	0.08 (.03)	19.8 (12.3)	0.04 (.01)	28.3 (13.5)	0.13 (.07)	21.0 (16.3)	0.04 (.02)
Amphipods	41.0 (31.2)	0.10 (.04)	36.3 (25.4)	0.15 (.08)	33.1 (21.1)	0.01 (.01)	26.4 (17.6)	0.03 (.01)	38.1 (27.3)	0.05 (.03)	27.1 (20.3)	0.12 (.05)	36.5 (25.5)	0.03 (.01)
Totals	452.8	0.85	794.5	1.58	218.3	0.24	242.5	0.38	420.2	0.59	1634.9	2.95	300.6	0.53
Biomass	37.8 (34.5)		70.4 (63.5)		10.6 (7.4)		17.0 (8.5)		26.3 (16.5)		131.0 (48.7)		23.7 (18.6)	

Table 4. Density of Diastylopsis dawsoni and biomass of total infauna for transect line samples collected in Agate Bay, California, on 21 September, 1991.

Sample Number (distance along line in meters)	Density (individuals / square meter)	Biomass (grams / square meter)
Line 1		
1 (0)	8341	36.1
2 (30)	10249	38.4
3 (60)	8911	27.8
4 (90)	17022	41.8
5 (120)	23819	62.7
Line 2		
1 (0)	4622	16.2
2 (30)	3244	9.9
3 (60)	12489	41.3
4 (90)	9422	27.6
5 (120)	16622	50.9
Line 3		
1 (0)	2755	8.4
2 (30)	4178	13.6
3 (60)	3378	6.2
4 (90)	5822	13.1
5 (120)	8133	19.8

Table 5. Comparison of greatest mean biomass estimate from Agate Bay, California, with reported levels from other gray whale feeding areas.

Location	Biomass grams / square meter (mean $\pm$ 1 SD)	Prey Item	Reference
Bering Sea	211 $\pm$ 167 482 $\pm$ 286	<i>Ampelisca macrocephala</i> <i>Ampelisca macrocephala</i>	Thomson 1984 Stoker 1978
Vancouver Island			
Ahous Bay	160 $\pm$ 39	<i>Ampelisca agassizi</i>	Kvitek and Oliver 1986
Pachena Bay	197 $\pm$ 71	<i>Ampelisca agassizi</i>	Oliver et al. 1984
Pachena Bay	211 $\pm$ 188 94 $\pm$ 61	<i>Neomysis rayii</i> <i>Holmesimysis sculpta</i>	Guerrero 1989 Guerrero 1989
Agate Bay, California	131 $\pm$ 49	<i>Diastylopsis dawsoni</i>	Mean biomass, August 1991 This study
Baja California Sur, Mexico	24 $\pm$ 1	<i>Ampelisca agassizi</i>	Oliver et al. 1983