Feeding, distribution, and reproductive behavior of cyamids (Crustacea: Amphipoda) living on humpback and right whales

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Abstract: Cyamids are little-known amphipod crustaceans that live only on cetaceans. Specimens were collected from strandings of three right whales (*Eubalaena glacialis*) and one humpback whale (*Megaptera novaeangliae*). The intestinal contents of cyamids from the humpback whale indicated that they feed on a layer of whale skin containing pigment. The single species of cyamid from the humpback whale had a male-biased sex ratio (70% male) and its distribution indicated that males were competing for access to females. Two species of cyamids from the callosities of right whales occurred in different microhabitats. No reproductive synchrony was found between cyamids and their hosts. A species of cyamid that occurs in large patches on the head of young right whale calves disappears from the head when calf growth slows at approximately 2 months of age; this habitat shift may indicate a change in the quality or quantity of new skin.

Résumé : Les cyamidés sont de petits crustacés amphipodes peu connus qui vivent exclusivement sur des cétacés. Des cyamidés ont été recueillis sur trois Baleines noires (*Eubalaena glacialis*) et un Rorqual à bosse (*Megaptera novaeangliae*) échoués. D'après leurs contenus intestinaux, les cyamidés sur le Rorqual à bosse se nourrissent sur une couche de peau qui contient les pigments. La seule espèce de cyamidé trouvée sur le rorqual avait un rapport mâles : femelles déséquilibré (70% de mâles) et sa répartition indiquait que les mâles se faisaient compétition pour avoir accès aux femelles. Deux espèces ont été trouvées dans les callosités des Baleines noires, dans des microhabitats différents. Il n'y avait pas de synchronisme entre le reproduction des cyamidés et celle de leur hôte. Une espèce de cyamidé dont la présence ce manifeste par la formation de grands groupes compacts sur la tête de jeunes Baleines noires disparaît de la tête lorsque la croissance des jeunes ralentit, à l'âge de 2 mois environ; ce déplacement est peut-être relié à des changements dans la qualité ou la quantité de la nouvelle peau.
[Traduit par la Rédaction]

Introduction

Cyamids are amphipod crustaceans that pass all life stages on cetaceans. For this reason they are difficult to study and their biology is poorly known. Much of the cyamid literature was written in the 1800s and describes the anatomy and systematics of specimens collected during whaling expeditions (for a review see Grüner 1975). Aspects of cyamid ecology are discussed in papers by Balbuena and Raga (1991), Berzin and Vlasova (1982), Best (1979), Brownell and Mead (1985), Leung (1967), and others referred to below. New information is presented here on feeding behavior, spatial distribution, reproduction, and ecological succession in species of *Cyamus* that live on humpback whales (*Megaptera novaeangliae*) and right whales (*Eubalaena glacialis*). An opening background section briefly reviews aspects of cyamid biology that provide a context for these new results. As an aid to organizing the diversity of findings, the results and discussion for each topic are presented together under separate subheadings.

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Background

Cyamids cannot swim (Roussel de Vauzème 1834), and if dislodged from a whale they will die unless another whale surfaces under them. They hold on with five pairs of legs (pereopods), each ending in a sharp, hooked claw (dactylus) (Fig. 1). Females carry eggs and maturing young in a marsupium (Fig. 1). Cyamids aggregate in areas of reduced water flow, such as the skin folds of the ventral grooves, eyes, flippers and blowholes; the margins of the lips; in wounds; around barnacles; and on callosities, the raised patches of roughened skin found only on the head of right whales (Leung 1970*a*, 1970*b*). Right and gray whales have more than one species of cyamid and the species have different spatial distributions (Leung 1976; Rice and Wolman 1971; Roussel de Vauzème 1834).

Examination of cyamid mouthparts, digestive tract, and the skin from which they were collected has led to speculation that cyamids eat whale skin (Agrawal 1967; Leung 1976; Roussel de Vauzème 1834; Samaras and Durham 1985; Sokolov and Evgen'eva 1988). Keith (1974) reported that large food particles in the stomach of a cyamid had the appearance of whale skin. The nearest relatives of cyamids (caprellid amphipods) feed by predation, scavenging, scraping, and filter-feeding on diatoms, protozoans, and crustaceans (reviewed by Caine 1974). E.A. Caine (personal

Fig. 1. Morphology of a cyamid (*Cyamus ovalis*). (*a*) Dorsal view of a female. (*b*) Ventral view of a female. (*c*) Ventral view of a male. *a*, antenna; *d*, dactylus or claw; *fg*, first gnathopod; *g*, gill; *m*, marsupium; *mp*, maxilliped palp and mouth region; *p*, pereopod.

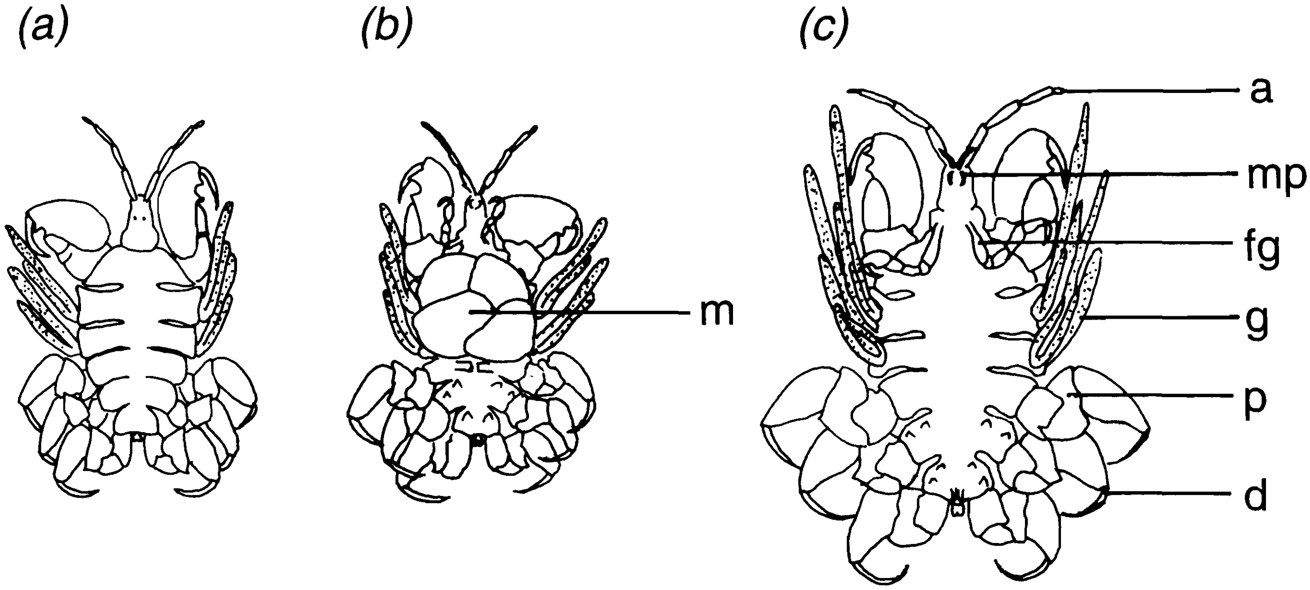


Table 1. Cyamid collections made at strandings of a humpback whale (*Megaptera novaeangliae*) and three right whales (*Eubalaena glacialis*).

	Sex	Length (m)	Location	Date of stranding	*Cyamus* spp. collected
Humpback whale	M	11	Truro, Mass.	6 Nov. 1982	*C. boopis*
Right whale	M	11	E. Hampton, N.Y.	5 Mar. 1979	*C. gracilis*
					C. ovalis
Right whale	M	11	Island Beach State Park, N.J.	24 Feb. 1983	*C. gracilis*
					C. ovalis
Right whale	F	11	Provincetown, Mass.	7 Aug. 1986	*C. gracilis*
					C. ovalis
					C. erraticus

communication) comments that "cyamid mouthparts are highly modified from those of caprellids; they have no setae on the maxillipeds, lack endites, and the other mouthparts are reduced and located on a projected oval area. The structure of the mouthparts precludes feeding on free-living organisms and suggests that cyamids are obligate ectoparasites."

Female amphipods mate immediately after molting (Conlan 1991). In amphipods that do not synchronize molts, such as cyamids, more males than females are available for mating at any one time and male competition for females has led to the evolution of precopulatory mate guarding (Adams and Greenwood 1987). Mate guarding begins before the molt and ends with fertilization (Caine 1991; Conlan 1991). In many cyamids, males are larger than females, and during mate guarding the male straddles the female while clasping the base of her external gills (Pouchet 1892).

Materials and methods

Cyamid collections were made at four whale strandings (Table 1). The right whales had been killed by collisions with ships. The humpback whale had been towing a fishing net for several months, as indicated by healed wounds on the tailstock. It was alive when it stranded, but died shortly thereafter. It had a very heavy infestation of cyamids, possibly because of its slow swimming speed. Photographs of right whale calves taken during their first 3 months of life are the source of data for the succession study.

Cyamids were collected at a number of different locations on the whales (three sites on the chin callosity of the New York right whale, five sites on the bonnet callosity of the New Jersey right whale, and six sites in different regions on the body of the humpback whale). At each location, all cyamids within a measured area were collected. The two largest collections from the humpback whale were from 300-cm^2 areas (7 × 45 cm on the flipper and 17 × 17 cm on the tailstock) where cyamids completely covered the skin; one was from white skin on the flipper and the other was from black skin on the tailstock. Collections from the right whales were from circular areas of roughly 30 cm^2 on the bonnet and chin callosities. Separate collections were made from deep pits (2–4 cm deep) and shallower areas of callosity tissue. The cyamids were preserved in 70% ethanol. Two collections of 300–500 cyamids (one from the humpback and the other from the New Jersey right whale) were kept alive in aerated salt-water aquaria maintained at 10°C, on whale skin and on neoprene wet-suit material, and were observed for periods of 2–6 weeks.

The preserved specimens were sorted according to species, sex, and body length. Lengths were measured along the dorsal midline between the anterior margin of the second and posterior margin of the seventh body segments. Although all ages were present in the collections, only individuals that could be sexed are reported in the results. Immatures can be recognized as female when their marsupial plates begin to develop. Individuals of this size (or larger) that did not show budding marsupial plates were considered male. Females were considered immature until their marsupial plates fully overlapped. Males were considered immature if they fell within the same size range as immature females.

Results and discussion

Conclusive evidence that cyamids feed on whale skin

The collections provided new information on cyamid feeding behavior. The color of the intestinal contents was examined in preserved *Cyamus boopis* Lütken collected from the flipper and tailstock of the humpback whale. Most (99%) of the 1011 cyamids from the black skin on the tailstock had black intestinal contents, and most (98%) of the 1319 cyamids from the white skin on the flipper had white intestinal contents (Rowntree 1983). These observations suggest that cyamids eat a layer of whale skin containing pigment. Some large juveniles still in the brood pouch had black intestinal contents, indicating that the young may leave the marsupium to feed and then return.

Cyamus ovalis Roussel de Vauzième in the aquaria appeared to feed on the whale skin to which they were clinging. They pressed the oval area of the mouth against the skin and alternately swept the left and right maxilliped palps across the whale skin in a lateral–medial motion. Four *C. ovalis* were removed from the whale skin and placed on neoprene wetsuit material in another tank. The position of the dark material in their intestines was recorded; it passed through at the rate of one body segment per hour.

The pigment that cyamids eat occurs only in the epidermis of whale skin (Sokolov 1982). Sokolov and Evgen'eva (1988) found that cyamids had removed only the outermost layer of gray whale epidermis. In most mammals, the cells of the outer epidermal layer are fully keratinized and are in the process of being sloughed. Whale skin is produced at an extraordinarily high rate (Geraci et al. 1979), and the sloughed skin cells are usually not fully keratinized (Sokolov 1982). The retained cytoplasm could provide added nutrition for cyamids. Skin cells probably accumulate in areas of reduced water flow, which are areas where cyamids typically concentrate.

Do cyamids also feed on plankton?

Although the primary diet of cyamids is probably whale skin, it is possible that they also feed on plankton. A single caprellid species may use several different feeding methods to take a variety of prey species (Caine 1974). The close relationship between caprellids and cyamids suggests that cyamids might also be opportunistic feeders; in addition to feeding on whale skin, they could scrape diatoms and protozoans from the skin. They might also prey on free-swimming plankton. When caprellids filter-feed or prey on passing plankton, they assume an upright stance with their six hind legs clasping the substrate and the anterior portion of the body held vertically (Caine 1978). Cyamids maintained in the aquaria occasionally assumed a similar upright posture. This observation suggests that cyamids could use a caprellid-like upright stance to prey on passing plankton. Right whales seek out plankton blooms and begin feeding when prey densities reach about 1000 zooplankters/m^3 (Mayo and Marx 1990). At such high plankton densities, the anterior surface of a moving whale, and its cyamids, would be bombarded by the zooplankton and by the protozoans, diatoms, and other organisms on which the zooplankon feed. Even without special structures to facilitate prey capture, cyamids might be able to feed profitably on some components of a plankton bloom.

This suggests that an interesting mutualistic relationship could exist between a feeding right whale and its cyamids. All baleen whales have sensory hairs around the outside of the mouth. It is speculated that the hairs are used to detect water currents and prey (Lillie and Hutchinson 1910; Nakai and Shida 1948; Sokolov 1982). In right whales, the sensory hairs are found on the tip of the snout, along the lower lip, and in the callosities. A small callosity looks like a volcanic crater and has a single sensory hair projecting from its center. The arrangement of the tissue around the hair suggests that callosities may enhance the functioning of the sensory hairs. They may serve as pedestals that raise the sensory hairs beyond the boundary layer, where they can more effectively detect changes in plankton density. The roughened surface of the callosities probably also disrupts the boundary layer and brings more water and thus more plankton closer to the hairs.

Callosities may have evolved to help a whale sense its environment but their roughened surfaces provide good attachment sites for cyamids. The cyamids that blanket a callosity could interfere with a whale's sensory reception by covering, breaking, or bending the sensory hairs. However, it is also possible that cyamids amplify the signal to the whale. They might sense a plankton bloom and change their activity patterns either by assuming a predatory upright stance or by crawling about in search of plankton caught in the pits of the callosity tissue. The change in activity of thousands of cyamid claws could signal to a whale that it had entered or left plankton-rich water.

Varying spatial distributions

Variation in the distribution of different ages and sexes within the same species of cyamid was studied in collections from the humpback whale, and variation in the distribution of different species of cyamids was studied in collections from the right whales. Cyamids are not stationary, and in the aquaria they walked at average rates of 4.5 m/h. This means they can move to preferred locations and are able to travel the length of a whale in about 3 h. The cyamids described here could have been collected from locations to which they had moved after their host stranded. However, even if they had moved after the stranding, there remain differences in distribution at various collection sites, as discussed below.

Cyamus boopis is the only species found on humpback whales. Table 2 shows the numbers of individuals in different age and reproductive categories. Most of the differences in distribution seem to be correlated with the reproductive states of individuals. There was a significantly higher proportion of gravid females in the small collections (fewer than 110 individuals) than in the larger collections from the tail and flipper ($\chi^2 = 63.0$, df = 1, $p = 0.00001$). Some collections were small because the sites where they were collected had only a few widely spaced cyamids. Gravid females may move to areas where there is less competition for their young or to "launching" sites where there is more

Table 2. Numbers of *Cyamus boopis* collected from a humpback whale that stranded at Truro, Massachusetts.

	Flipper	Tail	Tubercle on head	Back	Genital slit	Tip of lower jaw
Females						
Juvenile females	268	54	18	26	21	25
Nongravid females	97	86	2	16	6	67
Gravid females	13	17	19	—	4	14
Females with young	1	8	—	—	2	—
Mate-guarded females	15	61	—	17	—	—
Total	394	226	39	57	33	106
Males						
Juvenile males	269	310	—	14	13	62
"Adult" males	641	414	17	21	28	161
Mate-guarding males	15	61	—	17	—	—
Total	925	785	17	52	41	223
Total of cyamids	1319	1011	56	109	74	329
% males	70	78	30	28	55	68
% in precopulatory pairs	2	12	0	31	0	0

contact between whales and the cyamids have a greater chance of moving to a new host. The proportion of sexable juveniles ranged from 26 to 46% in all the collections. They did not appear to concentrate abundantly on any particular area of the whale.

The sex ratio of the entire cyamid collection from the humpback whale was male biased (70%). This, in addition to the operationally male-biased sex ratio resulting from the asynchronous molt of female cyamids, must have created strong competition among the males for mating opportunities. The highest proportion of individuals in precopulatory pairs (31%) was found in a small collection near a wound on the back. In contrast, in the collections of densely concentrated cyamids from the tail and flipper, 12 and 2% of the sexable individuals were in pairs, respectively. This implies that mate-guarding males attempted to decrease interference from other males by moving to areas of lower cyamid density. Observations of a precopulatory pair among the cyamids maintained in aquaria support this idea. When a single male approached the precopulatory pair, the males touched each other with their first antennae and then the paired male turned away. The single male grasped the base of the paired male's antennae but the paired male pulled free and walked away carrying the female. The single male did not follow. Paired females do not easily relinquish their hold on the whale and are pulled around by the males.

The intestinal contents of cyamids collected from the humpback whale provide evidence that male cyamids move about more than females. Twenty-nine cyamids collected from the white skin of the flipper had black intestinal material. They must have moved to the flipper from an area of black skin. The nearest black skin was about 30 cm from where they were collected. This small collection of cyamids with black intestinal material was highly male biased (28/29 male). There is a significant association of gender with color of intestinal material among the specimens from the flipper (G test with Williams' correction, $G = 12$, 1 df, $p < 0.001$; Sokol and Rohlf 1981). The fact that most of the cyamids containing black intestinal material collected from white skin were males indicates that the males were traveling more than the females. The highly male-biased sex ratio must have caused strong competition for mates, between the males and most likely drove males to travel in search of receptive females.

In general, natural selection strongly favors balanced sex ratios ($\sim$1:1) at birth or weaning (Fisher 1930; Charnov 1982). If this is so, why should an apparently male-biased sex ratio exist in cyamids? Possible causes could be a higher mortality rate of females or environmental sex determination. Females must be particularly vulnerable to being washed away when they are being carried by males, which use only the small first pair of gnathopods (Fig. 1) to hold onto the females. Environmental sex determination (ESD) occurs when the sex of an offspring is determined after conception by some environmental influence (Charnov and Bull 1977). It is believed to evolve in situations where a patchy resource distribution confers a relatively greater advantage on the members of one sex at some times or places and on the other sex at other times or places. ESD is known to occur in some amphipods (Naylor et al. 1988). Larger male cyamids enjoy a substantial reproductive advantage over smaller males. Males must be larger than the females they carry, and larger males can carry larger females that in turn produce more young. The humpback whale that stranded had been towing a fishing net and thus had been swimming slowly for months. The slow swimming may have opened up vast feeding sites that in turn allowed male cyamids to grow to a large size, or favored male development because growth to a large size was assured. Further work is needed to determine whether ESD really does occur in cyamids, but in any case there appears to have been fairly intense competition among the male cyamids on this humpback whale.

The right whale cyamids that were studied for distributional variation came from the callosities and contained only the two species restricted to callosities, *C. ovalis* Roussel de

Table 3. Cyamids collected from different regions of the callosities of right whales that stranded in New York and New Jersey.

Cyamus species	Stranding locality	No. in deep pits	No. not in deep pits
C. ovalis	N.Y.	64	149
C. ovalis	N.J.	24	261
C. gracilis	N.Y.	101	3
C. gracils	N.J.	126	50
Total		315	463

Vauzème and *Cyamus gracilis* Roussel de Vauzème. The cyamids did not show the within-species distributional variation that the humpback cyamids showed. However, the different species were found in different regions of the callosities (Table 3). *Cyamus gracilis* was significantly more prevalent in the deep pits of callosity tissue, while *C. ovalis* predominated in open areas (χ^2 = 198, 1 df, p = 0.00001 for the New Jersey collection; χ^2 = 126, 1 df, p = 0.00001 for the New York collection). Species composition did not vary significantly with distance from the edge of the callosity.

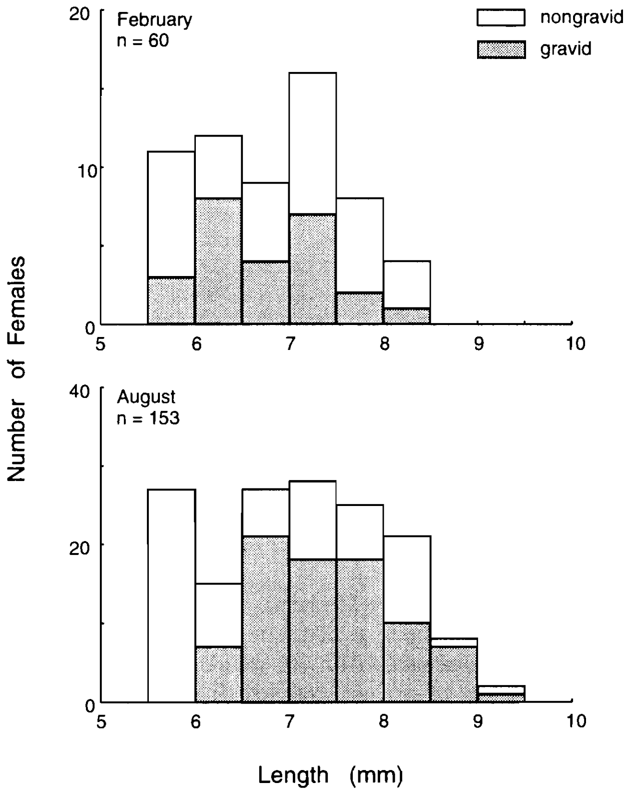
The sex ratios of the right whale cyamids were consistently female biased (21–42% male), in contrast to the strongly male-biased humpback whale sample. Sex ratios can fluctuate strongly under systems of environmental sex determination, in response to fluctuations of the cue (e.g., temperature) that directs individuals down either the male or the female developmental pathway (see Bull 1983). To understand sex determination and sex-ratio evolution in cyamids, many collections are needed. Where possible, different samples should be taken from all regions of the bodies of recently stranded whales.

Seasonal reproduction

Roussel de Vauzème (1834) suggested the possibility of seasonality in cyamids when he noted that there were relatively few cyamids on the last right whale of the expedition, which was taken at the beginning of winter. Leung (1976) reported seasonal reproduction in cyamids found on gray whales but gave no detailed data. If habitat is limited for cyamids, then it would be advantageous to have offspring when new habitat becomes available, such as when their hosts calve. In addition, offspring survival might be greater for gravid females that transfer to calves, where there will be less competition for feeding and for attachment sites with reduced water flow. The New Jersey right whale stranded during the calving season (February) and the Massachusetts right whale stranded 6 months later, during the feeding season (August). The numbers of female *C. ovalis* with and without eggs in their marsupia were compared in the collections taken from these two whales. Only female cyamids that were as long as or longer than the smallest female with eggs in her marsupium were used in this comparison.

Figure 2 shows the numbers of gravid and nongravid female *C. ovalis*. There is no significant difference between the numbers of females with and without eggs on the two whales (χ^2 = 2.41, 1 df, p = 0.12). However, since the whales that stranded were juveniles outside the normal

Fig. 2. Numbers and sizes of gravid and nongravid female *Cyamus ovalis* in collections made in February and August.



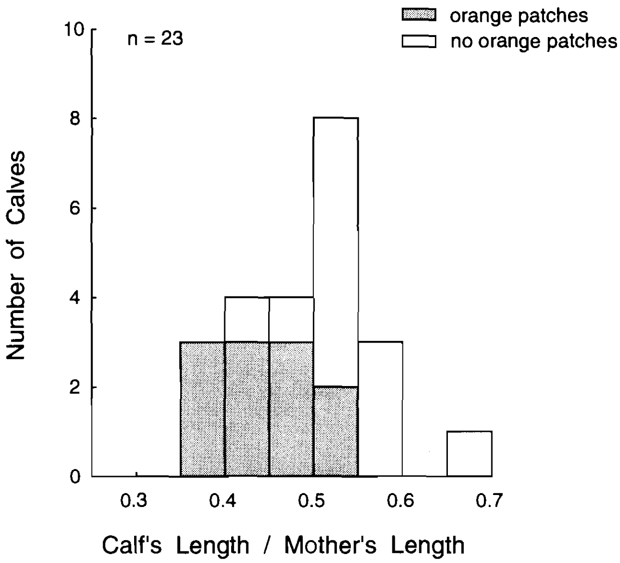
migratory route, these collections may be anomalous. Comparing cyamids from adult whales on high-latitude feeding grounds with those from adults on low-latitude calving grounds might show a different ratio of gravid to nongravid females. The data do show larger females and a greater percentage of gravid females in the larger size classes in August.

Succession

The species of cyamids on the heads of young right whale calves change as the calves grow. This successional pattern was studied by examining aerial color slides of right whale calves in their first 3 months of life. The photographs were taken as part of an ongoing study of the ecology and behavior of the southern right whale (Payne 1986). Twenty-three photographs of 13 calves were selected in which (*i*) the area between the calf's lower mandible and lip was clear enough for the presence or absence of patches of orange cyamids to be scored, and (*ii*) the calf and mother were parallel to each other with their snout tips and fluke notches visible, so that the calf's length could be measured with respect its mother's length. For some calves there was one photograph, while for others there were three photographs, each taken at a different time in the season; the longest interval between the first and last photographs was 101 days.

The change in species can be seen as a change in the color and location of patches of cyamids. The first notable infestations on a calf are large patches of orange cyamids, *Cyamus erraticus* Roussel de Vauzème, on the head, particularly in areas of smooth skin where there is no callosity tissue (for a photograph see Darling 1988). On adults, *C. erraticus* occurs in wounds and in folds of skin such as the genital

Fig. 3. Numbers of calves of different lengths with and without patches of orange *Cyamus erraticus* on their cheeks.



slit, and is seldom found on the head. The cyamids probably transfer from the mothers' genital and mammary slits to the calves when they are born or are nursing. As the calves grow, the patches of orange cyamids disappear and white cyamids (*C. ovalis*) colonize the callosity tissue.

When a calf grows to more than 55% of its mother's length, the patches of orange *C. erraticus* disappear from its cheeks (Fig. 3). *Cyamus erraticus* are not seen in such large and dense patches elsewhere on the calf's body unless it has a wound. The calf grows rapidly in its first month, with the head growing faster than the rest of the body (Whitehead and Payne 1981). Growth slows at 2 months of age, when the calf reaches about 55% of its mother's length (Whitehead and Payne 1981). Thus, the disappearance of patches of *C. erraticus* from calves' cheeks occurs at the time when growth slows. The dense concentrations of *C. erraticus* on the heads of young calves may therefore be a response to a high rate of skin production associated with the initial rapid growth of the head.

The disappearance of cyamids from the cheeks of calves is unlikely to be caused by a slow migration from the head to the genital slit (where *C. erraticus* is found in adults), since a cyamid can walk the length of a calf in 2 h. *Cyamus erraticus* is not displaced by *C. ovalis*, since the two species are found on different types of tissues (smooth skin versus callosity tissue; Roussel de Vauzème 1834). The disappearance of *C. erraticus* does not appear to be a response to faster swimming, and thus to greater flow rates over the head. Mother–calf pairs swim fairly rapidly early in the calf's life but at 1–1.5 months of age they slow down, the mothers spend more time resting, and calves develop mother-centered play behaviors that often include touching the mother (Thomas and Taber 1984). This change in behavior may contribute to the growth of the *C. ovalis* populations on the callosities, since the calves could pick up cyamids while touching their mothers' heads in play. A change in callosity tissue is the most likely cause of the appearance of *C. ovalis*. Callosities are smooth at birth and become pitted with crevasses (like tree bark) as the calves' heads grow (Payne et al. 1983). The appearance of ridges to which the cyamids can cling is undoubtedly an important factor facilitating the arrival of *C. ovalis*.

For the future

Cyamids are difficult animals to study because they live only on cetaceans. Knowledge of cyamid biology increases sporadically as specimens are collected at whale strandings. In the future, large collections should be made whenever possible, as they will provide the kinds of demographic and genetic data needed to unravel the complex relationships between these fascinating arthropods and their giant, far-ranging mammalian hosts.

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