

Giant aggregates: Importance as microbial centers and agents of material flux in the mesopelagic zone

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Abstract

By using a remotely operated vehicle (ROV), we studied large mucous aggregates produced by the larvacean *Bathochordaeus* in Monterey Bay, California. These fragile structures or “houses,” cannot be sampled by typical water or net collecting devices, and likely represent a class of cosmopolitan, widely spaced aggregates in subsurface waters. ROV samples allowed us to determine the contribution of the aggregate-associated communities to populations of microorganisms at depths of 100–500 m. Because the giant houses only average ~1 per 100 m³, they harbor <1% of the microorganisms in the water, although they are locally enriched. However, once abandoned, houses may play a significant role in transporting materials and organisms to depth. Flux calculations indicate they may seasonally account for 11–100% of some classes of sinking materials at 500 m. These calculations are based on house-flux contributions predicted from house age (estimated), house abundance (ROV measured), and particle flux (measured by a nearby sediment trap). Based on our ROV observations of spatial and temporal characteristics of the giant aggregates, we calculate the probability that sediment traps collect the correct number of sinking aggregates. Our results suggest that rare particles, such as large aggregates and some sarcodines and pteropods, may be undersampled by commonly used, small sediment traps. Furthermore, the predictably infrequent capture of such comparatively rare particles can lead to erroneous interpretations of temporal or spatial patterns in the flux of material through the upper ocean.

Studies of marine snow, readily visible particles >0.5 mm, have focused on particles in the millimeter to few centimeter size range. Nonliving particles many centimeters across, however, have been noted in literature dating back over a century (*see* reviews in Trent 1985; Alldredge and Silver 1988; Stachowitsch et al. 1990; Riebesell 1992). Because they are fragile and rare (their abundance and physical and biological characteristics are poorly known) large aggregates may be of considerable interest because they harbor concentrated, distinctive populations and may transfer associated populations and material to depth.

Several types of very large aggregates are known. Submersible and Scuba divers have described “comets” and “stringers” (Alldredge and Silver 1988), which may result from physical coagulation of smaller particles (Alldredge and Jackson 1995). In the Adriatic Sea, exceptionally large

and abundant aggregates occasionally result from a unique combination of physical and chemical conditions (Herndl and Peduzzi 1988; Stachowitsch et al. 1990). These large aggregates incorporate phytoplankton and range from centimeter-long comets to meter-sized “clouds” and stable “leathery” layers. In the Adriatic, these accumulate in 10–100-m-long surface mats and accrete through sequential flocculation events. Similar phytoplankton-derived aggregates have been described in the North Sea (Riebesell 1992). Other very large aggregates are formed by zooplankton, including mucous feeding webs of pteropod molluscs (Gilmer and Harbison 1986) and giant “houses” of larvaceans (Barham 1979; Hamner and Robison 1992). The large larvaceans occur in both eutrophic and oligotrophic environments (Youngbluth 1984; Alldredge and Silver 1988) but are poorly known because they cannot be sampled by traditional oceanographic sampling devices.

This study examines the role of very large (tens of centimeters) aggregates as plankton community centers in mesopelagic waters and as vertical transfer agents of organisms and materials, using houses of the giant larvacean *Bathochordaeus*. In this study, house size and abundance were determined and collected using a remotely operated vehicle (ROV) (Robison 1994). We consider whether neglect of such relatively rare and fragile particles could lead to biased views of the deep-water plankton community or to underestimates of material flux to the deep sea.

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Materials and methods

Field collections—We collected houses of the giant larvacean *Bathochordaeus* sp. at depths of 100 to 500 m at the seaward edge of Monterey Bay, California, at a ~1,000-m-deep site in the Monterey Bay submarine canyon (360°42'N, 122°02'W). Collections were made between 0900 and 1400 h from October 1989 to January 1993 by using the Monterey Bay Aquarium Research Institute (MBARI)-owned ROV, the *Ventana*. Equipment on the ROV included a high-resolution, broadcast-quality SONY video camera for viewing and recording images of houses, and samplers for capturing houses and water (Robison 1994).

Two ROV-mounted types of samplers (Harbor Branch Oceanographic Institute design) collected occupied (larvacean present) and discarded (empty) houses. The first was the 7.5-liter plexiglass detritus sampler with hydraulically activated lids. A specimen was captured by maneuvering the cylindrical sampler over the house and closing the lids. Turbulence created by the sampler caused the fragile houses to collapse so that even large houses were generally collected in their entirety. Fractions of houses collected were estimated visually from the Sony monitor. For this study, only samples where at least 50% of the house was captured were used. A paired seawater control was usually obtained within 50 m. The second type, the suction sampler, was a variable-flow vacuum system that pumped houses through a nozzle, depositing them into a rotating carousel of canisters with 165- μ m mesh net cod ends (see Steinberg et al. 1994).

In most of the analyses presented, data for the two types (detritus and suction) of samplers are pooled. Statistical differences in fecal pellet and organism counts between the sampler types were noted only for fecal pellets, (Student's *t*-test, $P < 0.05$). Pellets seemed to be undersampled by the suction device, perhaps because the suction sampler turbulence dislodged them so that they passed through the screen. Thus, we used only detritus sampler data for pellet counts.

House abundances were measured on 10-min horizontal video transects on 12 sampling dates. Duplicate transects averaging 500 m³ each were run at 100, 200, 250, 300, 400, and 500 m. Transect depths were chosen based on the distribution of *Bathochordaeus* obtained from >400 h of videotape from 1989–1992 and CTD datasets (C. H. Pilskaln pers. comm.). The volume of water surveyed was determined as the known field of view times the distance traveled, which was obtained from the current meter mounted on the ROV and the track point navigation system.

Concurrently, a 450-m-deep time-series sediment trap moored 5.5 km N–NE of the ROV study site provided bi-weekly samples of particles (Pilskaln et al. 1996). The sediment trap was cone-shaped and baffled, with a surface collection area of 0.05 m², and was deployed from August 1989 through November 1992 (Pilskaln et al. 1996). Individual bi-weekly flux events or samples were separated within the collecting cod end by layers of teflon beads dispensed every 2 weeks from an intervalometer device suspended inside the trap cone (Anderson 1977). Trap solutions were pre-poisoned with a 4% density-adjusted Formalin solution (Pilskaln et al. 1996).

Sample processing—We gently pipetted visible house material from detritus samplers aboard ship with a wide-bore pipette. Remaining small house fragments, possibly dislodged during sampling, were concentrated on a 53- μ m mesh filter and gently rinsed with filtered seawater into a 400-ml jar containing the pipetted material. After vigorous shaking, a 10% aliquot was removed for fecal pellet and microbial counts (in 2% glutaraldehyde) and the remainder chemically analyzed (Pilskaln et al. 1996). Seawater controls were 400 ml of unconcentrated seawater (in 2% glutaraldehyde) from the paired detritus sampler. Suction samples were already concentrated when retrieved from the ROV and were apportioned and preserved as described for detritus samples, but processed with a 165- μ m screen. We assumed that most house material and attached associates obtained with the suction sampler were retained by the 165- μ m screen in the canister, while free living plankton passed through the screen. For the suction sampler, this assumption seems reasonable, because most items we counted were <165 μ m. Because finer (53- μ m) mesh was used to process detritus sampler collections, we corrected for the additional >53- μ m items in the water obtained with the larvacean houses. Although the mesh sizes used allowed dislodged diatoms and protozoans to pass through, we assumed that this loss was negligible. Corrections were based on the numbers of fecal pellets and the various microorganism groups obtained from seawater controls (i.e. free-living or unassociated); that is, 7.5 liters minus house volume (estimated from video records; see below).

Sediment trap samples were split into quantitative aliquots for microscopy and chemical analyses, including total, organic, and inorganic carbon and dry weights, by using a Honjo-Erez rotary precision sampler. Carbon fluxes were determined using methods described in Pilskaln et al. (1996), after removal of metazoan swimmers.

Microscopy—Aliquots for microscopy were taken after gently shaking the samples. The same item classes were counted in larvacean house, water, and sediment trap samples, except for bacteria and *Synechococcus*, which were not counted in sediment trap samples. Fecal pellets with >50- μ m diameters were enumerated using an Olympus SZH zoom stereo dissecting microscope. Numbers of pellets counted varied with pellet densities but were usually ≥ 100 pellets. A 0.5–2-ml aliquot placed in a settling chamber was counted for intact diatoms (i.e. those containing protoplasm), dinoflagellates, ciliates, and sarcodines using an Olympus IMT-2 inverted microscope with epifluorescent attachment (Silver and Gowing 1991). At least 100 cells were counted by either counting the entire chamber or some fraction of the chamber (i.e. every third or sixth transect). DAPI (4'-diamidino-2-phenylindole) staining of samples facilitated identification of intact protozoans (Sherr et al. 1993). Two replicate slides of the cyanobacterium *Synechococcus* and DAPI-stained heterotrophic bacteria (Porter and Feig 1980) prepared from house and water samples were filtered on 0.2- μ m Nuclepore filters and counted using epifluorescence microscopy on a Zeiss Axioscope (MacIsaac and Stockner 1993).

Video data processing—House images were sized from video using a width-of-field measurement determined from calibration of the ROV-based SONY camera (Davis and Pilskaln 1992) and OPTIMAS software. We viewed the houses from the side with the ROV and were unable to maneuver the vehicle to determine the true shape of the top, or particle intercepting area, of the house. House surface areas were considered the square of the house horizontal dimension, a rough yet conservative estimate of the house-collecting surface. (Had we assumed that the houses were circular when viewed from above, collection surfaces would have been 21% smaller, resulting in younger houses and even greater house fluxes.) House volumes were calculated based on their roughly elliptical or spherical shape using formulae for sphere or ellipsoid.

Results

Field samples in this study were collected over a 2½-year period and subdivided into two oceanographic seasons. These seasons reflect the hydrography (Lenarz et al. 1995) and seasonal particle flux pattern in Monterey Bay (Pilskaln et al. 1996). In this paper, the high productivity upwelling period is considered to be April–September and the lower productivity nonupwelling period is October–March. Because the samples, even if grouped by season, were often highly variable, nonparametric statistical tests were used when data were not normally distributed, as indicated by Kolmogorov–Smirnov tests.

In our video survey of 507 houses, two types were observed: (1) inflated ones ($n = 366$) of parachute or balloon shape that were horizontally elongate and usually contained an animal; and (2) collapsed, stringy, vertically elongate houses ($n = 141$) that always lacked an animal (Fig. 1). Data from the two types of houses (occupied and abandoned, respectively) were combined, since numbers of organisms and particles associated with the two did not differ significantly ($P < 0.05$, Mann–Whitney U -test). Horizontal cross-sectional area of the houses (mean \pm SE) was estimated to be $0.08 \pm 0.02\text{m}^2$, with no significant difference between seasons (Mann–Whitney U -test, $P > 0.05$).

Microscopy revealed similar types of diatoms, protozoans, and fecal pellets in houses, seawater controls, and sediment trap samples (Table 1). Dominant diatoms included the gen-

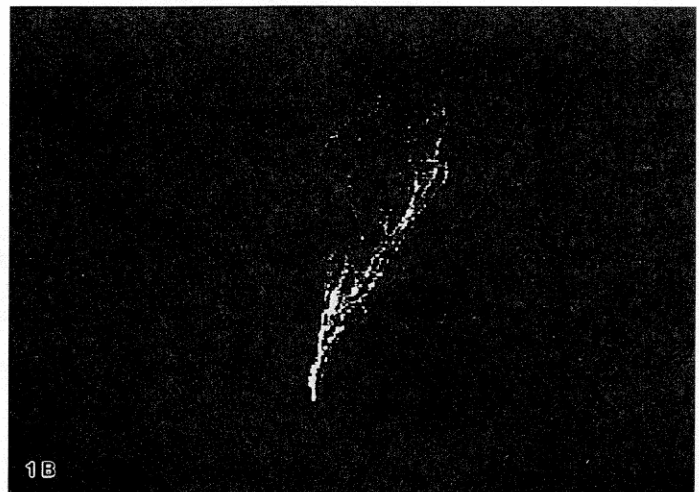
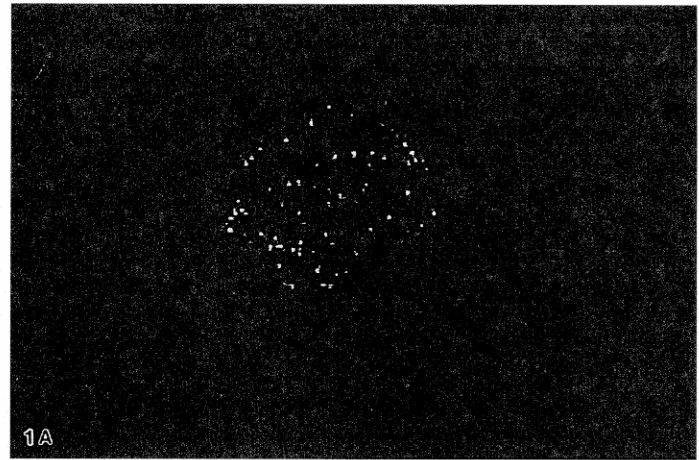


Fig. 1. Photographs of typical *Bathochordaeus* feeding structures (houses) obtained with the SONY camera system on the ROV *Ventana*. A. Inflated house (horizontal dimension of 0.35m) that is occupied by the animal. B. An abandoned, collapsed, and presumably sinking house (horizontal dimension of 0.14 m). Many small particles on the house surfaces are visible in these photographs.

on log-transformed abundances of items on houses to determine whether their numbers varied with season (upwelling and nonupwelling). For fecal pellets and all organism groups

Table 1. Items associated with larvacean houses, surrounding water, traps, and enrichment factors. Means \pm standard errors for houses were obtained by combining numbers of items associated with inflated and collapsed houses and, in all cases except for pellets, combining detritus and suction samples (*see text*). Water controls were obtained near houses. Sediment trap fluxes were provided by biweekly collections of traps deployed concurrently near sampling site from May 1990 through November 1992. Enrichment factors are enrichment of items on larvacean houses with respect to surrounding water obtained only from houses with paired water controls (*see text*). Significant differences between samples taken during upwelling (April–September) and nonupwelling (October–March) periods (two-way ANOVA or Student–Newman–Keuls test, $P < 0.05$) are denoted in boldface.

Item class	Houses (No. house ⁻¹ ; $n = 65$)	Water (No. liter ⁻¹ ; $n = 32$)	Trap flux (No. m ⁻² d ⁻¹ ; $n = 28$)	Enrichment factor ($n = 50$)
Diatoms				
Upwelling	4.2 \pm 1.9 $\times 10^5$	9.9 \pm 5.6 $\times 10^3$	9.2 \pm 4.2 $\times 10^6$	1.3 \pm 0.5 $\times 10^3$
Nonupwelling	6.0 \pm 2.0 $\times 10^4$	4.2 \pm 1.3 $\times 10^2$	4.2 \pm 1.5 $\times 10^5$	1.7 \pm 1.3 $\times 10^3$
Ciliates				
Upwelling	1.7 \pm 1.5 $\times 10^4$	1.2 \pm 0.3 $\times 10^2$	3.1 \pm 0.8 $\times 10^4$	3.2 \pm 1.2 $\times 10^1$
Nonupwelling	1.5 \pm 0.4 $\times 10^3$	5.7 \pm 0.8 $\times 10^1$	3.5 \pm 1.5 $\times 10^3$	2.7 \pm 0.8 $\times 10^1$
Fecal pellets				
Upwelling	1.1 \pm 0.6 $\times 10^4$	3.5 \pm 0.9 $\times 10^1$	4.6 \pm 0.9 $\times 10^5$	1.3 \pm 0.7 $\times 10^3$
Nonupwelling	8.4 \pm 2.9 $\times 10^3$	3.3 \pm 0.6 $\times 10^1$	3.6 \pm 0.7 $\times 10^5$	4.5 \pm 1.3 $\times 10^2$
Sarcodines				
Upwelling	2.3 \pm 1.0 $\times 10^2$	1.1 \pm 0.4 $\times 10^0$	6.4 \pm 2.7 $\times 10^3$	2.2 \pm 1.1 $\times 10^1$
Nonupwelling	2.2 \pm 0.8 $\times 10^2$	4.0 \pm 0.2 $\times 10^0$	3.5 \pm 1.0 $\times 10^3$	3.8 \pm 1.9 $\times 10^2$
Nonsarcodine protozoans				
Upwelling	3.8 \pm 3.7 $\times 10^4$	2.8 \pm 0.6 $\times 10^1$	1.2 \pm 0.3 $\times 10^4$	1.4 \pm 0.6 $\times 10^2$
Nonupwelling	2.1 \pm 1.6 $\times 10^3$	4.9 \pm 1.3 $\times 10^1$	2.3 \pm 2.3 $\times 10^2$	1.6 \pm 1.3 $\times 10^2$
Synechococcus				
Upwelling	1.6 \pm 0.9 $\times 10^6$	9.5 \pm 3.0 $\times 10^4$	Not available	4.5 \pm 3.1 $\times 10^1$
Nonupwelling	5.4 \pm 1.9 $\times 10^6$	3.1 \pm 1.3 $\times 10^5$		1.6 \pm 1.3 $\times 10^2$
Bacteria				
Upwelling	3.2 \pm 1.0 $\times 10^8$	3.2 \pm 1.1 $\times 10^8$	Not available	0.6 \pm 0.4 $\times 10^0$
Nonupwelling	5.4 \pm 4.0 $\times 10^8$	1.0 \pm 0.8 $\times 10^9$		1.6 \pm 1.3 $\times 10^1$

they detach and pass through the screen used to retain house fragments.

Generally, houses were enriched with respect to the surrounding water (Table 1). EFs ranged from 8 for bacteria to 1.7×10^3 for diatoms during nonupwelling periods. A two-way ANOVA or a Student–Newman–Keuls analysis (when data were not normally distributed) was applied to test whether the degree of enrichment of organisms on houses varied with season or year. Diatom and sarcodine enrichment differed significantly between seasons ($P < 0.05$). Statistical analyses also indicated that diatom enrichment on houses was significantly lower in 1992, an El Niño year, with an EF of 46, than in either 1990 (EF of 1.7×10^3) or 1991 (EF of 3.1×10^3) $P < 0.05$.

Microscopic examination of sediment trap material provided estimates of fluxes (No. m⁻² d⁻¹) of fecal pellets and organisms. Fluxes (Table 1) were calculated by dividing numbers by trap surface area, divided by the duration of individual sample collection periods (days) (Pilskaln et al. 1996). Fecal pellets showed little variability, with no statistically significant seasonal or yearly differences (ANOVA, $P > 0.05$).

To compare detritus from traps and houses, we calculated the numbers of fecal pellets and organisms per unit carbon (Table 2). Trap-measured carbon fluxes differed by about factor of two between upwelling and nonupwelling periods

(Pilskaln et al. 1996). On an organic carbon (OC) basis, no statistically significant differences between trap and house detritus were found for the concentration of diatoms, pellets, or sarcodines ($P > 0.05$, Mann–Whitney U -test), but differences were noted for ciliates and nonsarcodine protozoans ($P < 0.001$, Mann–Whitney U -test) (Table 3). A Student–Newman–Keuls test on house-associated particles and pellets showed no significant seasonal trends, and yearly values differed significantly only for diatoms ($P < 0.01$), with lower numbers in trap detritus during the El Niño year of 1992 (1.4×10^3 mg⁻¹ OC) than in 1990 (1.9×10^5 mg⁻¹ OC) or 1991 (2.2×10^5 mg⁻¹ OC).

House age—The ecological role of houses in midwater communities and house role in flux both depend on the length of time an individual house is occupied, or house age. (After the suspended houses are abandoned, they collapse and sink rapidly.) Average house ages were estimated using several independent methods. In the first, we used the abundance of particles on houses, particles with delivery rates that could be estimated. Three mechanisms deliver organisms or particles to houses: (1) sinking materials passively rain on them (the particle flux), (2) particles in surrounding water are actively pumped into the house by the larvacean, and (3) motile organisms immigrate to houses from surrounding waters. The rates of the first two processes can be

Table 2. Particle richness on houses and in traps (means \pm SE). Seasonal differences are presented although not statistically significant (OC, organic carbon).

Item class	House detritus (No. mg ⁻¹ OC; n = 56)		Trap detritus (No. mg ⁻¹ OC; n = 28)	
	Upwelling	Nonupwelling	Upwelling	Nonupwelling
Diatoms	2.4 \pm 1.5 \times 10 ⁵	3.6 \pm 1.1 \times 10 ⁴	1.2 \pm 0.6 \times 10 ⁵	4.5 \pm 1.6 \times 10 ³
Ciliates*	3.0 \pm 1.8 \times 10 ³	7.9 \pm 2.1 \times 10 ²	3.9 \pm 0.6 \times 10 ²	1.7 \pm 0.5 \times 10 ²
Fecal pellets	3.1 \pm 0.8 \times 10 ³	5.7 \pm 1.4 \times 10 ³	5.7 \pm 0.6 \times 10 ³	7.9 \pm 1.0 \times 10 ³
Sarcodines	8.8 \pm 2.8 \times 10 ¹	1.3 \pm 0.4 \times 10 ²	5.0 \pm 1.5 \times 10 ¹	4.7 \pm 1.2 \times 10 ¹
Nonsarcodine protozoans	5.1 \pm 4.5 \times 10 ³	1.1 \pm 0.7 \times 10 ³	1.6 \pm 0.5 \times 10 ³	5.2 \pm 1.6 \times 10 ¹

* Significant differences between houses and traps ($P < 0.01$, Mann-Whitney U -test).

estimated, whereas the third is currently not known. Combining the time it takes for the first two processes to deliver the observed particle loads provides a maximum house age, because immigration is neglected. That is, organisms such as ciliates and dinoflagellates that could migrate to the house may be misinterpreted as requiring additional time to collect via settlement and filtration. However, for nonmotile organisms, the first two (predictable) processes should give house age.

Fecal pellets best demonstrate delivery via the vertical particle rain, because their rain rate shows minimum variability (C.V. of 87% vs. 136–241% for other items) and they collect only through the first two, predictable processes (*see above*). Similarly, numbers of pellets per m² of house collection surface did not vary significantly between seasons or years, with a mean of 3.3×10^5 m⁻² for the inflated (detritus sampler) sampled houses we used for this calculation. Assuming that larvacean houses collect sinking material in proportion to their horizontal cross-sectional area (i.e. like sediment traps), their age is

$$\text{Age} = \frac{\text{No. pellets on houses (No. m}^{-2}\text{)}}{\text{Rain rate of pellets (No. m}^{-2}\text{ d}^{-1}\text{)}}$$

where rain rate is measured by the trap. By using only inflated, detritus sampler-sampled houses and pellet fluxes obtained from either corresponding sediment traps or mean pellet flux when paired sediment trap data were unavailable, estimates made by this method indicate houses are 1.1 ± 0.23 d old (mean \pm SE). A possible error is introduced if

Table 3. Time in days (mean \pm SE) required for larvaceans to accumulate the observed numbers of particles via passive sinking or active filtration by animal. Passive sinking rates are estimated from nearby sediment traps. Filtration is estimated from larvacean morphometrics and tailbeat frequency (*see text*). House age is estimated based on the simultaneous accumulation rates of the two processes.

Item class	Passive sinking (days)	Filtration by animal (days)	House age (days)
Diatoms	1.9 \pm 0.9	8.2 \pm 6.7	0.5 \pm 0.2
Ciliates	6.7 \pm 2.8	0.2 \pm 0.1	0.2 \pm 0.1
Fecal pellets	0.8 \pm 0.2	5.5 \pm 1.6	0.6 \pm 0.1
Sarcodines	2.3 \pm 1.1	1.4 \pm 0.8	0.7 \pm 0.5
Nonsarcodine protozoans	20 \pm 14	5.9 \pm 4.4	1.5 \pm 0.7

organisms on houses produce or consume pellets. To estimate the potential magnitude of such an error, using average numbers of metazoans on houses (Steinberg et al. 1994) and likely fecal pellet production rates (Corner et al. 1972; Paffenhoffer and Knowles 1979; Ayukai and Nishizawa et al. 1986; Butler et al. 1994), we determined that a maximum of half the pellets on houses could derive from residents, resulting in a two-fold overestimation of house age. Error in the opposite direction (i.e. causing underestimates of house age) may exist if some metazoans on houses consume pellets, a possibility suggested by Steinberg (1995). These errors do not appear large and may cancel each other to a degree.

Filtering by the larvacean is the second mechanism delivering particles to houses. Although the filtering rate of the giant larvacean has not been measured directly, it can be estimated. In oikopleurid larvaceans (the family to which *Bathochordaeus* belongs), Morris and Deibel (1993) found that rates can be predicted by tail length, width, and tail beat frequency. Based on our video measurements of these characteristics, we calculate a flow rate of ~ 2.8 ml s⁻¹, or ~ 250 liters d⁻¹. Items in the water stream drawn into the house are concentrated and consumed by the larvacean or adhere to house internal walls. Considering that a third of the particles in the entering water stream are retained by the house (Gorsky et al. 1984; data for diatom retention by house walls), that particle concentrations are those observed in the surrounding water (i.e. controls), and the water flow rate through the house, we can calculate the time required to collect the observed particles.

Table 3 shows the time required for houses to accumulate individual classes of items via passive sinking or via active filtration. It also shows the house age as a combination of these processes acting together; that is, observed numbers are divided by the hourly contribution expected from the detrital rain plus the filtration of the animal. Because total particle accumulation by larvaceans seems to be largely a function of passive sinking, differences in the estimate of particle retention by the animal do not greatly affect our house ages. Whether using one-half, one-third, or one-fourth as an estimate of particles retained by the larvacean, ages are still on the order of 1 d (0.6, 0.7, and 0.8 d, respectively). This age is a maximum, as noted above, if immigrants are present. Items usually are collected more rapidly by one mechanism than the other, and the combined processes supply houses in 1.5 d or less. (Below, we discuss additional

Table 4. Larvacean house contribution to water column biomass and potential contribution to total particle flux at 500 m (na, not available).

Item class	Water column	
	(%)	Particle flux (%)
Diatoms	0.05	17
Ciliates	0.13	200
Fecal pellets	0.34	11
Sarcodines	0.03	20
Nonsarcodine protozoans	0.65	1,164
Bacteria	0.001	na
<i>Synechococcus</i>	0.021	na

reasons why house age may be overestimated.) We consider the best estimate of house age to be the mean age estimated from ages derived from all item classes, i.e. 0.7 d (Table 4).

A second strategy for estimating house age uses the ratio of inflated to collapsed houses. For this estimate, we assume the ratio is approximately constant over time, although the absolute numbers of houses in the water can change. Constancy is expected if *Bathochordaeus* houses are normally used for about the same length of time before being discarded, if sinking rates of discarded houses remain about the same, and if vertical immigration or emigration of larvaceans in the 100–500-m stratum has not just occurred. Such vertical movements seem unlikely, because the observed species of *Bathochordaeus* appeared mostly restricted to the 100–500-m depth stratum (see Steinberg et al. 1994), where we made our inventory. Patchiness and even large local changes in abundances of larvaceans in the 100–500-m stratum would not affect the ratio and thus the age estimated by this method. Because in situ sinking rates of houses are known (avg of 800 m d⁻¹; Hamner and Robison 1992), the time of occupation can be calculated from field-observed ratios of occupied to collapsed houses during our study interval (366:141, or 72% inflated [occupied] and 28% collapsed [sinking] as follows:

$$\text{Age} = \frac{\text{No. occupied houses (sinking time)}}{\text{No. sinking houses}},$$

where the time a house spends sinking is equal to the average depth a house sinks within our depth stratum (i.e. bottom of stratum [500 m] – average depth in stratum [300 m] = 200 m) divided by house sinking rate (800 m d⁻¹), or 0.25 d (6 h). By this method, the average house age is 0.65 d (16 h), nearly the same age calculated by the particle accumulation method (see above).

Flux—When houses are discarded, they sink and transport their contents to depth, thus contributing to the overall rain of material through the water. Sediment traps at a nearby site measured flux but the contribution of houses to trap contents could not be determined directly because houses were usually not recognizable among the trap material. Thus, house flux was estimated indirectly by two different methods.

In the first method, we used house ages as determined by their particle loads. Here, the overall abundance of occupied, inflated houses is considered to be in steady state. That is,

when a house is abandoned and collapses, the larvacean builds another (Fenaux 1985). In steady state, the loss rate of collapsed houses from the stratum matches the production rate of houses, or

$$\text{Flux} = \frac{\text{No. inflated houses m}^{-2}}{\text{Age of inflated houses}}.$$

Using the average number of houses (4.6 m⁻²; C. H. Pilskaln pers. comm.) times the proportion inflated (i.e. 0.72) to calculate the number of inflated houses and the age estimated from the average time for item accumulation via filtration and passive sedimentation (0.70 d), we calculate a flux of 4.7 ± 7.8 houses m⁻² d⁻¹ (mean ± SD).

The second method for predicting house flux uses the average abundance of sinking houses times the proportion sinking (0.28) and their sinking rate—values determined directly from ROV observations.

$$\text{Flux} = \frac{\text{No. sinking houses m}^{-2}}{\text{Sinking time}}.$$

This method gives a flux of 5.2 ± 4.5 houses m⁻² d⁻¹ (mean ± SD).

The contribution of houses to individual classes of items in the observed particle flux, measured by the sediment trap, can now be calculated. Taking the average of our two estimates of house flux, i.e. 5 m⁻² d⁻¹, the flux of house-delivered particles and organisms is the numbers per house times the house flux. Table 4 presents the estimated percent contribution made by sinking houses to the overall trap-measured flux of items, as well as the likely contribution to populations in the water. Although items on larvacean houses represent a very small fraction of the numbers suspended in the water, the relative contribution of houses to the flux of particles is significant, with contributions always >10% and sometimes >100% for some items (Table 4). (Sometimes predicted fluxes exceed those observed in traps, i.e. for ciliates and nonsarcodine protozoans, as discussed below). A similar calculation that considers the average house OC (2.0 mg; C. H. Pilskaln pers. comm.), the OC flux at the site (68 mg OC m⁻²; Pilskaln et al. 1996), and the average house flux (see above) suggests that houses contribute ~15% of the OC flux at this site.

Trapping probability—Because the giant houses are relatively rare, single sediment traps may not collect them, especially during short deployments. If houses are undercollected by traps, overall material flux at the site may be underestimated when houses are very particle or carbon rich. This house contribution could explain why more items were observed in the sediment traps than we predicted (i.e. why estimated contributions to flux by houses are >100%; Table 4). The probability that a trap will incorrectly estimate particle flux, based on its collecting surface and the duration of collection time, can be calculated precisely. Our trap had a horizontal collecting surface of 0.05 m² and thus a 1 in 20 chance of collecting a house that settles through a square-meter area. In this model, house size is not considered directly in the calculation; collapsed houses settle like para-

chutes with small-diameter leading edges (Fig. 1B). We assumed that parachutes enter traps only if their leading edge falls within the trap cross-sectional area. We considered the probabilities of collecting the expected number of houses within a factor of 2 ($\pm 200\%$ of the flux). Based on the temporal and spatial characteristics of this distribution, the relative rarity of larvacean houses in the water, and the indeterminate number of houses that sank through the 400-m water column, probabilities were calculated based on a Poisson distribution (Sokal and Rolf 1969) using MINITAB statistics software.

To understand the scope of possible trap-collecting errors, we considered a broader range of possible particle rain rates. We also considered the effect of differences in the duration of trap collection periods and the consequences of using a small trap, the 0.0039-m² surface "MultiPIT" type (Martin et al. 1987) and a large 1.5-m² one (Honjo and Doherty 1988). When the predicted mean numbers of sinking houses exceeded 50 m⁻² d⁻¹, we used an approximation based on the normal distribution (Moses 1986).

The probabilities of successfully trapping houses within 200% of the correct number are presented in Fig. 2B. These results indicate that, given average numbers of houses observed, the 0.05-m² trap should normally collect the correct number of houses within a factor of 2 for 75% of the time during our 14-d collection period. If a smaller trap had been used (Fig. 2A), however, even a 30-d deployment would have been insufficient to collect the correct number of houses within a factor of 2 for 70% of the time, whereas the larger trap could easily accomplish this in a 1-week period (Fig. 2C). The distribution of probabilities is not symmetrical about the mean, with house flux usually underestimated.

Discussion

The mucous house of *Bathochordaeus* represents a near end-member in the size of naturally occurring aggregates. *Bathochordaeus* aggregates are particularly interesting because they occur in subsurface waters, where particle abundance and size is expected to be lower than in surface waters. *Bathochordaeus* and some other larvaceans produce centimeter and larger feeding structures in many subeuphotic environments in the Atlantic, Pacific, and Mediterranean, including those underlying oligotrophic waters (Barham 1979; Youngbluth 1984; Laval et al. 1989; Davoll and Youngbluth 1990). Other large zooplankton-derived aggregates have been observed at considerable depth, including those produced by foraminifera (Alldredge and Youngbluth 1985), the worm *Poeobius* (Uttal and Buck 1996), and thecosomateous pteropods (Youngbluth 1984). The presence of large aggregates at depths within and below the main thermocline may be related to reduced turbulence in the water column, which can break apart fragile aggregates (Alldredge et al. 1990; Riebesell 1992). The thermocline may provide the most favorable mix of physical stability with proximity to a food source.

What special role might large mesopelagic aggregates serve if they are a widespread phenomenon? Ecologically, distributions of organisms on aggregates may follow prin-

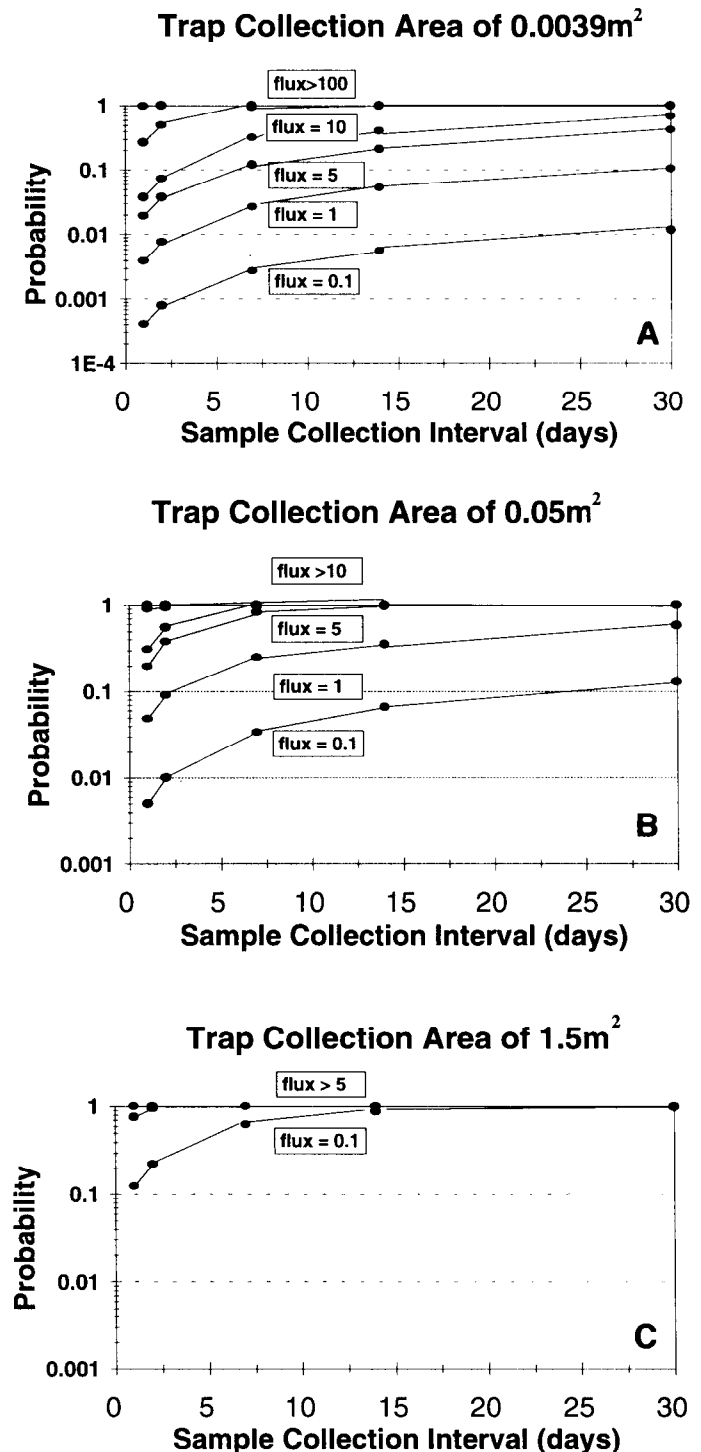


Fig. 2. Probabilities of accurately trapping larvacean houses within a factor of 2 using three commonly deployed sediment traps. Probabilities are calculated on a Poisson distribution for fluxes ranging from 0.1 to >100 m⁻² d⁻¹ and for deployment periods of 1–30 d. A. Trapping probabilities for sediment traps having cross-sectional collection area of 0.0039 m². B. Probabilities for sediment traps used in this study having cross-sectional collection areas of 0.05 m². C. Trapping probabilities for traps having cross-sectional collection area of 1.5 m².

ciples described for island biogeography. As relatively large substrates (compared with the more typical millimeter-sized marine snow), the houses may host more species because of the positive correlation between species number and habitat size. Certainly, large predators that forage on substrate-associated prey might find only large aggregates to be sufficiently food rich (see Steinberg et al. 1994; Steinberg 1995; Silver et al. 1995). Our ROV collections confirm the presence of zooplankton (Steinberg et al. 1994), microorganisms, and detrital particles on the houses (Fig. 1, Table 1).

Another biological role of such aggregates could be to provide important foraging substrate by collecting rapidly sinking items that otherwise pass quickly through the water. Most of the phytoplankton, procaryotes, and protozoa studied here are concentrated on houses (Table 1) enriched 1–3 orders of magnitude over populations in the surrounding water. Evidence for the midwater utilization and reworking of sinking particles is widespread (e.g. Urère and Knauer 1981) and large suspended aggregates could provide important feeding centers (Steinberg 1995).

In Monterey Bay, the deep-water houses are not quantitatively important for populations of microorganisms because houses are relatively rare, averaging ~1 per 100 m³ (Pilskaln et al. in prep.) House associates contribute <1% to the total plankton (Table 4). Giant houses, however, may be important habitats for particular species of associated organisms. Other studies on aggregates indicate that specialized communities occur here: bacteria (DeLong et al. 1993), small flagellate protozoans (Patterson et al. 1993), larger sarcodine protozoans (Gowing 1986), and copepods (Ferrari and Steinberg 1993).

On an OC basis, the giant houses are typical mesopelagic detritus. Concentrations of pellets, diatoms, and sarcodines on the *Bathochordaeus* detritus, although variable, do not differ significantly from those in trap-collected detritus (Table 2), with the exception of motile ciliates and nonsarcodine protozoans (often mostly dinoflagellates).

Role of giant aggregates in the vertical particle flux—By scavenging slowly sinking particles, giant aggregates could enhance sinking rates or, alternatively, slow the sinking rates of faster particles (Trent 1985). Our data indicate that the protozoans (ciliates, sarcodines, and nonsarcodines) accumulate on houses primarily through larvacean filtering—feeding draws in organisms from surrounding waters, and thus most were suspended or slowly sinking. In contrast, it appears that the giant houses acquire most of their diatoms and fecal pellets by passive settlement onto house surfaces (Table 3).

The expected contribution of house-associated organisms to the vertical particle flux is significant (Table 4). Despite the low standing crop of houses in the water column (~1 per 100 m³), the house presence throughout the 100–500-m depth stratum and their relatively frequent replacement rate (about once per day) result in a substantial house flux of 5 m⁻² d⁻¹ (see results). Thus, giant houses should contribute 10–100% of the organisms and fecal pellets observed in traps, thereby playing a much more important role in the vertical transport of organisms and particles than they do as community centers in the water column. By a similar cal-

ulation, their contribution to the overall carbon flux appears modest, ~15% of the sinking detritus at 500 m.

Traps as collectors of rare particles—There are a number of reasons to expect that the giant houses may be undersampled by sediment traps. First, many traps (including ours) contain entry baffles that may prevent them from entering. Second, cone-shaped traps might scavenge houses on their sloping sides, allowing the material to decompose or wash out (Laws et al. 1989). Other potential errors related to mooring line motions and trap hydrodynamics have been discussed (see Gust et al. 1994). Possibly owing to these or other reasons, predictions of flux based on particle numbers in the water and expected sinking rates differ from field-measured values of flux (Asper et al. 1992). Another error, that can be predicted quantitatively is the probability that a trap of limited size will capture a relatively rare particle, especially over a short deployment. This error has received scant attention in the literature, although Goldman (1993) described the difficulty of collecting large, spatially rare phytoplankton aggregates that may contribute substantially to carbon sedimentation rates.

The efficiency of a sediment trap depends on its collecting surface and duration of deployment (as well as hydrodynamic and other characteristics not considered here). Our predictions regarding the potential role of giant houses to total organism flux were based on flux estimates of 5 houses m⁻² d⁻¹ (see results). Our 0.05-m² trap should collect 1 in 20 of the houses that sink per square meter. Thus, most houses would not enter a trap. (Less likely, however, traps can also overcollect rare items; for example, a rare, large particle obtained during a short deployment could lead to erroneously high flux estimates.) This same 0.05-m² sediment trap, however, would usually correctly estimate house flux within a factor of 2, in a 2-week deployment (Fig. 2B).

Because traps have become a primary tool for measuring vertical mass flux, we consider it useful to calculate the ability of a variety of traps to collect the correct number of rare particles such as the giant larvacean houses. Traps with very small surface areas, e.g. the typical 0.0039-m² MultiPIT design traps used in the VERTEX and some JGOFS observations (Knauer et al. 1990), would usually not sample the correct numbers of the large Monterey Bay aggregates over deployments as long as even a month (Fig. 2A). In contrast, our calculations predict that a trap with 1.5-m² surface (Honjo and Doherty 1988), also commonly used in JGOFS and other studies (Fig. 2C), is nearly certain to collect the correct number within a factor of 2 over deployments of only a few days.

Are rare but relatively important contributors to mass flux common in pelagic environments? There is evidence from the literature that pteropods (Fabry and Deuser 1992; Deuser and Ross 1989) and foraminifera (Deuser and Ross 1989), which contribute 10–20% of the sinking CaCO₃ at three particular sites, have fluxes of <100 m⁻² d⁻¹, within the problematic range for small traps (Fig. 2A). Likewise, radiolarians can contribute up to one-fourth of the silica flux while numbering ≤100 m⁻² d⁻¹ (Bernstein et al. 1990). Our calculations indicate that deployments <2 weeks for MultiPIT traps pose collection difficulties for particles less frequent

than $10 \text{ m}^{-2} \text{ d}^{-1}$, whereas the larger 1.5-m^2 traps are good collectors of all but the extremely rare sinking particles. Our calculations address the problems of collecting rare sinking particles using a single trap of variable collecting surface. Possibly such an error contributes to the carbon imbalance noted by Michaels et al. (1994) at the Bermuda time-series site. The authors suggested that the most consistent explanation for the imbalance is a serious underestimate by sediment traps, which in that case were small MultiPIT collectors deployed for relatively short periods. The presence of rare but carbon-rich aggregates could explain the imbalance, although our calculations (above) suggest this error is a modest one for carbon in the Monterey Bay system. Another approach, the use of the $^{234}\text{Th} : ^{238}\text{U}$ disequilibrium, which provides an estimate of carbon export from surface waters (Coale and Bruland 1985, 1987), likewise suggests that sediment traps may under- or overcollect to varying degrees (Buesseler 1992). This discrepancy has been attributed to the design and hydrodynamic attributes of individual traps. Our study indicates that the frequency and quantitative importance of individual sedimenting particles also play a role in influencing the discrepancy between the observed disequilibrium and the measured flux. The rare but significant signal of a large aggregate may be an example of a potentially misleading, stochastic event that can lead to errors in interpreting patterns. The chance collection of a rare but carbon-rich aggregate is especially problematic because its presence could be interpreted as a temporal or spatial signal. Because of the costs of oceanographic sampling gear and shiptime, it is particularly important that researchers recognize that enriched, often sizable particles exist and that, although rare, they pose special sampling problems.

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