

Floating and algal rafting as potential dispersal mechanisms in brooding invertebrates

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ABSTRACT: Many benthic marine invertebrates brood their young to a crawl-away stage and thus lack a swimming dispersal phase on their life histories. Results of flotation experiments on brooding infaunal tanaids, amphipods and bivalves from intertidal habitats show that many of these animals, especially small individuals, may remain suspended on the water surface from a few hours to a few days, indicating that floating is a potential dispersal mechanism for these species. Because animals suspended on the water surface are likely to contact algae or logs to which they can attach, floating also increases the probability of dispersal by rafting. The presence of eel grass reaching the surface initially accelerated the rate at which organisms returned to the bottom, but did not alter the final results. The non-wetting characteristic of the crustacean species studied decreased with time, so that most of the animals were eventually able to resubmerge. In addition, data on abundance of brooding organisms in algal mats on a mudflat and in drift algae suggest export of algae and associated fauna, including several brooding species, from the mudflat occurs during spring tides. With respect to dispersal by floating or rafting, small adult size probably contributes to the evolutionary success of shallow-water brooders. The increasing representation of brooding species in benthic communities at higher latitudes is considered with respect to Thorson's (1950) hypothesis that low temperatures (slow development rate) and short periods of algal productivity at high latitudes limit planktotrophy and favor non-pelagic direct development. Two alternative hypotheses are suggested: (1) the geographic distribution of brooding species is correlated with rafting opportunities; (2) the abundance of potential pelagic predators on planktotrophic larvae at high latitudes selects for brooding or lecithotrophy in less fecund species and, conversely, intense benthic predation pressure at low latitudes restricts brooding and favors planktonic larval forms.

INTRODUCTION

Dispersal capability, whether a morphological or behavioral adaptation, is a major component in the life history evolution of most organisms. Among benthic invertebrates, dispersal is typically accomplished by the inclusion of a swimming larval phase in the life history. In contrast to this pattern, benthic peracarid Crustacea (most Amphipoda, Isopoda, Tanaidacea, Cumacea) brood their young to a crawl-away stage, thus lacking a swimming dispersal phase in their life histories. Similarly, various species ranging from cnidarians (e.g. the anthozoan *Epiactis prolifera*) to echinoderms (e.g. the asteroid genus *Leptasterias*, the holothurian *Leptosynapta clarki* and the ophiuroid *Amphipholus squamata*) brood their offspring to a

benthic stage (Himmelman et al. 1982, Kozloff 1983). An analogous situation occurs among those gastropods, e.g. *Littorina sitkana* (Behrens 1971) and *Nucella emarginata* (Morris et al. 1980, Palmer 1984), in which crawl-away juveniles hatch from egg capsules cemented to the substratum.

Many of these species have broad geographic distributions in spite of not having a specialized dispersal phase. This study focuses on one such species, *Leptochelia dubia* (Kroyer 1842) (Tanaidacea), which has a cosmopolitan distribution (Miller 1968, Morris et al. 1980), and 2 potential dispersal mechanisms, floating and rafting. Other species studied were the amphipod *Pontogeneia* sp. cf. *P. ivanovi* Gurjanova (an undescribed north-temperate species of probable Arctic origin: Staude pers. comm.), the leptostracan *Nebalia pugettensis* (Clark 1932) (Puget Sound to Baja California: Morris et al. 1980), the bivalve *Transennella tantilla* (Gould 1853) (Alaska to Baja California: Kozloff

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1983), the sea star *Leptasterias hexactis* (Stimpson 1862) (Alaska to California: pers. obs., Morris et al. 1980), and the small brittle star *Amphipholus squamata* (Delle Chiaje 1829) (nearly worldwide: Morris et al. 1980). Each of these broods and releases benthic larvae or juveniles directly into the adult habitat. The crustaceans are capable of swimming but they normally burrow or build tubes in soft-bottom habitats and apparently only enter the water column when disturbed.

Another aspect of the study was to determine if those species with non-wetting (hydrophobic) exoskeletons, such as *Pontogeneia* sp. cf. *P. ivanovi*, *Nebalia pugettensis* and especially *Leptochelia dubia*, became helplessly trapped when suspended on the water surface and eventually perished, and whether animals suspended on the surface encounter objects to which they could attach and crawl down to overcome the hydrophobic forces.

METHODS

This research was conducted at the Friday Harbor Laboratories, San Juan Island, Washington, May to August 1982 and July to August 1984.

Floating. *Pontogeneia* cf. *ivanovi* was collected from False Bay by sieving sand in the field, and transported to the laboratory in containers of seawater. For *Leptochelia dubia*, *Nebalia pugettensis* and *Transennella tantilla*, sand was collected from False Bay and taken to the laboratory for sorting. *L. dubia* and *N. pugettensis* were collected by agitating the sand with a probe, which resulted in animals becoming suspended on the surface of the water (Highsmith 1983). *T. tantilla* was collected with an 0.5 mm sieve.

The floating experiments were conducted by suspending animals on the surface of the water in 0.95 l plastic freezer containers. To permit water circulation, 2 large holes were cut on opposite sides of the containers and covered with 355 μ m Nitex. The containers were placed in a seawater table with the water level approximately 2 cm lower than the height of the containers. A thin layer (5 to 10 mm) of 0.5 mm sieved sand sufficient for tube building (*Leptochelia dubia*) or burrowing (other species) was placed in the bottom of each container. Small eel grass plants (*Zostera marina*) were placed in half of the containers so that 3 blades reached and floated on the surface. For experiments with juvenile tanaids ($\bar{x} = 1.51 \pm 0.31$ mm length) and bivalves (0.5 to 0.8 mm length), 100 ml plastic containers were used.

The crustacean species, which all have non-wetting exoskeletons, were transferred gently to the water surface in the experimental containers using a probe. The bivalves were suspended by resubmerging the collect-

ing sieve, which resulted in a number of the animals floating. They were then transferred, while still floating, to the experimental containers. Juvenile *Transennella tantilla* were suspended by placing them in a shallow bowl of water, tilting it until the bivalves were exposed, and then levelling the bowl.

The number of animals on the surface of the water in each container was recorded periodically. The sand in the bottom of each container was sorted and sieved at the end of the experiment and the number of live animals present recorded.

Rafting. A thick algal mat composed primarily of *Ulva* and *Monostroma* spp. develops each year on the mudflat at Mitchell Bay with peak cover in late spring to mid summer (Woodin 1974). Eight 0.01 m² random quadrats in the algal mat were collected in order to estimate the density of *Leptochelia dubia* present. The algae were cut at the margin of the quadrat and placed in plastic bags for later sorting at the laboratory. In addition 12 0.25 m² algal quadrats were collected to estimate the abundance of *Amphipholus squamata* and *Leptasterias hexactis*.

Twenty drift samples were collected from Mitchell Bay in buckets or plastic bags on rising spring tides with the use of a row boat. Four additional samples, originating from Beaverton Cove, were collected in front of the Friday Harbor Laboratories. After sorting, the algae in each sample were squeezed gently to remove excess water and weighed.

RESULTS

Floating

The tanaids *Leptochelia dubia* were able to survive on the surface and to resubmerge over periods of a few hours to a few days (Fig. 1, 2, 3; Table 1). These data suggest that the hydrophobic nature of the exoskeleton is actively maintained rather than an intrinsic skeletal characteristic. In addition, dead or preserved animals are not hydrophobic. Males (Fig. 1) tended to remain on the water surface for a shorter period of time than females (Fig. 2) or juveniles (Fig. 3). The shorter floating time of the males could be due to differences in morphology (see Highsmith 1983, Highsmith & Mace unpubl.), swimming capability, or secretion of a non-wetting substance. The juveniles resubmerged at about one-half the rate of the females, perhaps due to their small size relative to surface tension forces.

The presence of *Zostera marina* accelerated the initial rate at which male and female tanaids resubmerged (Fig. 1, 2) but there was no difference in the mean proportion of animals floating at the end of the experiments (Mann-Whitney U-tests: females, $P=0.35$;

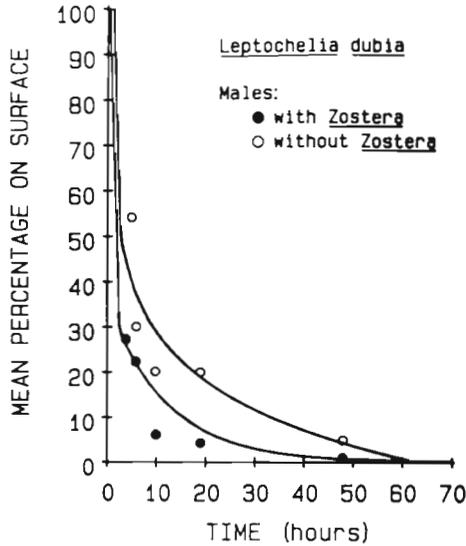


Fig. 1. *Leptocheilia dubia*. Resubmergence rate of floating males with and without eel grass *Zostera marina*. Mean percentages are for 6 replicates per treatment. Containers with eel grass: N = 62; containers without eel grass: N = 58. See Table 1

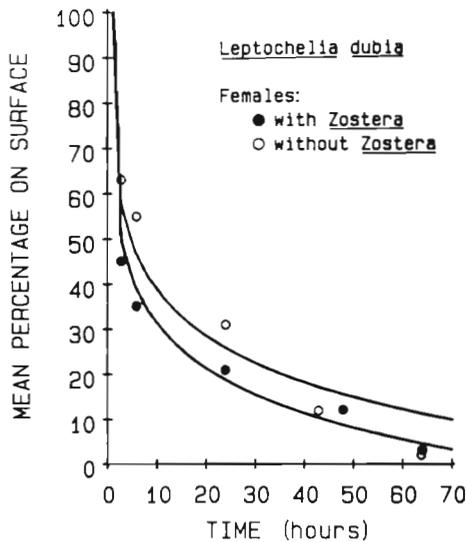


Fig. 2. *Leptocheilia dubia*. Resubmergence rate of floating females with and without eel grass *Zostera marina*. Mean percentages are for 6 replicates per treatment. N = 90 for each treatment. See Table 1

males, $P=0.29$). Eel grass had no effect on resubmergence of juveniles (Fig. 3).

Nearly all of the tanaids that resubmerged were alive (Table 1) and had constructed tubes in the sand. This suggests that being 'trapped' on the surface by the non-wetting feature of the exoskeleton may result in dispersal rather than mortality *per se*. Being carried to an unsuitable location, contact with a predator, or being stranded by an ebbing tide are, however, risks

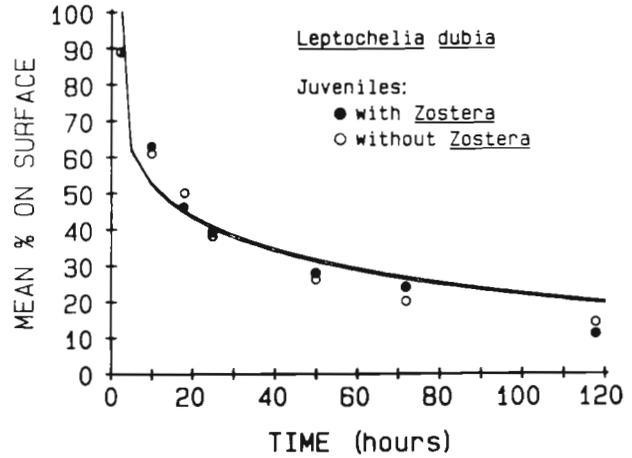


Fig. 3. *Leptocheilia dubia*. Resubmergence rate of floating juveniles with and without eel grass *Zostera marina*. Mean percentages are for 6 replicates per treatment. N = 90 for each treatment. See Table 1

Table 1. Percentage of animals alive, dead or not found at termination of flotation experiments. Bottom = in sand at bottom of container. Surface = on surface of water. Number of containers in parentheses

	Without <i>Zostera</i>	With <i>Zostera</i>
<i>Leptocheilia dubia</i>		
Females	N = 90 (6)	N = 90 (6)
Live:		
bottom	96	84
surface	2	2
Dead	2	11
Not found	0	2
Males	N = 58 (6)	N = 62 (6)
Live:		
bottom	86	90
surface	0	0
Dead	12	10
Not found	2	0
Juveniles	N = 90 (6)	N = 90 (6)
Live:		
bottom	69	64
surface	14	14
Dead	3	3
Not found	13	18
<i>Transennella tantilla</i>		
Adults	N = 99 (7)	N = 90 (6)
Live:		
bottom	87	93
surface	11	6
Dead	1	1
Not found	1	0

associated with floating (Highsmith 1983). The juvenile *Leptocheilia dubia* ingested floating colored particles (visible through the body wall) while on the water surface, suggesting that they could survive for a

considerable time. Over 10% of the juveniles were still floating after 5 d (Fig. 3).

Adult *Pontogeneia* cf. *ivanovi* are larger and much stronger swimmers than the tanaids. Within the first hour, 46% of the large ($\bar{x} = 9.9 \pm 1.1$ mm length) amphipods had returned to the bottom (Fig. 4). The

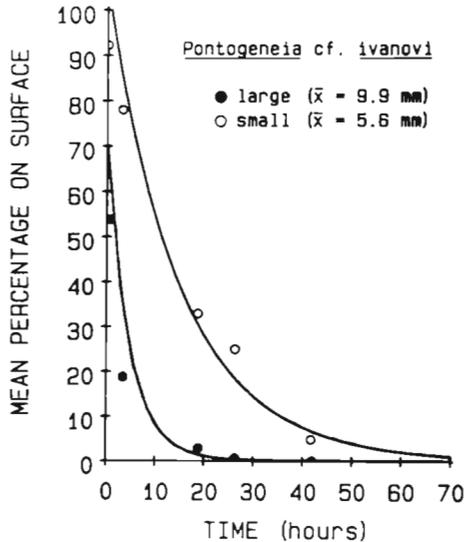


Fig. 4. *Pontogeneia* sp. cf. *P. ivanovi*. Resubmergence rate of floating specimens. Mean percentages are for 6 replicates for small individuals and 4 replicates for large individuals. Large individuals: N = 37; small individuals: N = 55

resubmergence rate of small ($\bar{x} = 5.6 \pm 0.98$ mm length) *P. cf. ivanovi* was slower and similar to that of female tanaids (Fig. 2). This difference appeared to be due to the superior swimming ability of the larger animals, which enabled them to overcome the hydrophobic forces. The rate for the smaller animals, again, suggests that the non-wetting characteristic of the exoskeleton is actively controlled (preserved *P. cf. ivanovi* do not have non-wetting exoskeletons).

Nebalia pugettensis has a less hydrophobic exoskeleton than the other species. The nebalians were difficult to suspend on the surface for more than a few moments, so only 1 container of 10 specimens was used. Only 3 remained on the surface after 15 min, although 2 were still on the surface at 9 h. At 18 h, 4 individuals were on the surface, 1 of which was dead. Because some animals were returning to the surface, the experiment was terminated.

Like the tanaids, *Transennella tantilla* initially resubmerged more rapidly in containers with eel grass, and a higher proportion of juveniles than of adults remained suspended for a longer period of time (Fig. 5). All but 2 or 3 of the specimens were alive after 10 d, including those still on the surface (Table 1). The bivalves usually had their siphons extended, so were probably able to feed while suspended.

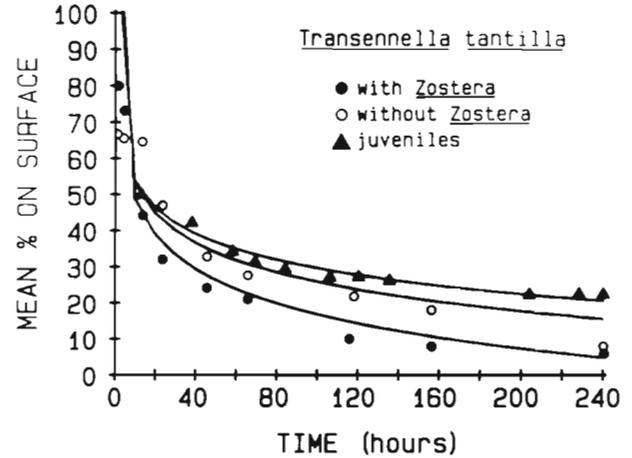


Fig. 5. *Transennella tantilla*. Resubmergence rate of floating adults with and without *Zostera marina* and juveniles without *Z. marina*. Mean percentages are for 6 replicates for adults with eel grass and for juveniles and for 7 replicates without eel grass. Adults with eel grass and juveniles: N = 90; adults without eel grass: N = 99. See Table 1

Rafting

The density of *Leptochelia dubia* in the algal mat, exclusive of the underlying substratum, was 14200 m⁻² (Table 2) and that of *Amphipholus squamata* was 484 m⁻² (Table 2). Woodin (1974) found 26680 *L. savignyi* (= *L. dubia*) m⁻² in the sediment at this location. The

Table 2. *Leptochelia dubia*, *Amphipholus squamata* and *Leptasterias hexactis*. Abundance m⁻² in the algal mat at Mitchell Bay, San Juan Island

	\bar{X}	SD	Range	N
<i>Leptochelia dubia</i>	14200	6690	3300-22700	8
<i>Amphipholus squamata</i>	484	437	0-1416	12
<i>Leptasterias hexactis</i>	0.33	1.15	0-4	12

density of the brooding sea star *Leptasterias hexactis* was very low (Table 2). Normally, *L. hexactis* is found in the rocky intertidal or in eel grass beds (Kozloff 1983). Also, the distribution of *L. hexactis* may be very patchy. Six individuals (mean diam. 2.3 ± 1.5 cm, range 0.26 to 5.0) were found in a limited area with just a few minutes of searching and 2 additional sea stars crawled onto the outside of a plastic collecting bag left on the mud flat for approximately 1 h.

The number of organisms found in the drift-algae samples was not correlated with sample wet weight (Table 3; Spearman rank correlation, $r = 0.004$). Samples that contained members of a group usually con-

Table 3. Weight of and number of animals present in samples of drift algae (mostly *Ulva* and *Monostroma*). 'Other' includes nemerteans, nematodes, *Mytilus edulis*, *Nebalia pugettensis*, *Cancer productus*, holothurians and *Amphipholus squamata*; number of *A. squamata* in parentheses

Algal wt (g)	Amphipods	Tanaids	Shrimp	Polychaetes	Gastropods	Other	Total
Mitchell Bay							
95	2	0	1	4	2	0	9
95	68	1	1	41	4	5	120
100	15	0	0	9	2	2	28
100	17	0	0	10	4	4	35
103	40	3	0	31	3	7 (2)	84
105	39	0	0	24	3	6 (2)	72
110	20	0	0	5	0	2	27
117	43	0	0	17	7	2	69
185	3	0	0	0	3	0	6
185	2	0	0	2	1	0	5
195	0	0	0	0	0	0	0
195	3	0	0	0	0	0	3
275	0	0	0	1	0	0	1
280	3	0	0	35	0	0	38
285	0	0	1	0	3	0	4
290	10	5	1	3	0	0	19
350	23	20	0	31	0	8 (3)	82
375	326	28	13	19	4	12 (2)	402
455	2	12	0	8	2	1 (1)	25
580	0	0	2	3	5	4	14
Beaverton Cove							
398	12	0	1	1	22	0	36
412	10	0	0	0	15	1	26
572	18	5	1	3	82	9	118
686	0	3	0	8	51	2	64
Total	656	77	21	255	213	65	1287
\bar{X}	27	3	1	11	9	3	54
\bar{X}^*	36 (18)	10 (8)	3 (8)	13 (19)	13 (17)	5 (14)	56 (23)

* Means for samples (N in parentheses) actually containing members of the group

tained several to many individuals. Amphipods were the most abundant group and included *Ampithoe lacertosa*, *Aoroides* sp., *Pontogeneia (rostrata ?)*, and *Melita (desdichada ?)*. In 11 of the samples, the number of amphipods brooding was determined. None in 3 samples, 5% in 3 samples, 33% in 2 samples and 10, 15 and 17% in 1 sample each were brooding.

Polychaetes were also abundant, occurring in all but 5 of the samples (Table 3). The most common species was *Ophiodromus pugettensis* (Johnson 1901) (Hesionidae) followed by the nereid *Platynereis bicanaliculata* (Baird 1863), which uses the algae for tube building as well as feeding (Woodin 1974). Other polychaetes included *Exogone lourei* Berkeley & Berkeley 1938 (Syllidae), *Harmothoe imbricata* (Linnaeus 1766) (Polynoidae), *Eupolyornia heterobranchia* (Johnson 1901) (Terebellidae), and unidentified lumbrinerids, eunicids and phyllodocids.

One-third of the drift samples contained from 1 to 28 *Leptochelia dubia* (Table 3), most of which were adult

females (Table 4) with a mean length of 3.35 ± 0.82 mm. Seven females were brooding. Had the samples been collected a few weeks earlier or later, a

Table 4. *Leptochelia dubia*. Number and sex collected from drift algae (Table 3). Number of females brooding in parentheses

Sample wt (g)	Females	Males	Juveniles
Mitchell Bay			
95	1	0	0
103	2	1	0
290	2 (1)	2	1
350	20 (3)	0	0
375	26	1	1
455	11 (2)	0	1
Beaverton Cove			
572	2	2	1
686	2 (1)	1	0

much higher proportion of the females would have been brooding (Highsmith unpubl.). The low percentage of males is characteristic of *L. dubia* populations (Highsmith 1983).

Gastropods were considerably more abundant in the Beaverton Cove samples, possibly because the substratum is more gravelly than at Mitchell Bay. At both locations members of the genus *Lacuna* were predominant (88%). Other species included *Margarites pupillus* (Gould 1849) and *Littorina sitkana* Philippi 1845.

Other animals included 10 *Amphipholus squamata*, 1 *Leptosynapta clarki* Heding 1928, 2 juvenile *Cancer productus*, 4 nemerteans (2 *Tetrastemma candidum* and 2 *Zygonemertes virescens*), 1 *Nebalia pugettensis* and a few nematodes and flatworms.

Of the above animals found on the drifting *Ulva* and *Monostroma*, all the amphipods, *Leptochelia dubia*, *Exogone lourei*, *Amphipholus squamata*, *Leptosynapta clarki* and *Nebalia pugettensis* brood their young to a crawl-away stage. In addition, *Littorina sitkana* hatch from attached egg masses as benthic juveniles.

DISCUSSION

Floating

The literature on flotation as a dispersal mechanism for benthic, brooding invertebrates appears to be limited to the small bivalve gem clam *Gemma gemma* (Sullivan 1948, Bradley & Cooke 1959, Sellmer 1967, Carriker, cited in Sellmer 1967). Sullivan (1948) collected juvenile *G. gemma* in plankton tows, Carriker found *G. gemma* in plankton traps placed from 0.25 to 1.5 m off the bottom, and Sellmer (1967) reported their occurrence in the water just above the sediment. These findings suggest that gem clams, which are similar in size and shape to *Transennella tantilla*, are dispersed by wave action and currents (Bradley & Cooke 1959, Sellmer 1967), especially if algal tufts occur on the shells (Bradley & Cooke 1959). Other, non-brooding bivalves may disperse partially or redisperse by drifting with the aid of threads similar to byssal threads (Sigurdsson et al. 1976, Lane et al. 1982, 1985), while the freshwater bivalve *Corbicula fluminea* secretes a mucous strand that results in drifting of adults in currents (Prezant & Chalermwat 1984). Nelson (1925) reported that *Mytilus edulis* post-larvae were able to remain pelagic by secreting a gas bubble into the mantle cavity. None of these mechanisms was observed in *T. tantilla*.

Adult tanaids are occasionally collected in plankton nets (Smith 1977), as are other peracarids (Watkin

1941, Colman & Segrove 1955, Jansson & Kallander 1968, Williams & Bynum 1972). Infaunal haustoriid amphipods sometimes enter the water column for unknown reasons, perhaps disturbance or limited food supply, and may be redistributed by drifting in tidal currents before returning to the bottom (Grant 1980). Amphipods were found on 99% of 379 offshore buoys, isopods on 25% and tanaids, including *Leptochelia dubia*, were found on less than 4% (Miller 1968). These occurrences might be due to flotation but could be due to rafting, swimming or colonization by benthic individuals living near the anchor. Following a storm, the abundance in the water column of benthic amphipods and other infauna was much greater than before the storm (Dobbs & Vozarik 1983). Some species in the water column samples did not occur locally, suggesting storm transport of animals over distances on the order of kilometers.

Among species with egg capsules and crawl-away juveniles, floating occurs in the gastropod *Hydrobia* (Newell 1964, Anderson 1971, Little & Nix 1976, Levinton 1979), resulting in local dispersal of adults.

Floating would seem to be a more likely dispersal mechanism for brooding invertebrates with non-wetting exoskeletons than for those without, although *Transennella tantilla* tended to float longer than *Leptochelia dubia* in the laboratory experiments (Fig. 5). In *L. dubia*, the non-wetting characteristic appears to be an active process which can be halted to permit resubmersion. Because some pelagic crustaceans have hydrophobic exoskeletons and the majority of *L. dubia* individuals probably do not ever contact the surface of the water, non-wetting exoskeletons and hence floating may be a coincidence of some other aspect of these organisms' biology.

The experiments in this study indicate that floating is a potential dispersal mechanism for *Leptochelia dubia*, *Pontogeneia* cf. *ivanovi* and *Transennella tantilla*. Small individuals and juveniles remained suspended on the water surface the longest (Fig. 3, 4 & 5) and are hence more likely to be dispersed in this manner, although one would predict that adults, especially brooding females, would be more successful colonizers.

One possible outcome of floating is that it provides an opportunity for animals to raft. Floating material is usually concentrated by wind and currents into drift lines. Floating animals could thus well come in contact with floating algae or logs within a few hours or days. Floating *Leptochelia dubia* will often clutch at any object with which they come in contact (own obs.) and *Transennella tantilla* is capable of attaching to objects with byssal threads. Thus, floating may serve as a dispersal mechanism in itself, but also provide the opportunity for rafting.

Rafting

It is commonly assumed that animals are frequently dispersed by rafting on algae (e.g. Soot-Ryen 1960, Fell 1967, Miller 1968, Dell 1972, Arnaud et al. 1976, Gerlach 1977, Simpson 1977, Vermeij 1978, Pearse 1979, Averincev 1980). To be sure, many brooding organisms, including amphipods, isopods, tanaids and cumaceans, inhabit attached algae (Colman 1940, Mukai 1971, Gunnill 1982, Ojeda & Santelices 1984) and are, hence, potential rafters, as detachment or fragmentation of algae is commonplace (Norton & Mathieson 1983). Quantitative data, however, are rather sparse (Scheltema 1977). Mortensen (1933) found the South African sea star *Asterina exigua* at the mid Atlantic island of St. Helena and concluded that it had rafted on kelp because this species has direct development. Further, Arnaud et al. (1976) found a South African kelp species drifting near St. Helena, a straight-line distance of over 3000 km from Cape Town, with 14 invertebrate species living on it. However, the authors suggested that very few species originating from South Africa successfully colonize St. Helena because of the different environmental regimes.

Birkeland (1971) reported that the gastropod *Searlesia dira*, which hatches as a crawl-away juvenile, and the brooding seastar *Leptasterias* spp. were abundant on Cobb Seamount, 450 km from the Washington (USA) coast. Algae and driftwood were observed floating over the area and Birkeland (1971) suggested that both species had colonized the seamount by rafting.

In the Antarctic, a high proportion of benthic invertebrate taxa brood or produce egg capsules from which benthic juveniles hatch, yet most species are widely distributed (Dell 1972, Simpson 1977, Pearse 1979, Picken 1980). All four of these authors suggest algal rafting as a dispersal mechanism and Dell (1972) posits that a brooding female is a better colonist than a larva. Some species live on or around algae and are probably rafted routinely (Dell 1972, Simpson 1977). How the other species disperse, on drift algae or by other means, e.g. anchor ice (Dayton et al. 1970), is uncertain.

Although corals normally have a dispersal phase in their life histories, adult colonies may be transported great distances as a result of larval settlement on floating objects, such as pumice (Jokiel 1984). The adults may colonize new locations or they may release gametes or larvae at widely separated locations while rafting.

In the present study, no correlation was found between the wet weight of the drift algae and the number of invertebrates present (Table 3), although other studies have shown such a correlation (Thorhaug

& Roessler 1977, Gore et al. 1981, Stoner & Greening 1984). One observation that may account for the lack of correlation in this study is that clean, bright-green samples had very few animals whereas the oldest-appearing and most sediment-laden algal samples had the largest numbers of animals. The clean samples probably represented recent algal growth in the upper layers of the mat that had not yet been colonized to any degree by benthic invertebrates from the sediment below. This is probably why *Leptochelia dubia* and *Amphipholus squamata* were not as abundant in the drift samples as expected from the densities found in the quadrats (Table 3 & 4). The algae are lifted off the mudflat when the upper layers are dried out during summer spring tides and air (oxygen?) bubbles become trapped in folds of the algae. In some instances, currents alone provide enough lift to carry detached algae. In the fall and winter, when productivity has declined and the weather is less mild, these green algal mats break up entirely (Woodin 1974, Price & Hylleberg 1982). Many invertebrates are probably rafted away at that time. Further, the clumped distribution of organisms among the drift samples indicates that potential colonists arrive at new sites in groups, which should increase their probability of success.

Scheltema (1977) claimed that infaunal deposit feeders have no chance of dispersal by rafting. The data presented here show that, in fact, there is potential for dispersal by rafting for at least some of these animals, e.g. *Leptochelia dubia*, *Pontogeneia* cf. *ivanovi*, *Exogone lourei*, *Amphipholus squamata* and *Leptosynapta clarki*. The first 3 species probably are more selective than the last 2, but all probably have rather broad feeding capability. For example, *L. dubia* feeds primarily on diatoms but is also a facultative predator (Highsmith 1982). These animals are so small, especially the juveniles, that an almost negligible amount of sediment or the ability to utilize epiphytic diatoms or the alga itself would probably sustain them long enough to permit dispersal.

General

Generalizations about both brooding and dispersal are complicated by problems of ancestry and taxonomy. For example, sibling species probably should be lumped when considering an organism's geographic distribution relative to dispersal mechanisms. This immediately raises problems of how broadly a 'species' is distributed, of distinguishing endemic species, and even of what constitutes a species in some cases. These difficulties will not be considered further here but they should be kept in mind during the following discussion.

Most brooding invertebrates have a small adult size. The reason for this correlation has been the subject of considerable speculation and debate (Menge 1975, Christiansen & Fenchel 1979, Himmelman et al. 1982, Strathmann & Strathmann 1982). Whatever the reason, small size is an advantage for shallow water brooding species with respect to dispersal by floating or rafting. Small animals are more likely to live on algae or sea grass before it becomes detached, especially in high enough numbers to be good potential colonists (see Cheetham 1960). As pointed out by Scheltema (1977), rafting can be a successful mechanism only for those species able to survive on floating objects for extended periods. Macrophytes and sea grasses would provide shelter and food or foraging habitat for small organisms for a considerable period of time (Norton & Mathieson 1983) but would be less likely to do so for large animals. As broadly-distributed species are likely to have lower extinction rates than species with narrow distributions (MacArthur 1972, Scheltema 1977, Vermeij 1978, Hansen 1980), small size may contribute to the success of brooding species by facilitating dispersal.

With regard to the geographic distribution of brooding species, presumably they should have lower extinction rates and be more common in regions where dispersal opportunities, such as rafting, are good. Thorson (1950) pointed out that a higher proportion of benthic invertebrates brood, or otherwise have non-pelagic development, at high latitudes than in the tropics (see also Spight 1981). Thorson suggested that the reason for this gradient is that larvae grow slowly in cold temperate and polar waters and the period of high algal productivity is so brief that planktotrophic larvae cannot reach metamorphic competence during this limited time of food availability. However, the notion that planktotrophy is favored in the tropics by virtue of temperature and food availability is troublesome (Clark & Gotzfried 1978, Birkeland 1982). Larval metabolic rates and, hence, food requirements tend to increase at higher temperatures (Clark & Gotzfried 1978, Wienberg 1982, Paul & Nunes 1983, Sprung 1984) but plankton primary production is generally quite low in tropical seas (e.g. Koblentz-Mishke et al. 1970). Because of this and the fact that planktotrophic larvae can be extremely abundant at high latitudes (Johnson 1937, Mileikovsky 1968, 1970, Makarov 1969, Edinburgh Oceanographic Laboratory 1973, Falk-Peterson 1982, Townsend 1984, A. Springer pers. comm.), Thorson's hypothesis needs to be reexamined. Perhaps the question should be why there is so little non-pelagic development in the tropics rather than why there is so much at high latitudes. Two alternative hypotheses may provide at least a partial explanation for the lower proportion of brooders in the tropics.

First, because of the scarcity of macroalgae in the tropics (Vermeij 1978, Gaines & Lubchenco 1982), in contrast to high latitudes (Scheltema 1977), rafting would be less available as a dispersal mechanism. Also, floating is probably not a very good long-distance dispersal mechanism (Table 1 to 5) and suitable habitats often are separated by considerable distances, e.g. coral reefs, which account for much of the high species diversity on which Thorson calculated the percentage of planktotrophic vs non-planktotrophic species.

Second, the abundance of persistently aggressive, predatory reef fish (e.g. Bakus 1981, Foster 1984) such as wrasses, triggerfishes, puffers and certain damselfishes would make external brooding, such as occurs in many asteroids at high latitudes (Himmelman et al. 1982), very risky and difficult, especially in combination with the variety of fishes that turn over rubble and/or break corals while foraging (e.g. Glynn 1974). Most tropical, benthic invertebrates have evolved chemical or mechanical defenses against this intensive predation pressure (Bakus & Green 1974, Vermeij 1978). Mechanical defense often limits space available for internal brooding, e.g. shell thickening in prosobranch gastropods, one of the main groups on which Thorson (1950) based his hypothesis. In addition, release of juveniles from a point source could very well result in loss of the entire brood to small predatory reef fishes which are often attracted by the feeding activities of other individuals (Bakus 1967, author's own obs. at Enewetak, Panama & Belize). Broods and egg capsules could also be lost due to incidental predation by schools of scraping grazers such as parrotfish, surgeonfish and puffers. With regard to the planktonic phase, the abundance of potential pelagic predators (e.g. cnidarian medusae, chaetognaths, predatory holoplanktonic crustaceans, decapod larvae, fish larvae and juveniles, and filter-feeding fish; e.g. Lebour 1922, 1923, Nelson 1925, Korrington 1940, Thorson 1950, Legare & Maclellan 1960, Bright 1967, Cooney 1981, Waldron 1981) on planktotrophic larvae is certainly much lower in the tropics than at higher latitudes. Also, benthic filter feeders such as barnacles, mussels, and infaunal bivalves and polychaetes, that are capable of ingesting larvae swimming near the bottom (Korrington 1941, Thorson 1946, 1950, Mileikovsky 1974), become more abundant at higher latitudes (Highsmith 1980). Thorson (1950) emphasized the importance of predation on larvae but did not discuss latitudinal differences in predator abundance. At high latitudes, planktotrophic larvae are produced during the spring and summer when plankton primary productivity is greatest (Mileikovsky 1970, Falk-Petersen 1982) but this is also the period of greatest predator abundance and activity. Consequently, high latitude

benthic invertebrates with planktotrophic larvae must generally be long-lived and produce huge numbers of larvae, or else utilize alternative modes of reproduction such as brooding or production of lecithotrophic eggs that have brief planktonic periods, that can be released at times when predators are less abundant (e.g. Falk-Petersen 1982), or that can remain at depths where predators are less concentrated.

To demonstrate that a species is dispersed by rafting or floating, it is necessary to show that sufficient numbers of an existing population drift away from an inhabited site and arrive at a new, uninhabited site and that the species is able to persist at the new location. Consequently, the work reported here does not prove that the species studied disperse by floating or rafting, but it does provide quantitative data showing the potential for these methods of dispersal.

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