OBSERVATIONS OF INVERTEBRATE COLONIZED FLOTSAM IN THE EASTERN TROPICAL PACIFIC, WITH A DISCUSSION OF RAFTING

C. Josh Donlan and Peter A. Nelson

The dispersal of marine invertebrates enjoys a long history of research. In the context of larval biology, rafting, the physical association between organisms and flotsam, has received relatively little attention. Although rafting has been suggested as an alternative dispersal agent, in select species this process may serve as a primary means of dispersal (e.g., Dooley, 1972; Ó Foighil, 1989; Ingólfsson, 1995). However, direct evidence of successful dispersal by rafting is scarce (Jokiel, 1984; Jokiel, 1990; but see Jackson, 1986; Ó Foighil, 1989; Ó Foighil et al., 1999).

A number of physical oceanographic processes tend to aggregate flotsam. Fronts and eddies tend to collect biological and non-biological material through processes such as Langmuir circulation, small-scale frontal systems, internal waves and tidal fronts (Pingree, 1974; Shanks, 1983; Kingsford and Choat, 1986; Franks, 1992). A wide diversity of organisms aggregate around these processes: seabirds, marine mammals, marine turtles, sea snakes, a variety of fishes, and many invertebrates (Hunter and Mitchell, 1967; Hunter and Mitchell, 1968; Barstow, 1982; Fedoryako, 1982; Shanks, 1983; Kingsford and Choat, 1986; Le Fèvre, 1986; Haney, 1987; Silber, 1990; Au, 1991; Kingsford et al., 1991; Pitman, 1993; Arenas et al., 1999). While detached macroalgae (Highsmith, 1985; Helmuth et al., 1994), pumice (Jokiel, 1984; Jokiel, 1989), and eelgrass (Worcester, 1994) have received some attention as means of dispersal mechanisms, woody flotsam has been relatively ignored as habitat or as a dispersal agent for marine invertebrates.

Here, we document invertebrate organisms rafting on woody flotsam in the Eastern Tropical Pacific and provide a simple measure of rafting frequency for the species observed. We also test the importance of flotsam surface area and distance from shore in determining species richness of the invertebrate flotsam community, and report the frequency of different flotsam types in Bay of Panama. We propose a simple scheme for classifying organisms associated with floating debris, and discuss the natural history of select rafting invertebrates with an emphasis on how certain life history traits may be advantageous to dispersal by rafting. These observations provide a preliminary indication of the invertebrate species associated with floating woody debris in this nearshore geographic region, and the importance of this resource to some of these organisms.

**Methods**

Flotsam was observed and collected by haphazard searches (CJD) in the Bay of Panama, Panama. Collecting trips originated from the Smithsonian Naos Marine Laboratories, located at the southern entrance of the Panama Canal. Using small boats (15-25 ft), trips were conducted out to and around the vicinity of the Pearl Islands, approximately 70 km SE of Panama City, during the Spring and Summer of 1997 (April 11, 25, May 5, 16, 20, June 2, 9, Fig. 1). Flotsam small enough to bring into the boat were measured and colonized animals collected for identification. Only invertebrates physically associated on flotsam were collected and reported. The flotsam were approached slowly by boat and flotsam collected swiftly (with a large net (5mm mesh) when possible), to prevent the loss
of attending animals. With flotsam too large to bring aboard (e.g., trees), measurements and animal collections were made in the water. An estimate of flotsam surface area (m²) was calculated by measuring length, width, and height or length and circumference (depending on the flotsam type). The distance (km) of each collection from shore was also recorded using GPS.

Colonized flotsam were separated by type: woody and non-woody categories, along with natural and anthropogenic categories. ‘Woody’ flotsam was further divided into sub-categories including (1) tree (included attached branches or roots), (2) coconut, (3) bamboo, (4) conglomerate, variegated mat of vegetative matter often with anthropogenic trash, (5) log (no roots or branches attached), (6) palm frond, (7) wood (anthropogenic—lumber) and (8) other plant material, which included material such as sticks, leaves and roots. A linear regression model was used to investigate potential relationships between flotsam species richness and both surface area and distance from land (Neter et al., 1996). Statistical analyses were conducted using SYSTAT™ with an α-level of 0.05 (Wilkinson, 1998).

A relative rafting frequency observed (Rₙ) for each species was derived by the equation.
\[ R_o = \frac{x}{n} \times 100 \]

where \( x \) = the number of rafting events encountered with the specific taxon (i.e. the number of times the organism was observed rafting) and \( n \) = the total number of rafting events recorded with at least one colonized organism for the entire dataset.

Rafting invertebrates can be separated into three categories of resident organisms: obligate, facultative, and accidental rafters (see also Gooding and Magnuson, 1967). Obligate rafters are species with adaptive characteristics attributable to selective forces unique to rafting, and at least a portion of their life history includes a rafting stage. Facultative rafters are species that possess attributes which facilitate rafting, but are also regularly observed on fixed, benthic substrate. Accidental rafters are species with characteristics that may permit them to survive a rafting episode, but probably have not been selected for this possibility. The latter two categories form a continuum, with facultative rafters relatively frequently found in association with flotsam; accidental rafters are rare occurrences.

RESULTS

Organisms from six phyla were observed rafting; a minimum of 23 species were recorded (Table 1; certain taxa were identified only to family). With the exception of a single cricket [Insecta: Orthoptera], all observations were of marine organisms. Decapod larvae (i.e. megalopae) were observed with the greatest frequency (\( R_o = 50.0\% \)). Commonly observed taxa included stalked barnacles (\( Lepus \) spp., \( R_o = 26.6\% \)), three species of grapsid crabs (\( Plaguris imiculata, Planes cyanus, \) and \( Pachygrapsus transversus \)), an annelid worm, \( Amphipneus vagans \) (Polychaeta: Amphipneidae), and boring bivalves (Teredinidae, Table 1). Members of the Teredinidae are not discussed here, since they are addressed extensively elsewhere (e.g., Ray, 1958; Edmonson, 1962). The mean number of species per flotsam was 1.88 ± 1.5 (SD, \( N = 203 \)).

Of the flotsam observed with at least one colonizing organism, 191 (94\%) were woody (Table 2). The few non-woody, colonized flotsam were plastic and other trash. Common flotsam types included plant material, lumber, and logs (Table 2). Multiple regression analysis indicated that the relationship between species richness and flotsam surface area and its distance from land was statistically significant; however, the relationship was weak (\( R^2 = 0.256 \); Table 3).

DISCUSSION

Woody flotsam made up the majority (94\%) of the observed colonized flotsam in the Bay of Panama. While anthropogenic trash was common, it was not often colonized. Small logs, sticks, leaves and anthropogenic wood (e.g., lumber) made up over 50\% of the colonized flotsam. Other colonized flotsam included bamboo, coconuts, palm fronds and entire trees. Species richness and both surface area and distance from land were weakly correlated. This weak relationship suggests that other factors may be important in the ecology of rafting communities.

The following discussion of individual species is divided into obligate, facultative, and accidental rafters. An important component to these species treatments is our justification for these categories. While data to support or refute the categorization of these species are admittedly slim, we hope that by proposing these categories and providing these tentative examples we will stimulate further research.
Table 1. Rafting invertebrates and their rafting frequencies.

<table>
<thead>
<tr>
<th>Phylum</th>
<th>Class/Order</th>
<th>Family</th>
<th>Species</th>
<th>No. of rafting events</th>
<th>$R_o$, rafting frequency</th>
</tr>
</thead>
<tbody>
<tr>
<td>Annelida</td>
<td>Polychaeta</td>
<td>Amphinome vagans</td>
<td>7</td>
<td>3.7</td>
<td></td>
</tr>
<tr>
<td>Arthropoda</td>
<td>Amphipoda</td>
<td>Pachygrapsus transversus</td>
<td>2</td>
<td>1.1</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Brachyura</td>
<td>Plagusiella immaculata</td>
<td>15</td>
<td>8.0</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Planes cyanus</td>
<td>14</td>
<td>7.4</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Portunidae</td>
<td>Portunus asper</td>
<td>8</td>
<td>4.3</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Callinectes spp.</td>
<td>6</td>
<td>3.2</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Juvenile</td>
<td>4</td>
<td>2.1</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Megalopa</td>
<td>94</td>
<td>50.0</td>
<td></td>
</tr>
<tr>
<td>Isopoda</td>
<td></td>
<td></td>
<td>4</td>
<td>2.1</td>
<td></td>
</tr>
<tr>
<td>Natantia</td>
<td></td>
<td></td>
<td>1</td>
<td>0.5</td>
<td></td>
</tr>
<tr>
<td>Orthoptera</td>
<td></td>
<td></td>
<td>1</td>
<td>0.5</td>
<td></td>
</tr>
<tr>
<td>Thoracica</td>
<td>Balanomorphoidea</td>
<td>Balanus spp.</td>
<td>6</td>
<td>3.2</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Chthalamoidea</td>
<td>Euphia sp.</td>
<td>2</td>
<td>0.1</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Lepadidae</td>
<td>Lepas sp.</td>
<td>50</td>
<td>26.6</td>
<td></td>
</tr>
<tr>
<td>Bryozoa</td>
<td></td>
<td>Membranipora sp 2</td>
<td>2</td>
<td>0.1</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Membranipora tuberculata</td>
<td>7</td>
<td>3.7</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Membranipora sp 1</td>
<td>2</td>
<td>1.1</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Membranipora tenella</td>
<td>3</td>
<td>1.6</td>
<td></td>
</tr>
<tr>
<td>Cnidaria</td>
<td>Hydroida</td>
<td></td>
<td>6</td>
<td>3.2</td>
<td></td>
</tr>
<tr>
<td>Mollusca</td>
<td>Bivalvia</td>
<td></td>
<td>17</td>
<td>9.0</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Teredinidae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Gastropoda</td>
<td>Fossaridae</td>
<td>Fossarida sp.</td>
<td>3</td>
<td>1.6</td>
</tr>
<tr>
<td></td>
<td>Octopoda</td>
<td>Argonautidae</td>
<td>Argonauta sp.</td>
<td>1</td>
<td>0.5</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>5</td>
<td>2.7</td>
<td></td>
</tr>
</tbody>
</table>

Platyhelminthes

2 *Balanus amphitrite* complex and possibly *Fistulobalanus* spp. (W. Newman, pers. comm.).
3 Likely *Euphia eutropacensis* (W. Newman, personal communication).

Table 2. Distribution of flotsam type collected in the Bay of Panama, with at least 1 rafting organism ($N = 203$). See text for definitions of flotsam types.

<table>
<thead>
<tr>
<th>Flotsam Type</th>
<th>%</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Woody</td>
<td>94</td>
<td>191</td>
</tr>
<tr>
<td>Wood (anthropogenic)</td>
<td>25.7</td>
<td>49</td>
</tr>
<tr>
<td>Log</td>
<td>16.2</td>
<td>31</td>
</tr>
<tr>
<td>Palm frond</td>
<td>7.3</td>
<td>14</td>
</tr>
<tr>
<td>Coconut</td>
<td>7.3</td>
<td>14</td>
</tr>
<tr>
<td>Bamboo</td>
<td>4.7</td>
<td>9</td>
</tr>
<tr>
<td>Conglomerate</td>
<td>2.1</td>
<td>4</td>
</tr>
<tr>
<td>Tree</td>
<td>1.0</td>
<td>2</td>
</tr>
<tr>
<td>Other plant material</td>
<td>35.1</td>
<td>67</td>
</tr>
<tr>
<td>Non-woody</td>
<td>6</td>
<td>12</td>
</tr>
</tbody>
</table>
Table 3. Multiple linear regression with species richness as the dependent variable and (1) log area (m²) and (2) distance from land (km) as independent variables. The overall model was significant: n = 129, F = 23.04, P < 0.001, adjusted r² = 0.256.

<table>
<thead>
<tr>
<th>Effect</th>
<th>Coefficient</th>
<th>SE</th>
<th>Tolerance</th>
<th>t</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>0.854</td>
<td>0.219</td>
<td></td>
<td>3.91</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Log area</td>
<td>0.594</td>
<td>0.109</td>
<td>1.0</td>
<td>5.43</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Distance</td>
<td>0.022</td>
<td>0.005</td>
<td>1.0</td>
<td>3.96</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

The graspid crab *Planes cyanus*, the polychaete *Amphinome vagans*, the stalked barnacle *Lepas* sp., and bryozoans of the genus *Membranipora* are flotsam obligates—true rafting species with adaptations attributable to a rafting existence. The graspid crab, *Plagostoma tuberculata* has been reported both on flotsam and among rocky littoral zones (Rathbun, 1918; Williams, 1968) and thus is a facultative rafter. No clear life history patterns were correlated with rafting frequencies (R) for organisms observed during this study; while both graspids and *Lepas* spp. have long planktonic larval stages (Wilson and Gore, 1980; Rabbaibis and Gore, 1985; Moyse, 1987), the polychaete *A. vagans* is a brooder (Pettibone, 1963; personal observation, CJD).

**Obligate Rafters**

*Planes cyanus* (Dana) [Brachyura: Grapsidae].—*Planes cyanus* was commonly observed rafting (Rₙ=7.4%, Table 2). Multiple individuals were associated with one raft. In total, 10 males (including 1 juvenile) and 4 females were observed, including one gravid female.

This ditypic genus is restricted to floating substrata in pelagic systems and is circumtropical in distribution, occasionally penetrating temperate waters (Rathbun, 1918; Chace, 1951; Davenport, 1992). The Atlantic *Planes*, *P. minitus*, occurs in large numbers amongst *Sargassum* rafts and as an epibiont on sea turtles (Chace, 1951; Davenport, 1992; Davenport, 1994). The taxonomic and ecological differences between the two species are minimal and unresolved (Chace, 1951).

*Planes minitus* is an opportunistic omnivore that possesses specialized foraging techniques. The diet of *P. minitus* includes fish post-larvae and juveniles (*Exocoetidae, Lagoccephalus, Naucrates*), euphausids, isopods, sea skaters (*Halobates*) and their eggs, *Lepas* spp. and their spat, small squid, hydroids, *Membranipora* spp., flatworms, *Sargassum* and detritus (Geiselman, 1983; Davenport, 1992). *P. minitus* is able to swim continuously for 35–45 min; after this time, the crab sinks (Davenport, 1992). *Planes* spp. are anatomically similar to the intertidal graspids, and may have developed their limited swimming abilities to extend prey capture to items otherwise out of reach (Hartnoll, 1971; Davenport, 1992). Limited swimming ability would also facilitate flotsam to flotsam dispersal in areas where flotsam is at high densities. In *Sargassum* communities, adult *P. minitus* and *Portunus sayi* are near the top of the food web (Geiselman, 1983).

*Amphinome vagans* (Savigny) [Polychaeta: Amphinomidae].—Members of the polychaete family *Amphinomidae* are cosmopolitan in distribution, found both in tropical and temperate waters. While most amphinomids are restricted to intertidal and subtidal habitats (with a few deep-sea exceptions), *Amphinome vagans* is a flotsam obligate. Collections from driftwood have also been reported off the Marquises Islands, Acapulco,
Mexico, and South Africa (Day, 1967). The feeding habits of A. vagans have not been studied. The majority of Amphimedon browse on sessile cnidarians (i.e., corals, hydroids, and anemones), sponges, and ascidians (Dales, 1963; Day, 1967). Five stomachs of A. vagans were dissected, all revealing Lepas sp. testes. These barnacles are often at high densities on flotsam (pers. obs., CJD).

A. vagans were observed brooding young on their backs. We also observed juveniles on flotsam without adults. Amphimedon vagans likely has few, if any, predators due to poisonous notosetae (Fauchois and Jumars, 1979). Therefore, dispersal and density-dependent effects may play important roles in the population dynamics of this species. Observations suggest that A. vagans are poor swimmers; consequently, the aggregation of flotsam in convergent zones may be important for flotsam-to-flotsam dispersal.

Lepas spp. — Species of Lepas settle gregariously solely on floating objects (Anderson and Underwood, 1994). Characteristics due to their neustonic lifestyle include the thinning of capitular plates and insensitivity to light and water movements (Anderson and Underwood, 1994). Both of these characteristics may lead to higher susceptibility to predation. The polychaete, A. vagans, appears to prey almost exclusively on Lepas spp.

Membranipora spp. [Cheilostomata: Anasca]. — Membranipora including two undescribed species. Three of these species are considered obligate rafters, and the fourth is a facultative rafter (below). Membranipora spp. were observed on 34 of the 203 colonized flotsam (Rₙ=16.7%), however rafting frequencies of the individual species are less because a proportion of rafting bryozoans were not collected and identified to species (Table 2).

M. tenella has been reported rafting on a variety of flotsam, including wood and plastic; it has not been reported on Sargassum (Winston, 1982a; Winston, 1982b). The reported distribution ranges from Florida to Brazil in the Atlantic Ocean (Winston, 1982b). To our knowledge, this is the first account of M. tenella from the Pacific Ocean. M. tenella was observed rafting on woody flotsam, including coconut and bamboo (Rₙ=1.6%). Despite few records of this species over the past 100 yrs, M. tenella is now one of the most abundant bryozoans on the Atlantic coast of Florida; its recent abundance may be explained by its ability to colonize drift plastic, which has recently become abundant (Winston, 1982a).

Membranipora sp. 1 has been reported once before from the east coast of Florida (Winston, 1982b). Winston (1982b) collected this species from wood and plastic objects among beach drift. We observed this species rafting exclusively on woody debris, including a palm frond (Rₙ=1.1%). Winston notes the similarity of Membranipora sp. 1 to Electra bisticata, described and reported from two littoral locations in the Pacific (Mazatlan, Mexico and the Secas Islands, Panama; Osburn, 1950). A taxonomic relationship may exist and rafting may play a role in the biogeography of these species. Membranipora sp. 2 is an undescribed species of bryozoan (A. Herrera, pers. comm.). This species was collected only twice during the study (Rₙ=1.1%).

Facultative Rafters

Plagusia immaculata (Lamarck) [Brachyura: Grapsidae]. — Plagusia immaculata was commonly encountered on flotsam (Rₙ=21.8%). While these crabs, often referred to as the ‘Pacific log rider’, are commonly found on logs (pers. observ., Rathbun, 1918), they are also found rafting on leguminous fruits (Finnegan, 1940), cayucas (Garth, 1948), trash, and a few have even been found on drifting coconuts and plastic sandals (personal
observation, CJD). This species is also a permanent inhabitant of the littoral zone (Rathbun, 1918; Williams, 1968). This animal’s ability to exist on flotsam may contribute to its wide distribution. Plagusia immaculata is a cosmopolitan species, reported from the Atlantic coast of the United States to Brazil, the West African coast, the Indo-Pacific region, and Costa Rica to Ecuador in the eastern Pacific (Finnegan, 1940; Rathbun, 1918; Garth, 1948; Williams, 1968).

Membranipora tuberculata (Cheilostomata: Anasca).—Membranipora tuberculata commonly colonizes floating Sargassum (S. natans and S. fluitans) and attached algae in subtidal waters (Osburn, 1950; Shier, 1964; Ryland, 1974; Winston, 1982b). Winston (1982a) also reports this species as the second most abundant colonizer of drift plastic off the Atlantic coast of Florida. M. tuberculata is cosmopolitan in tropical waters, found throughout the Pacific, Atlantic and Indian Oceans (Osburn, 1950; Brusca, 1980; Winston, 1982b). We observed this species on logs and branches. While M. tuberculata larvae do show settlement preferences toward Sargassum natans, its presence on other algae, drift plastic, and woody flotsam indicates that M. tuberculata is plastic with regard to settlement requirements (Winston, 1982a).

ACCIDENTAL RAFTERS

Pachygrapsus transversus (Gibbes) [Brachyura: Grapsidae].—P. transversus is a small intertidal grapsid crab commonly found in rocky, sandy, and mangrove habitats (Abele et al., 1986). This grapsid is one of the most cosmopolitan in its family, ranging on the east American coast from North Carolina south to Montevideo, Uruguay (including most of the Caribbean islands). On the Pacific, this species is found from California to Peru, including the Galápagos, Cocos, and Easter Islands (Garth, 1946). This grapsid has also been reported off Australia, the West Coast of Africa, and the Indo-Pacific region (Rathbun, 1918; Boone, 1928; Garth, 1948; Abele and Kim, 1989). With the exception of collection on a whaling ship in Cape Cod, Massachusetts (Rathbun, 1918), P. transversus has not been reported rafting previously.

Certain life history traits of P. transversus may be advantageous to rafting. It is omnivorous, feeding on fish, algae, and other P. transversus. A diverse foraging strategy would be advantageous to survival in habitat with unpredictable and ephemeral food sources such as flotsam. This species commonly occupies small holes, a behavior that has been attributed to high predation pressures (Crane, 1937; Abele et al., 1986). Bored holes, often left by shipworms (Mollusca: Teredinidae) and boring isopods, are common in floating woody debris; both P. transversus and unidentified megalopa utilize these holes (pers. observ.).

Megalopa Larvae [Brachyura].—Brachyuran crab larvae at the megalop stage were the most abundant organisms observed (R = 50.0%). It is likely the observed P. transversus colonized flotsam during the megalop stage rather than as an adult crab from the littoral zone. Pachygrapsus transversus lacks well-developed appendage setae and is not well adapted to swimming (Hartnoll, 1971). Observations in the lab and field show that P. transversus is a poor swimmer. In addition, megalopa collected from flotsam and transferred to an artificial sea-table molten into P. transversus (personal observation, CJD).

Hydrozoa.—Dozens of cosmopolitan, benthic hydroid species are considered to be rafters (Cornelius, 1992a, b). Many of these rafting hydroids foul vessels (Millard, 1959) or are found in Sargassum communities (Morris and Mogelberg, 1973). Cornelius (1992a, b) argues that rafting may play an important role in the distribution of hydroids.
Many of the rafting hydroids have a suppressed medusa stage (Cornelius, 1992a; Cornelius, 1992b); these species include taxa that have colonized islands such as the Azores and could reach remote destinations only by rafting during the polyp stage. Many of these rafting species are substrate generalists, which may contribute to successful rafting.

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LITERATURE CITED


**ADDRESSES:** (C.J.D., P.A.N.) Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Ancón, Panama. (P.A.N.) Comisión Interamericana del Atún Tropical, Laboratorio Achoyines, Las Tablas, Provincia Los Santos, Panama. **CURRENT ADDRESSES:** (C.J.D.) Island Conservation & Ecology Group, University of California, Long Marine Lab, 100 Shaffer Road, Santa Cruz, California 95060 E-mail: <jdonlan@islandconservation.org>, (P.A.N.) Living Links, Yerkes Regional Primate Research Center, Emory University, Atlanta, Georgia 30329 E-mail: <peteranelson@earthlink.net>. **CORRESPONDING AUTHOR:** (P.A.N.)