THE NUMBERS OF FRESHWATER GASTROPODS ON PACIFIC ISLANDS AND THE THEORY OF ISLAND BIOGEOGRAPHY

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ABSTRACT

The freshwater gastropod fauna of the Pacific islands of Beqa, Vanua Levu, Waya, Rotuma (Fiji); Upolu, Savai'i, Tutuila (Samoa); Tongatapu, Vavatu (Tonga); Raratonga (Cook Islands); New Georgia (Solomon Islands); Guam, Truk and Ponape (Micronesia) is described. Thirty eight species were found; 20 species belonged to the Neocyprea, 10 to Thordisa, and one each to Assimineidae and Planorbidae. Using multiple regression analysis, the numbers of species on these and 11 other Pacific islands were shown to be correlated with the water area on the island and the distance the island was from a source of freshwater gastropods (accounting for 79% of the variation). Distance by itself was not a significant contributor. Islands with a small area of water showed a steeper species-water area curve, and the number of species on these islands was more correlated with distance than to water area. This was probably due to a higher extinction rate brought about by the drying up of the limited number of habitats.

Key words: freshwater, gastropods, Pacific islands, island biogeography.

INTRODUCTION

Faunal studies of angiosperms, birds and land snails in the Pacific have documented the ranges and distributions of the species in these taxa and have revealed examples of endemism and of species radiation (Carlgquist, 1974; Diamond, 1984; Solem, 1959). These studies have also been used in discussions of the theory of island biogeography developed by MacArthur & Wilson (1967). This theory suggests that because the immigration rate to island areas is greater than that to more distant islands and because the extinction rate is greater on smaller islands than on larger islands, the equilibrium number of species tends to increase with island area. In the past, freshwater snail diversity has been discussed in relation to this theory, with lakes and ponds being considered as islands of water isolated by land barriers (Lassen, 1975; Aho, 1984).

The aims of this work were to establish what species of freshwater gastropods are present on Pacific islands and to find if the island faunas, some of which had already been described (Haynes, 1985, 1988a; Star mhinner, 1976), supported the theory of island biogeography.

METHODS

Freshwater Gastropod Survey

From 1985 to 1987, freshwater gastropods were collected from the islands of Beqa, Rotuma, Vanua Levu, Waya (Fiji); Guam; Truk (Federated States of Micronesia); Savai'i (Western Samoa); Raratonga (Cook Islands) (Fig 1). The fauna of these islands is described for the first time. Collections were also made from Pohnpeia (Federated States of Micronesia); Upolu (Western Samoa); Tutuila (American Samoa); Tongatapu, Vavatu (Tonga) (Table 1). All islands are within the tropics. Guam is the most northerly at 14°N and Raratonga is the most southerly at 22°S.

Freshwater gastropods were collected by hand from rocks, boulders and vegetation or were swept with a 1 mm mesh lonic gravel and mud from streams, rivers and pools. Sampling took place both near the coast and inland to ensure that the gastropods found were representative of the whole fauna. Each site was searched for at least an hour, and all collections were made within the volume of water flowing in each stream was low to normal.


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Water temperature was recorded, and water samples were collected on New Georgia, Uolou, Savaii, Tutuila, Tongatapu and Vavau. These were analysed for pH, total ionic (µS cm⁻¹) and hardness (mg CaCO₃ l⁻¹) by the Institute of Natural Resources, University of the South Pacific. Some collections were made on islands that were visited not primarily for collecting gastropods; on these islands no water samples were taken.

All gastropod collections are housed in the Biology Department, University of the South Pacific.

Island Biogeography

Data for the 14 islands investigated are presented in Table 2, along with data already published for other Pacific islands. The islands previously investigated are Viti Levu (Fiji) (Haynes, 1985); Vanua Levu, Ovalau, Gau, Kadavu, Taveuni (Fiji) (Haynes, 1984); Guadalcanal (Solomon Islands); Efate (Van-

uabu); Tahiti (Stürmühler, 1976); New Caledonia (Stürmühler, 1970); and Kausal (Hawai) (Burch & Patterson, 1971; Maciolek, 1978).

Stream length was estimated by measuring the length of all streams and rivers on 1:50,000 or 1:25,000 government maps of the islands. The water area was estimated by multiplying the stream length by a mean river or stream width of 10–50 m (depending on the island size) and by adding the area of standing water to it.

The large, geologically old islands of New Guinea, New Caledonia and Viti Levu were considered to be the most likely sources of freshwater immigrants to the islands, so that the distances in Table 2 were measured from the nearest of these three islands to the island in question. The three large islands together with nearby islands form three generally accepted biogeographical subregions of the Pacific islands (Thorne, 1963). The source islands possessed all freshwater pulmonate species found on the smaller islands in their regions, with the exception of endemic species. Apart from Kausal (Hawai), the endemic
TABLE 1. Study Sites

Micronesia
1. Guam. Largest island in Micronesia. Formed from the union of two volcanoes. Yung River, Cett and Afiapu streams were sampled.

2. TRUK (Moen). Moen is one of the many islands in the Truk Lagoon. Winchen River and several small streams near the Continental Hotel were sampled.

3. PONPEE. A rugged island with high rainfall. Nanapi, Lohalii, and Pilenikiupu rivers and Eniap Stream were sampled. The collections were made by John Mavor and John Ford (MacKinnon & Ford, 1987), who assisted the author with collections on Guam and Truk.

Salomon Islands
4. NEW GEORGIA. A high volcanic island. Sampled along the length of Puta and Byron rivers.

Western Samoa
5. SAVAII. Streams are confined to the south coast because of extensive lava flows on the north coast. Lotsa Plantation Stream, Sili Village Stream, Mata'ave Pool, Asaga Spring, and Sapa'si Water holes were sampled.

6. UPOULI. A high volcanic island. Sampled Falele'a Falls, Le Mata Ras Stream, Mulvahil Stream, and along the Vassegano River.

American Samoa
7. TUTULU. Volcanic with short streams. Sampled Alotau, Lama's Saddle and Le'e'e streams, and Pala Lagoon.

Tonga
8. TONGATAPU. A coral island with no running water. Sampled coastal and inland ponds.

9. VAVAVU. An elevated limestone plateau with no running water. Sampled pools and Lake Tuansu.

Cook Islands
10. RAROTONGA. The only true volcanic island in the Cook Islands. Sampled Avatiu, Vaimango and Aana streams and taro patches. (Lower courses of all streams were dry in September 1983.)

Fiji
11. BULA. 14 km offshore from the main Island of Viti Levu. Sampled the length of the stream at Nakalava and in Nenedruvei Creek.

12. WAYA. In the Yasawa group. Sampled the two streams in the Yobole area.

13. VANUA LAVUA. Largest island in the northern Lau group. Northern part upland coral, southern part volcanic. Sampled the two streams near Lomaloma.

14. ROTUMA. An isolated volcanic island 500 km north of Viti Levu. The rock is porous, and there are no permanent streams. Wells and taro patches were sampled.

were Fluvio-pupa brevis on Estate and Melanoides ponti and Melanoides peringina on Upolu. New Caledonia, the source island for Estate, has three species of Fluvio-pupa that could have given rise to Fluvio-pupa brevis. Melanoides is a genus that shows much variation within species, and the isolation on Upolu of one or more of the 7-9 Melanoides species from the source island Viti Levu could have given rise to Upolu’s two endemic species.

The freshwater gastropods on Kauai, like most taxa in the Hawaiian group, show considerable speciation. It has eight endemic freshwater gastropod species. Four of these, Neritina granosa Sowerby, N. vespertina Sowerby, Clitonia cariosa (Wood), C. natalis (Easton), probably arose from species arriving from Southeast Asia or New Guinea. The four Lymnaeidae endemics (Fifine sawcombii, E. australasia, Pseudotrochia novaezelandiae and P. producta) probably had their origins in America, Melanoides tuberculata, Tanekila granulata (found elsewhere on Pacific islands), and Fernissia sharp probably arrived accidentally in recent times whereas Jalba viridis was introduced from Asia about 1890.
<table>
<thead>
<tr>
<th>Island</th>
<th>Area (km²)</th>
<th>Height (m)</th>
<th>Distance (km)</th>
<th>Stream length (km)</th>
<th>Water area (km²)</th>
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<td>16750</td>
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<td>31</td>
<td>10429</td>
<td>1323</td>
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<td>11</td>
<td>1709</td>
<td>1856</td>
<td>800</td>
<td>300</td>
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<tr>
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<td>843</td>
<td>200</td>
<td>1080</td>
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<tr>
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<td>12</td>
<td>1452</td>
<td>1598</td>
<td>(6000)</td>
<td>604</td>
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<tr>
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<td>1113</td>
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<td>15</td>
<td>1042</td>
<td>2241</td>
<td>2440</td>
<td>735</td>
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<td>887</td>
<td>546</td>
<td>500</td>
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<td>406</td>
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<td>470</td>
<td>894</td>
<td>10</td>
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<td>411</td>
<td>838</td>
<td>85</td>
<td>398</td>
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<td>19</td>
<td>740</td>
<td>0</td>
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<td>1000</td>
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<td>290</td>
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<tr>
<td>Bega</td>
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<td>35</td>
<td>438</td>
<td>14</td>
<td>37</td>
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<tr>
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<td>19</td>
<td>369</td>
<td>1300</td>
<td>6</td>
</tr>
<tr>
<td>Wegi</td>
<td>9</td>
<td>17</td>
<td>580</td>
<td>48</td>
<td>20</td>
</tr>
</tbody>
</table>

(Burch & Patterson, 1971; Maciak, 1978). Therefore, in the case of Kaua'i, distance from a source island is irrelevant. It was thought that little bias was introduced by using Starmüller's figures for New Caledonia, Guadalcanal, Elate and Tahtí. He collected from Upolu and Tuvalu (Samoa) in 1985 (Starmüller, 1996) and reported 23 species (one doubtful), which compares favorably with the 22 species I found in 1987. Bishop Museum shell collections of freshwater gastropods from Pacific islands were studied in 1985, and I undertook a revision of their nomenclature. The Bishop Museum collections, which are not extensive, contain no species additional to those I found.

The data in Table 2 were the basis of multiple regression analysis using the method described by Bliss (1970). The number of gastropod species on an island was used as the dependent variable and the other factors — island area, island height, island distance from the presumed source of gastropods, stream length and water area — were the independent variables. The four first-order independent variables were converted to logs whereas, for convenience, water area was first multiplied by 100 before being converted to logs. The quantity of calcium ions (hardness) and total ions (conductivity) in the water can determine whether gastropods will be present. However, as the figures for hardness and conductivity for all streams and rivers tested (Table 2) were above 4.0 mg Co 1−2 × 12.0 mg Mg 1−1, the amount that limits the presence of gastropods in freshwater (Aho, 1984), they were not used in the multiple regression analysis.

**RESULTS**

Freshwater Gastropod Survey

Thirty eight species of freshwater gastropods were collected from the 14 islands. Twenty six were Nairidae, 10 Thiadidae, one Planorbidae and one Assimineidae (Table 3). The species found most frequently was the parthenogenetic land Menerobrancus.
It was present on 11 of the 14 islands investigated. This species is also found in East Africa, the Middle East, Asia and the Caribbean (Starmüther, 1976).

The stream-dwelling natalis, Nentilia vari-
ageata (on 9 islands) and Septaria porcellana (on 5 islands), were the next most wide-
ground. These were followed by the brick-in-
water gastropod Nentilia turnita on 7 islands.

Twelve of the species were present on both North and South Pacific islands. These were Melanoides tuberculata, Nenilia turnita, N. vari-
ageata, N. pustulosa, N. magnilabris, N. aqua-
puncta, Nentiloides subulata, Clithon corona, Septaria porcellana, S. brevis, S. xaniposus and Tarebia granifera.

Although in this study Thia cancellata, Nentiloides cornea, Nenilia labiosa, N. asper-
ulata and Clithon nucleus were found only on New Georgia, the first three have been recorded from Papua New Guinea (Reich, 1937; Starmüther, 1975) and the last two from New Caledonia (Starmüther, 1975).

The only endemic species recorded were two trahis species, Melanoides lata and Mel-
anoidea peregrina, U'pou.

Water temperature, pH, hardness and con-
ductivity for the islands studied and results already published from other Pacific islands are given in Table 4. Gastropods were absent from Lake Tagimouca, Tānui on where total ions (conductivity) 14-18 µs cm⁻¹ and hardness (0.5-5.0 mg Ca × Mg ¹ / l) were low (Southern et al., 1986) (Table 4). Hard-
ness and conductivity of other freshwater were sufficient to support gastropods (Table 6).

Island Biogeography

Because island area (Xₐ) was correlated with stream length (Xₐ) (r = 0.9377) and with water area (Xₐ) (r = 0.8737), and water area (Xₐ) was correlated with stream length (Xₐ) (r = 0.9522), each made a similar contribution to the variation in the number of species (y).

However, the variable water area correlated best with species numbers (r = 0.8412) (Table 4).

Using the stepdown method of reducing the number of variables until only those having significant influence were left (Biss, 1970), the best correlation obtained was with the variable water area, distance from the source of gastropods (Xₐ) and island height (Xₐ). These variables accounted for 80% of the variation in species numbers. When is-

land height was omitted, 92% of the correla-
tion was still accounted for by water area and distance. As the contribution of island height was not significant, the residuals of species numbers (y - y') from the equation Y = 9.699 + 4.944Xₐ - 3.798Xₐ were plotted as de-
viations from the partial regression of species numbers against water area in Fig. 2. They did not depart much from linearity or from uniform scatter about the line of original distance was omitted, the correlation fell to 94%, showing that water area is the major contributor to the variation, but distance is a significant com-

menter (p < 0.001) when taken in combina-
tion with water area. However, distance by itself is not significant (r = 0.3215) for 23 is-
lands.

When the eight small islands with least wa-
ter area (i.e. Chal, Raratonga, Tongatapu, Waya, Vavau, Vava'u and Ro-
tuma) were considered separately, distance from source of gastropods was the largest contributing factor to the number of species per island. When combined with water area, the two factors contributed 91% of the corre-
lation, whereas distance alone contributed 81%. Species numbers were plotted against water area for the 25 islands in Figure 3. It is seen that the slope is steeper for the eight islands with small areas of water.

DISCUSSION

The pantophagous trahis Melanoides tu-
berculata, which was found on 11 of the 14 islands, can easily be spread on plant mate-
rial as it gives birth to live young. One speci-
men reaching an island can start a new pop-
ulation and as it inhabits ponds, ditches and lacustrine areas as streams and rivers, it can survive on such islands as Tongatapu, Vava'u and Rotuma which have no running wa-
ter.

The bird-uniform planorbid Physastra nasuta, which inhabits ponds as well as running wa-
ter, was present on Tongatapu, Raratonga and Tutuila. It has been found on other Pacific islands, such as New Caledonia (Starmü-
ther, 1970), Vava'u (Haynes, 1984) and Vava'u (Haynes, 1986a). Walker (1984) suggested that the genus Physastra evolved in the Australian region and spread into Southeast Asia and the Pacific through New Guinea. Physastra nasuta was collected from Tonga in 1832 (Solem, 1859), and it may
<table>
<thead>
<tr>
<th>Island</th>
<th>Guam</th>
<th>Truk</th>
<th>Ponape</th>
<th>N. Georgia</th>
<th>Savai'i</th>
<th>Upolu</th>
<th>Tutuila</th>
<th>Tongatapu</th>
<th>Vava'u</th>
<th>Ranotonga</th>
<th>Beqa</th>
<th>Waya</th>
<th>VanuaBALavu</th>
<th>Rotuma</th>
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<tr>
<td>Area (km²)</td>
<td>541</td>
<td>19</td>
<td>324</td>
<td>1470</td>
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<td>1114</td>
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<td>118</td>
<td>67</td>
<td>35</td>
<td>17</td>
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<tr>
<td>Height (m)</td>
<td>406</td>
<td>369</td>
<td>772</td>
<td>843</td>
<td>1856</td>
<td>1113</td>
<td>652</td>
<td>19</td>
<td>179</td>
<td>653</td>
<td>439</td>
<td>580</td>
<td>200</td>
<td>206</td>
</tr>
<tr>
<td>Number of species</td>
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<td>4</td>
<td>11</td>
<td>20</td>
<td>11</td>
<td>15</td>
<td>13</td>
<td>3</td>
<td>1</td>
<td>3</td>
<td>13</td>
<td>9</td>
<td>4</td>
<td>1</td>
</tr>
</tbody>
</table>

**THARIDAE**

- *Thiar anaxia (l inei)*
- *T. canosilata Röding*
- *T. rostrata (Müller)*
- Melanodoides tuberculata (Müller)
- *M. aperta (Hinds)*
- *M. mosai (Gould)*
- *M. lata (Mousson)*
- *M. perringius (Mousson)*
- *M. arnottii (brict)*
- *Tarebia granifera (Lamarck)*

**NERITIDAE**

- *Nerita sumula (Gmelin)*
- *N. auriculata (Lamarck)*
- *N. variata (Lessone)*
- *N. pedis Meduz*
- *N. pulchra (Linne)*
- *N. squamiplicata Röd* STA
- *N. canaliculata Stover* STA
- *N. porosa Gould*
- *N. appendiculata Röd* STA

<table>
<thead>
<tr>
<th>Haynes</th>
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<tr>
<td>Island</td>
</tr>
<tr>
<td>----------------</td>
</tr>
<tr>
<td>Sua'1</td>
</tr>
<tr>
<td>Upena</td>
</tr>
<tr>
<td>Tubuia</td>
</tr>
<tr>
<td>New Georgia</td>
</tr>
<tr>
<td>Vatavu (L. Tu'anuku)</td>
</tr>
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</table>

Tongatapu coastal pools:
- 7.4 1435-4061 42-9-177 3

Poroporo:
- 21-104 6-46 11

Upe Levu:
- 23-30 5.0-7.5 2.8-231 19.5-39 31

Vanua Levu:
- 23-30 6.0-7.0 111-195 36-232 26

Ovalau:
- 25-26 6.7-7.0 147-152.3 56-60 30

Taveuni:
- 21-32 5.0-6.5 14-9 0.8-5(Ca + Mg) 0

Kadavu:
- 25-26 6.7-7.5 36.1-46.7 9-19.7 15

Savo:
- 26-27 7.0-7.7 123-134 52-55 16


| TABLE 5. Freshwater gastropod habitats on Fiji Islands and the gastropods that may inhabit them. |
|-----------------------------------------------|-----------------------------------------------|
| **Habitats**                                  | **Gastropods**                                 |
| 1. Pond's, dolotaro patches, dry areas & lakes| Melanoides tuberculatus, Physastra nasuta, Ferrisia roumemensis, Curatula montipennis |
| 2. Brackish water (shaded or mangrove areas)  | Neritina turpis, N. turpis, Clithon oualaniensis |
| 4. Freshwater (influenced by the tide, lower courses of streams & rivers) | C. polita, C. diadoma, S. lineata, Septaria polyclita, Neritina aquaquinla, Thars amara, T. balcanica, T. siagria, T. turritata, Melanoidea olivaria, M. albiturris, M. aspersa |
| 6. Cascade (substrate boulders & rocks) | S. polyclita, S. sanguisuga, S. suffreni, S. macrocephala |

have been transported to Tongatapu and Ranatonga on taxi plants in recent times by man.

The majority (26 species out of 38) of the snails collected were nerites (Table 5). It has been suggested that the brackish and freshwater neritid genera, Clithon, Neritina, Neritilla, Neritoidea and Septaria, evolved at different times from the marine genus Nerita probably in the Southeast Asia region (Gowland & Natarajan, 1972; Stemberger, 1982). A few species have spread westward into the Indian Ocean, whereas many have spread eastward across the Pacific Ocean. In this survey, many more species of nerites were found in the South Pacific (25 species) than in the North Pacific (11 spe-
GASTROPODS ON PACIFIC ISLANDS

FIG. 2. Residual species numbers (N - Y) of freshwater gastropods plotted as deviations from the partial regression of species numbers against water area.


(continued) All species found in the North Pacific were also present in the South Pacific (Table 3). It appears that more species have moved south through the New Guinea-Solomon Island region than have moved north into Micronesia. Such species as Clithon nuculoides, Nentina asperulata and N. labrosa malaniscia do not appear to have dispersed further east than Solomon Islands and New Caledonia, whereas Clithon pintochea, Septaria macrocephala and S. suffruti probably arose in the South Pacific as they are not found as far north as Vanuatu and Solomon Islands (Fig. 1). Unlikely land snails, which show considerable speciation on Pacific islands, e.g. Partula on Samoa and zonitids and Fiji, are not endemic to New Caledonia, whereas Clithon pintochea, Septaria macrocephala and S. suffruti probably arose in the South Pacific as they are not found as far north as Vanuatu and Solomon Islands (Fig. 1).

Although man has probably helped in the distribution of Melanoides tuberculata and Physastra nasuta, which live in taro patches, it is unlikely that man has been responsible for the spread of other species to Pacific islands. Most freshwater gastropods do not live on vegetation but are found on the mud or rocks at the edge of the stream or river bottoms. They are not favored as food and therefore the chance of them being spread purposely by man is small. Some brackish-water natalis species may cling to wooden boats and be carried to nearby islands. Other neritid and zonal spe-

1970, 1976; Haynes, 1986b; Burch & Patter-

don, 1971; MacRae, 1970).
all nontidal species, but Nentilia, Clitina and Septana veligers left in the laboratory can be acclimatized to sea water, and they have re-

mi-allow a few days without settling. This allows them time to be carried by currents to quite distant islands. Usually they are more likely to reach and become established on is-

lands that are near the source of the gastro-

pod veligers.

Island Biogeography

According to the equilibrium theory of is-

land biogeography (MacArthur & Wilson, 1967), the greater the distance of an island from a source of colonization, the smaller the probability of colonization. However, if islands are the same distance from the source, immi-

gration will be greater to the larger island. Iso-

lated small populations on small islands will have a higher rate of extinction due to com-

petition and population fluctuations. If further immigration occurs after all potential niches are filled, interspecific interactions will in-

crease, and the extinction rate will increase and keep the species number in equilibrium.

On the 25 Pacific islands considered, the to-

tal area of water was the main factor influ-

encing the number of freshwater gastropod species present (expressing 86% of the vari-

ation). Because island area and stream length are strongly correlated with water area, their influence on the number of species is incorporated in water area. Distance from the source contributes 8% to the variation in the number of species and unknown factors 7%. The correlation of island area is also largely incor-

porated in water area (r = 0.7312) be-

cause an island with an altitude less than 300 m usually will be without streams, and in gen-

eral the higher an island the greater its stream length, water area and habitat diversity.

The importance that distance contributes to species variation on small islands may be due to the strong possibility of the small area of water drying up and the consequent likelihood of extinction of some or all gastropods. The nearer such islands are to a source of gastro-

pods the more likely immigration is to occur and the number of species to be restored. Ovalau (20 species) and Beqa (13 species), which are close to Viti Levu, have a relatively large number of species, whereas the more distant islands, such as Nanouga (2 spe-

cies), Tug (4 species), Nanouga (8 species) and Poga (11 species), have few species (Tables 2, 3).

Freshwaters on Pacific islands can be di-

vided into six distinct habitats: 1) ponds, taro patches, dec-ovine; 2) shaded brackish water; 3) open brackish water; 4) freshwater influ-

enced by the fale; 5) fast flowing streams and rivers; and 6) cascades (Table 5). Some are inhabited by only a few gastropods, and others are suitable for colonization by a large number of gastropod species. Small islands and islands of low elevation do not have all these different habitats, but those they do have fall into one of these categories. The species inhabiting the habitats are not all the same for each island group.

The number of gastropod species on an is-

land will partially depend on the number of each kind of habitat and their size. These are factors which account for some or all of the unknown 7%, in variation of the number of gastropod species on islands.

The steepest slope for islands with a small area of water has been observed in species-

area curves before (Fig. 3). Williams (1957) gives a similar plot for birds on the Solomon Islands, and Lassen (1975) drew another for freshwater snails in small eutrophic lakes in Denmark. This steepest slope for smaller ponds Lassen (1975) explained by lower im-

migration and an increased extinction rate with decreasing area. Birds carrying immi-

grant snails are less likely to visit small ponds, and small ponds are more likely to freeze.

Similarly, a steeper slope was obtained for Pacific islands with small water area, because the extinction rate increased due to ponds and lower courses drying up and because the survival rate of immigrants is low due to rela-
tively few available habitats.

Most investigations into which factors de-

termine the number of species on islands have involved plants or birds. Johnson & Heyen (1970) found that island area, latitude and soil types were important in the species diversity of plants on the British Isles and on California islands. Harris (1973), using multi-

variate analysis, established that the vari-

ables that contributed to the variation of num-

bers of breeding land birds on the Galapagos Islands were total plant area and altitude (87.7%) and distance (60.9%). Power (1972) found by multivariate analysis that the variation in the numbers of bird species on California islands was caused by the interaction of these vari-

ables: numbers of native plant species and distance from other islands and from the mainland. The variation in numbers of plant species was mainly explained by island area and latitude.
In this investigation, island area and height were important because they determine the diversity and size of the freshwater habitat available. The habitat diversity is best expressed as water area for purposes of multiple regression analysis. Distance from a possible source of new immigrants is also important in determining species numbers, probably because of the high rate of extinction caused by water flowing up and sometimes by whole populations being washed away during tropical cyclones.

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LITERATURE CITED


