RECURRENT GROUP ANALYSIS OF HYPERIID AMPHIPODS FROM THE NORTH PACIFIC CENTRAL GYRE *

ERIC SHULENBERGER

Scripps Institution of Oceanography
La Jolla, California 92093

ABSTRACT

A preliminary analysis of the hyperiid amphipod assemblage of the North Pacific Central Gyre is presented. "Recurrent group" analysis indicates the existence of such amphipod groups in the gyre. These groups frequently include congeners, a result unexpected in light of the "competitive exclusion" principle. More detailed analysis indicates how these congeners, although occurring together, may be dividing up space differently and so coexisting.

INTRODUCTION

This is a report of preliminary results of a detailed analysis of the hyperiid amphipod assemblage of the North Pacific Central Gyre community. The research is part of an intensive, long term investigation, under the leadership of Dr. J. A. McGowan, into the structure ("what lives there and how are the animals distributed in time and space?") and function ("how do the organisms interact, and what are the control mechanisms of the area's biology?") of the gyral community.

The North Pacific Central Gyre was selected as an appropriate site for investigating a pelagic ecosystem because of a-priori reasons to feel that it is a genuine ecosystem in the classical sense (Odum, 1959): a nearly closed system of highly co-evolved organisms, regulated by in-situ processes. The major circulation patterns of the Pacific seem to have remained essentially unchanged since at least the pliocene (Riedel and Funnell, 1964), and the gyre has therefore had a long period of evolution in which to fine tune its internal workings and arrive at some sort of long-term stability. The gyre is a much better approximation to an ideal "closed" system than are most oceanic study areas; at least it is not beset by massive horizontal advection, and it gives indications that its biology is controlled by in-situ processes rather than advective events (McGowan, 1974).

The first step in analysis of any system should be to determine "What is out there and where is it located?" This question is the basis for my current work on gyral hyperiids. Other aspects of gyral ecology are under intensive investigation: copepods (McGowan and Walker, in prep.), microzooplankton (Beers, Reid, and Stewart, 1975), chaetognaths (Lyons, in prep.), nutrients (Eppley et al. 1973), phytoplankton (Venrick, 1971, 1972), mesopelagic fishes (Barnett, 1975), physical microstructure (Gregg and Cox, 1972), primary productivity (Eppley et al. 1973), patchiness (Haury, 1973; Wiebe, 1970, 1971), and other parameters.

*This research was supported in part by NSF grant GA-38002 for improvement of doctoral dissertation research in the biological sciences. Various other support was also received from NSF, the Office of Naval Research, and the Marine Life Research program of Scripps Institution of Oceanography.

METHODS

Over the last decade a large number of month long cruises have been made by Scripps Institution of Oceanography to 28° N, 155° W, about 600 km north of Oahu; this site was selected in expectation that is would be representative of most of the gyre. The cruises cover most seasons of the year, and all used the same central sampling plan and equipment in order to permit direct comparisons. Most sampling procedures are done in intensive replication. Cruises involved with this investigation of the North Pacific Central Gyre are: Climax I (Sept 1968), Climax IIA (Aug 1969), Aries IX (Sept 1971), Cato I (June 1972), Southtow XIII (Feb 1973), Tasaday I (June 1973), Tasaday II (July 1973), Tasaday III (Aug 1973), and Tasaday XI (Mar 1974).

My data are from cruise Climax I during which two parachute drogues were deployed at ten m depths about 10 km apart and a ten day series of around-the-clock depth stratified bongo net (S.I.O. 1966) tows was made between them (see S.I.O. 1974 for drogue tracks and details of sampling plan). Six depth ranges were covered (0–25, 25–50, 50–75, 75–100, 100–350, and 350–600 m); depths were monitored using a Benthos time-depth recorder. Nets were opened at the bottom of a depth range, fished obliquely upwards, and closed at the top of the range; nets were closed automatically by a frame-mounted flowmeter after fishing 400 m^3 per side. All nets were 505 u mesh with 333 u cod ends, and all tows were at a nominal 2½ kts.

I have identified and counted all hyperiid amphipods from 79 of these Climax I bongo samples (one sample = one side of a bongo frame). For the present analysis all samples were designated either "day" (0600–1900) or "night" (2000–0500). All "day" samples taken at the same depth were considered replicates regardless of date taken, as were all "night" samples at a given depth.

RESULTS AND DISCUSSION

Structural Overview of the Hyperiid Assemblage

From analyses of zooplankton catches made in the same area with the Isaacs-Kidd plankton trawl (505 u mesh, 3 m x 3 m mouth), we know that hyperiids rank fifth in overall numerical abundance of major taxa in the gyre (Table 1). They comprise some 5–7% of total individuals in the macrozooplankton (i.e., zooplankton caught by 505 u nets) and are therefore a major portion of the community.

TABLE 1.

Overall Rank-Order of Numerical Abundance of Major Taxa in the North Pacific Central Gyre *

1. COPEPODS	7. "jellies"
2. EUPHAUSIIDS	8. PTEROPODS
3. CHAETOGNATHS	9. DECAPODS
4. OSTRACODS	10. FISH LARVAE
5. AMPHIPODS	11. HETEROPODS
6. THALIACIANS	12. POLYCHAETES

* From samples collected with the Isaacs-Kidd plankton trawl (505 u mesh, 3 m x 3 m mouth) in open oblique nighttime hauls from 0–300 m at 28° N, 155° W.

I have found representatives of over half (13 of 21) the world's hyperiid families, over half (42 of 71) the world's genera, and about ⅓ of the world's species (83 of approximately 300) in these samples. Lumping counts from all samples, a total of 14,851 individuals was taken, with overall abundances ranging from 1 to 3695 individuals per species. Individual samples contained from 1 to 38 species and from 1 to 658 individuals.

Wiebe (1971) studied the ability to accurately rank species (in terms of numerical abundance) using samples consisting of varying numbers of individuals. Accuracy of ranking is a function not only of sample size but also of the underlying community structure, especially degree of dominance and patchiness. However, his results suggest that with nearly 15,000 animals we can be fairly certain of the first 10 to 15 ranks. If we deal mainly with the top 10 to 15 hyperiid species, we are including 75–85% of the total individuals (Figure 1), and what is happening within that group is basically "what is going on among amphipods in general."

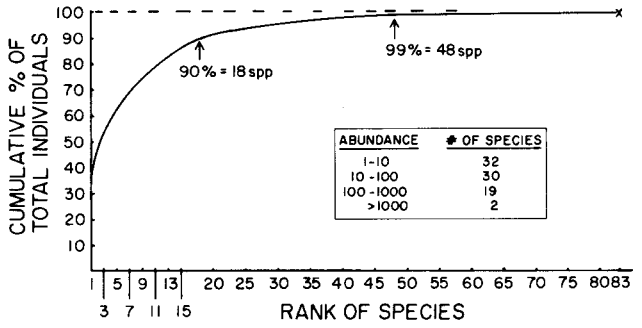

FIGURE 1. Cumulative percentage curve of hyperiid amphipod fauna from the North Pacific Central Gyre; totals for 79 bongo net tows are used. Grand total individuals = 14,851.

Relationships Among Hyperiid Species

As previously stated, this community has had a long time to evolutionarily fine tune its internal workings. The series of cruises listed above has shown that many factors, from primary productivity to rank order of abundance (abbreviated ROA) of species within major taxa, tend to be relatively constant within the gyre. Therefore, when we try to examine the internal workings of any portion of the community we are probably looking for subtle shifts and changes in internal structure. We must at present use rather unsubtle sampling (bongo net tows integrate over a horizontal distance of hundreds of meters) and statistical techniques (generally rank-order statistics). Because we must seek out subtle effects with unsubtle techniques, small changes or non-spectacular results (which might otherwise be viewed with skepticism) may have to be accepted as being true indicators of what is actually going on within the community.

In general, species (particularly small planktonic organisms) must encounter one another in order to interact, and it is in the interactions of species that one may seek control mechanisms for the ecosystem if it is in fact regulated by in-situ processes. An appropriate question is, then, "what species occur together?" If we know this, then we may further examine those sets of co-occurring species, hoping to answer such questions as "How do similar species manage to co-exist in an apparently physically unstructured environment?"

To aid in sorting out such groups of co-occurring species from a large mass of data (here 83 species and 79 samples), we have a technique available called "recurrent group analysis," Regroup for short (Fager, 1957). The object of this technique is to locate and identify groups of species which are commonly part of one anothers' environment ("part of" in the sense of being caught in the same bongo tow).

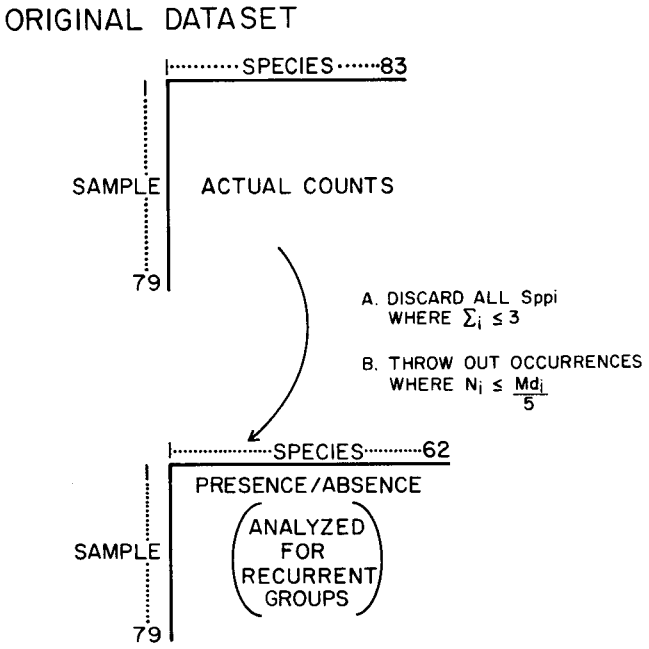

FIGURE 2. Original raw-data matrix of hyperiid species and their occurrences by samples, and the data matrix as reduced for recurrent group analysis.

Regroup calculates an index of affinity (ranging from 0.0 to 1.0) for every possible species pair. This index is based on presence and absence data arranged by sample (i.e., what species occurred in what samples; Figure 2). If we assume as a null hypothesis that species co-occur purely at random (i.e. that there is no pattern to nature), program AFFIN (Fager, MS) can calculate probability levels for affinity indices. For instance, the probability of "affinity index of sp. X and sp. Y being greater than 0.70 due strictly to chance" is less than .002 (Figure 3). Probability levels ("P") for indices of affinity depend on the number of occurrences for each species, and must be calculated anew for each new set of data.

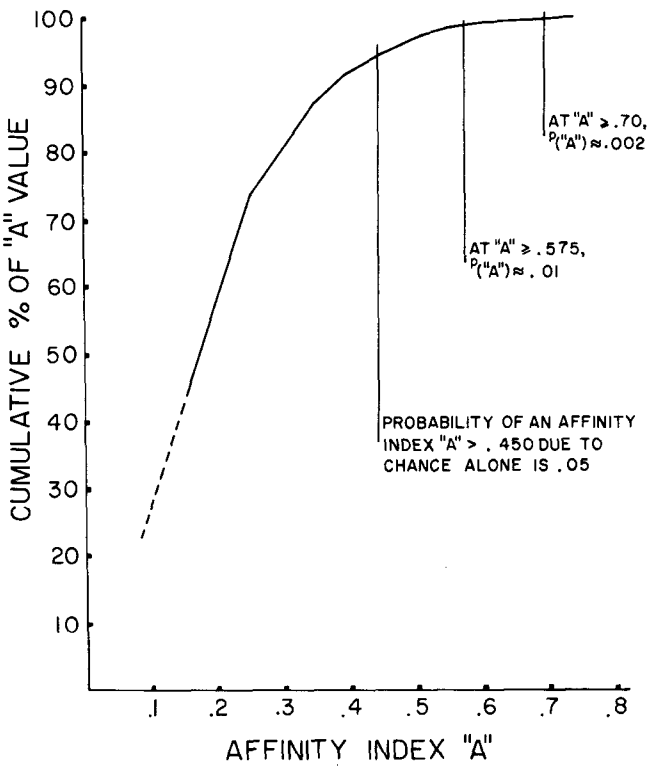

FIGURE 3. Cumulative percentage curve for indices of affinity assuming random associations of species in samples. Generated from the reduced data matrix of Figure 2.

Regroup forms the largest possible group of species within which all species have an affinity index greater than, say, 0.575 (P about .01 for present data) for one another. This represents a stringent grouping criterion; each species must have a high affinity index for all others in the group in order to be included. The idea is to sort out closely knit groups of species, (recurrent groups), wherein the rate of co-occurrence is much larger than can be expected due to chance alone. However, this does not require that all members of a group be present whenever any one member is present, merely that the rate of such occurrences be very high. Once the largest possible such group has been formed, it is removed from the analysis and the Regroup procedure applied to the remaining species to check for the existence of other groups. In Regroup, a species not included in a group may still be an "affiliate" of the group if that species has affinities only with group members.

It is unreasonable to include some species in such an analysis, particularly very rare species; all species for which the total caught was three or fewer were eliminated (Figure 2). In addition, contamination, minor net leakage, and so forth call into suspicion very low occurrences of otherwise common animals. To adjust for such problems, all species counts where "number of sp. X caught" was less than "20% of the median for sp. X" were reduced to zero. This cleans up the data considerably and allows us to seek clear cut patterns.

We do in fact get such recurrent groups among the hyperiids. Regroup analysis of the final data matrix (Figure 2) produced six groups, containing from two to seven members per group (Table 2). These groups are remarkably clearcut. In Regroup analysis of copepod data from samples taken during the same Bongo series, most groups had affiliates as well: no such affiliates were found for any amphipod group.

TABLE 2

Membership of Groups as Determined by Recurrent Group Analysis

Group #	Species ID #	Overall ROA*	Species	
I	6	11th	*Brachyscelus crusculum*	
	20	16th	*Hyperietta luzoni*	CONGENERS
	23	10th	*Hyperietta stephenseni*	CONGENERS
	24	2nd	*Hyperietta vosseleri*	CONGENERS
	29	5th	*Lestrigonus bengalensis*	
	35	18th	*Lycaeopsis themistoides*	
	52	13th	*Phronimopsis spinifera*	
II	7	12th	*Anchylomera blossevillei*	
	13	9th	*Eupronoe armata*	CONGENERS
	15	4th	*Eupronoe sp "A"*	CONGENERS
	26	3rd	Hyperioides sibaginis	
III	2	22nd	*Amphithyrus bispinosus*	
	32	17th	*Lestrigonus schizogeneios*	
	44	8th	*Paratyphis parvus*	
IV	53	14th	*Phrosina semilunata*	CONFAMILIALS
	56	1st	*Primno rectimanus*	CONFAMILIALS
V	25	7th	*Hyperioides longipes*	
	61	15th	*Scina sp "A"*	
VI	60	6th	*Scina sp "B"*	
	76	25th	*Vibilia armata*	

* Rank-order of numerical abundance (for lumped counts from 79 samples).

The hyperiid groups did not necessarily consist only of very high-ranked species, nor did all the high-ranked species group together. For instance, Group I includes species whose overall ROA were 11, 16, 10, 2, 5, 18, and 13 (Table 2). Group II included ROAs 12, 9, 4, and 3. The most common species was *Primno rectimanus*[1], which grouped in Group IV. Group IV consists of only two species, the other of which is *Phrosina semilunata:* these two species are confamilial and quite similar morphologically.

The three most abundant species fell into different groups. There is a tendency for at least some members of each group to be close relatives. Group I includes three very similar congeners, Group II includes a pair of very similar congeners, and Group IV consists of similar confamilials (the only two species of that family found in the gyre). It is frequently the case that morphological similarity implies functional similarity. If this is true for hyperiids, a tendency for similar species to occur together is disturbing, for ecological theory states that two species cannot do overly similar things at the same place and time or one will be eliminated in the resultant competition. These groups therefore warrant closer examination.

TABLE 3

Overall Rank-Orders of Abundances by Species within Depth*

Depth	Species ID # (Group I only)						
	6	20	23	24	29	35	52
A) Day							
0–25 m	2	4	3	5	1	6	7
25–50	6½	6½	2	1	3½	5	3½
50–75	4½	6	2	1	3	7	4½
75–100	5	2	3½	1	7	6	3½
100–350	5	6	2	3	4	7	1
B) Night							
0–25 m	2	6	5	1	3	4	7
25–50	4½	4½	3	1	2	6	7
50–75	7	4	5	1	2	6	3
75–100	6	2	5	1	4	7	3
100–350	5	4	2	1	7	6	3

* Ranks were obtained by summing all replicates at a time/depth, and ranking those species-sums within the time/depth. Numbers of replicates are given in Table 4.

Because it is the largest group, I will deal only with Group I for detailed analysis. The least sensitive question one might ask is, "Does the group as a whole exhibit a tendency towards internal ROA stability across depths?" This is really asking, "Did Regroup select a batch of species, based on presence/absence, which appears to have even stronger internal structure?" The answer is 'yes' for Group I for both day and night. Using the Kendall Concordance ("W") test for five sets of seven ranks (Table 3) to check the null hypothesis "there is no agreement over depths as to ROA within Group I", we must reject the hypothesis for both day ($W = .414$, $p \leq .05$) and night ($W = .485$, $p \leq .01$). Despite some impressive changes in within-group ROA of individual species from depth to depth (e.g., during the day, species #29 is ROA 1 at the surface but ROA 7 at 75–100 m) there is an overall significant ($p < .05$) agreement as to ROA.

[1] *Primno rectimanus = Primno latreilleri.*

A more detailed question is to ask whether there is repeatability of intragroup ROA at a given time of day and depth. This may again be checked using Kendall Concordance: the null hypothesis is "there is no agreement between replicates at a time and depth as to rank order of abundance of Group I species." There is very highly significant ($p < .01$) agreement between replicates at each time and depth (Table 4), and we reject the null hypothesis for all times and depths. In other words, the "replicates" at a time and depth, which often include samples taken on different dates within the 10-day sampling period, do in fact appear to be replicates of a constant condition.

TABLE 4

Analysis of Group I for Agreement between Replicates as to Rank-Order of Abundance at a Time/Depth

Depth	Day			Night		
	n*	W*	P*	n	W	P
0–25 m	8	.74	$<<.01$	7	.63	$<<.01$
25–50	7	.46	$<.01$	5	.65	$<<.01$
50–75	11	.44	$<<.01$	4	.62	$<<.01$
75–100	9	.51	$<<.01$	4	.65	$<<.01$
100–350	7	.63	$<<.01$	6	.67	$<<.01$

* n = Number of replicates at time/depth. W is the Kendall Concordance statistic calculated for n sets of seven ranks. P is the approximate probability that such a W value might be due to chance alone.

Another question of interest is "Do the various Group I species agree on where, horizontally (i.e., in which tows) to be abundant?" Because there is agreement on overall ROA structure within the group, we expect the answer to be 'yes'. If any one species becomes more abundant they must all become more abundant, or else the ROA agreement should fail to appear. Null hypothesis is "there is no agreement among species as to where (i.e., in which replicate) to be abundant." Again we test using Kendall Concordance; there is significant agreement ($p \leq .05$) on where, horizontally, to be abundant in only six of ten time/depths (Table 5). Due to the problems of multiple testing, only $P \leq .01$ should be regarded as truly statistically significant, reducing the number of positive agreements to four. This implies that while there exists an overall trend towards such agreement, it is not very strong; this in turn implies that multispecies patchiness is not particularly pronounced.

TABLE 5

Analysis of Group I for Agreement between Species as to Where (in which replicates) to be Abundant

Depth	Day			Night		
	n*	W*	P*	n	W	P
0–25 m	8	.34	$\sim.01$	7	.38	$<.01$
25–50	7	.63	$<<.01$	5	.40	$<.01$
50–75	11	.15	$>.20$	4	.05	$>.20$
75–100	9	.33	$\sim.01$	4	.11	$>.20$
100–350	7	.31	$\sim.05$	6	.22	$\sim.20$

* n = Number of replicates at time/depth. W is the Kendall Concordance statistic calculated for seven sets of n ranks. P is the approximate probability that such a W value might be due to chance alone.

Searching further for structure we may ask, "Do the species of Group I agree on a depth at which to be most abundant?" This requires re-ranking of the

average abundance data; ranks are now *within* each species *across* depths (Table 6). For both day and night we accept the null hypothesis "there is no agreement among Group I species as to the best depth (i.e., depth of maximum abundance) at which to be caught". (Kendall Concordance test for seven sets of five ranks: day $W = .266$, $p = .10$; night $W = .078$, $p \simeq .50$). We must then accept the inverse, that the species of Group I find different depths to be "best", which implies that vertical as well as horizontal patchiness is not very strongly multispecific. This is the first clue to the puzzle of recurrent groups containing congeners.

TABLE 6

Group I Species Ranked (Within Each Species) as to Average Abundance at Each Time/Depth

A) Day

Depth	Species ID# (Group I only) 6	20	23	24	29	35	52
0–25 m	1	4	5	5	1	4	5
25–50	3	2½	3½	2	2	1	3
50–75	2	2½	2	1	3	2	2
75–100	4	1	1	3	4	3	4
100–350	5	5	3½	4	5	5	1

B) Night

0–25 m	1	4	2	2	2	1	3
25–50	2	5	5	1	3	5	5
50–75	4	2	3	3	1	2	4
75–100	3	1	4	4	4	3	2
100–350	5	3	1	5	5	4	1

Looking for evidence of diurnal vertical migration is even more enlightening. A species may exhibit "normal" (upwards at night) vertical migration, lack of vertical migration, or "reverse" (downwards at night) vertical migration. The seven species in Group I are as evenly split as is possible among the three alternatives (Table 6): three species (ID nos. 6, 20, 52) show no migration, two species (ID nos. 23 & 29) show reverse migration, and two species (ID nos. 24 & 35) show normal migration. What is most interesting is that each of the three congeners does one of these three distinctly different things, thus providing evidence for the separation of roles which theory requires of closely related species found living together.

CONCLUSIONS

A number of fairly firm conclusions may be stated even at this preliminary stage in the analysis.

1. A species list has been generated for the gyre.
2. There are recurrent groups of amphipods in the gyral community.
3. These groups can and do include congeners.
4. The groups have a significantly consistent internal rank structure both within and across depths, but much more so within depths.
5. Both horizontal and vertical patchiness appear not to be strongly multispecific in nature.
6. There is evidence, from within Group I alone, of normal, reverse, and absence of diurnal vertical migration.
7. The ecological problem of coexistence of morphologically very similar congeners may yield to detailed examination of spatial and temporal distributions.

There appears to be an enormous amount of structure to the community in spite of the superficial homogeneity of the environment. The gyral community is a finely tuned system and we badly need better ways of examining it, but detailed analyses of existing samples and data can yield considerable insights.

REFERENCES

Barnett, M.A. 1975. Studies on the patterns of distribution of mesopelagic fish faunal assemblages in the central Pacific and their temporal persistence in the gyre. PhD thesis, Scripps Institution of Oceanography, Univ. Calif. San Diego. 145p.

Beers, J.R., F.M.H. Reid, and G.L. Stewart. 1975. Microplankton of the North Pacific Central Gyre. Population structure and abundances, June 1973. Int. Revue ges. Hydrobiol., 60: 5, p 607–637.

Eppley, R.W., E.H. Renger, E.L. Venrick, and M.M. Mullin. 1973. A study of plankton dynamics and nutrient cycling in the central gyre of the North Pacific Ocean. Limnol. and Oceanogr., 18(4): 534–551.

Fager, E.W. 1957. Determination and analysis of recurrent groups. Ecology 38(4): 586–595.

Gregg, M.C. and C.S. Cox. 1972. The vertical microstructure of temperature and salinity. Deep-Sea Res., 19: 355–376.

Haury, L.R. 1973. Studies on the sampling and small-scale pattern of marine zooplankton. PhD thesis, Scripps Institution of Oceanography, Univ. Calif. San Diego. 176 p.

McGowan, J.A. 1974. The nature of oceanic ecosystems p9–28 *in* The Biology of the Oceanic Pacific, C.B. Miller, Ed. Oregon State Univ. Press, Corvallis.

Odum, E.P. 1959. Fundamentals of Ecology, 2nd Ed. Saunders, Phila. 546 p.

Riedel, W.R., and B.M. Funnell. 1964. Tertiary sediment cores and microfossils from the Pacific Ocean floor. Quart. J. Geolog. Soc. Lond., 120: 305–368.

S.I.O. 1966. A new opening-closing paired zooplankton net. Scripps Instit. Oceanog. Ref., 66-23: 1–56.

_____ 1974. Data report; physical, chemical, and biological data, Climax I expedition, 19 Sept–28 Sept 1968. Scripps Instit. Oceanogr. Ref., 74-20: 1–41.

Venrick, E.L. 1971. Recurrent groups of diatom species in the North Pacific. Ecology 52(4): 614–625.

_____ 1972. Small-scale distributions of oceanic diatoms. Fish. Bull., U.S., 70(1): 363–372.

_____, J.A. McGowan, and W.A. Mantyla. 1973. Deep maximum of photosynthetic chlorophyll in the Pacific Ocean. Fish Bull., U.S., 71(1): 41–52.

Wiebe, P.H. 1970. Small-scale spatial distribution in oceanic zooplankton. Limnol. and Oceanogr., 15(2): 205–217.

_____ 1971. A computer model study of zooplankton patchiness and its effects on sampling error. Limnol. and Oceanogr., 16(1): 29–38.