

# Length-Weight Regressions and Condition Indices of Lutjanids and Other Deep Slope Fishes from the Mariana Archipelago

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**Abstract**—Predictive length-weight regressions for 23 commercial species of Marianas bottom fish are derived, based on a resource assessment program of hook-and-line sampling over deep slope (165–240 m) fishing grounds. Species in the snapper (Lutjanidae), grouper (Serranidae), and jack (Carangidae) families predominated in the catch, especially members of the deep-sea lutjanid genus *Pristipomoides*. Of the species examined, eight were characterized by allometric growth. An index of fish condition was calculated for individuals from the most abundant species, and this was analyzed for regional variation. It was found that bottom fish populations from the seamounts of the West Mariana Ridge were consistently heavier and more robust for their length than those sampled elsewhere.

## Introduction

Tropical deep slope fisheries for demersal fishes have assumed increased importance to many of the developing countries of the Pacific Basin (Hume, 1975, 1976; Hume and Eginton, 1976; Eginton and Mead, 1978; Mead, 1978; Taumaia and Crossland, 1980). A number of stock assessments have shown the existence of resources of significant commercial value, and these are now beginning to be more fully exploited and utilized (Ralston and Polovina, 1982; Ralston, 1984; Brouard and Grandperrin, 1985; Polovina and Ralston, 1986). Most of the species concerned are deepwater (50–300 m) forms belonging to the snapper (Lutjanidae), grouper (Serranidae), and jack (Carangidae) families, groups for which notably little information exists with which to manage the developing resource base.

One of the most basic relationships used in fisheries stock assessment and management is the length-weight regression (Ricker, 1975; Anderson and Gutreuter, 1983). An equation relating biomass to length is particularly useful in yield analysis. Although some studies have presented length-weight parameter estimates for a number of deep slope fishes (Forster *et al.*, 1970; Loubens, 1980; Uchiyama *et al.*, 1984; Brouard and Grandperrin, 1985), many species are currently harvested from throughout the Indo-Pacific region, for which this simple but useful relationship has not been determined. Significantly, most of these fishes are known to have wide geographic ranges (Druzhinin, 1970).

Presented here are the results of a study on length-weight relationships and condition indices for a variety of commercial fishes harvested during a resource assessment of the deep slope bottom fish community in the Mariana Archipelago, undertaken by the Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service.

### Materials and Methods

All sampling was conducted from the National Oceanic and Atmospheric Administration's ship *Townsend Cromwell* over a 2-year span from April 1982 to May 1984. During this time six 40-day cruises were completed and samples were obtained during all months of the year except March, September, and October (Table 1). Fishing was done throughout the Marianas (Fig. 1), including the offshore seamounts of the West Mariana Ridge, as part of an investigation of demersal bottom fishes and deep-sea shrimp (*Heterocarpus* spp.).

Virtually all the fishes reported on here were caught during the day by hook-and-line gear on hydraulically powered fishing gurdies. Numbers 20 and 28 Tonkichi round fish hooks, baited with stripped squid, were used exclusively while fishing. Four hooks were attached by short (30 cm) gangions to each of four separate drop lines. Fishing was targeted between depths of 165 and 240 m, although some catches were made shallower and deeper. In addition, specimens of *Selar crumenophthalmus* (Carangidae) and *Lutjanus kasmira* (Lutjanidae) were obtained at anchored 40 m depth night-light stations using handlines with small feathered jigs.

All fish landed were identified to species, measured to the nearest 0.1 cm fork length (FL) on a measuring board, and weighed to the nearest 0.01 kg on a balance scale.

To test for differences in condition factor the K statistic was computed (Weatherley, 1972; Anderson and Gutreuter, 1983). This is defined as:

$$K = \frac{\text{Weight}}{\text{FL}^b} \times 100,000$$

where b is the slope of the regression of log(weight) on log(FL) if growth is significantly allometric, and is 3 otherwise. In any comparison, large values of K reflect heavy weight,

Table 1. Dates and locations of *Townsend Cromwell* research cruises (see also Figure 1).

Cruise	Dates	Locations Visited
TC-82-02	4/19/82–6/2/82	Esmeralda Bank, Anatahan, Pagan, Guam, Sarigan, Tinian, Aguijan
TC-82-03	6/4/82–7/16/82	Guam, Esmeralda Bank, 38-Fathom Bank, Alamagan, Farallon de Medinilla, Pagan, Guguan, Agrihan, Arakane Reef
TC-82-04	7/20/82–8/31/82	Pathfinder Reef, Pagan, Saipan, Maug, Asuncion, Esmeralda Bank, Rota, Bank A, Arakane Reef, 38-Fathom Bank
TC-83-05	11/18/83–12/20/83	Bank C, Pagan, Alamagan, Guguan, Saipan, Anatahan, 38-Fathom Bank, Esmeralda Bank, Arakane Reef
TC-84-01	1/4/84–2/12/84	Esmeralda Bank, Alamagan, Sarigan, Pagan, Agrihan, Bank D
TC-84-04	4/7/84–6/1/84	Esmeralda Bank, Pathfinder Reef, Rota, Farallon de Medinilla, Guam, Bank A, Pagan, Alamagan

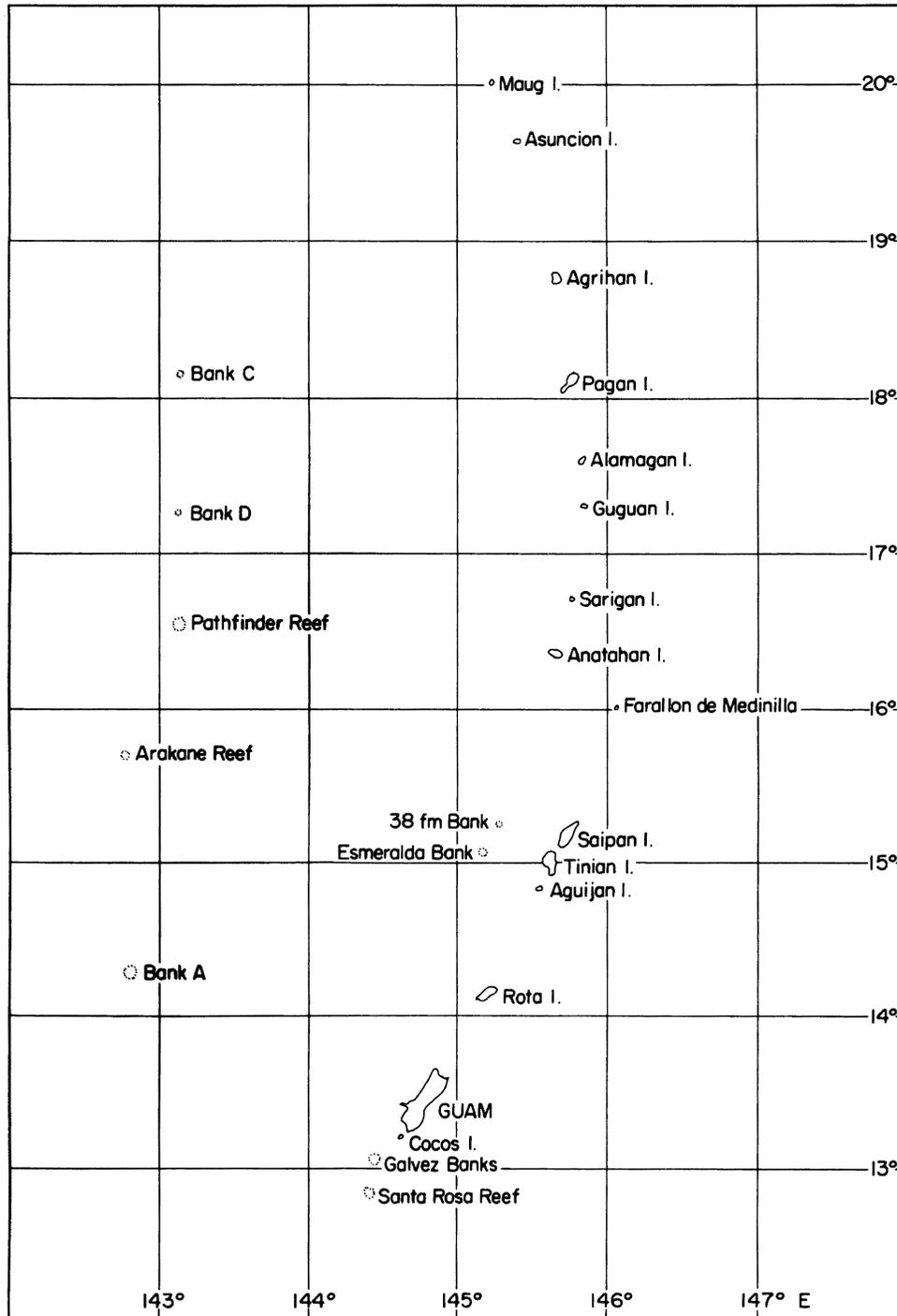


Fig. 1. Map of the Mariana Archipelago showing sampling locations.

after correcting for differences in length. Consequently, the statistic is a useful indicator of fish condition.

### Results

Seventy-one species of fish were caught during the six cruises, comprising a total of 10,127 individuals. Of these, however, 97.4% were represented by the 23 species listed in Table 2. Deepwater lutjanids, including especially the genus *Pristipomoides*, were by far the most abundant. The catch composition, by family and genus, is typical of tropical deep slope fish communities worldwide (Munro, 1983; Ralston and Polovina, 1982; Forster, 1984; Brouard and Grandperrin, 1985; Ralston *et al.*, 1986). Further, many of the species listed command unusually high prices in the marketplace.

Table 2. Length-weight regressions for Mariana bottom fish. Given for each species are the sample size (N), the fork length (FL) size range over which the data were fitted (LB = lower bound, UB = upper bound), the regression  $r^2$  value, and the estimates of intercept and slope with their respective standard errors (S.E.) for the model  $\log(Wt) = a + b \cdot \log(FL)$ . Fork length is in cm and weight in kg. Species demonstrating significant allometric growth ( $P = 0.05$ ) are marked with an asterisk.

Family Species	N	Size Range LB-UB	$r^2$	Intercept (S.E.)	Slope (S.E.)
<b>Lutjanidae</b>					
<i>Pristipomoides zonatus</i>	3890	19-47	90%	-10.76 (0.0566)	2.995 (0.0157)
<i>P. auricilla</i>	1166	22-42	95%	-11.04 (0.0763)	3.049 (0.0216)*
<i>P. flavipinnis</i>	507	24-50	93%	-10.42 (0.1260)	2.854 (0.0344)*
<i>P. filamentosus</i>	192	24-64	98%	-10.56 (0.1090)	2.890 (0.0283)*
<i>P. sieboldii</i>	55	26-43	96%	-11.88 (0.3114)	3.258 (0.0893)*
<i>P. amoenus</i>	23	23-33	96%	-11.27 (0.4521)	3.140 (0.1366)
<i>Etelis carbunculus</i>	969	21-55	94%	-10.91 (0.0867)	2.984 (0.0243)
<i>E. coruscans</i>	197	45-96	97%	-10.97 (0.1692)	2.961 (0.0394)
<i>Aphareus rutilans</i>	73	42-98	97%	-11.08 (0.2625)	2.961 (0.0623)
<i>Lutjanus bohar</i>	31	26-75	99%	-11.32 (0.1952)	3.120 (0.0504)*
<i>L. kasmira</i>	13	16-28	96%	-11.40 (0.5725)	3.154 (0.1827)
<i>Aprion virescens</i>	15	55-83	97%	-12.17 (0.6689)	3.264 (0.1585)
<b>Lethrinidae</b>					
<i>Lethrinus rubrioperculatus</i>	39	27-40	85%	-10.19 (0.6565)	2.774 (0.1883)
<i>Gymnocranius japonicus</i>	20	34-54	86%	-8.60 (0.8756)	2.431 (0.2315)*
<b>Carangidae</b>					
<i>Caranx lugubris</i>	320	24-76	99%	-10.83 (0.0588)	3.001 (0.0153)
<i>Seriola</i> sp.	44	40-114	98%	-10.60 (0.2861)	2.876 (0.0653)
<i>Selar crumenophthalmus</i>	747	15-30	93%	-11.51 (0.1048)	3.180 (0.0324)*
<b>Serranidae</b>					
<i>Epinephelus</i> sp.	26	52-148	99%	-12.02 (0.3278)	3.231 (0.0723)*
<i>E. morrhua</i>	15	34-84	99%	-11.61 (0.3237)	3.130 (0.0764)
<i>Saloptia powelli</i>	47	33-47	91%	-11.70 (0.5634)	3.175 (0.1525)
<i>Cephalopholis igarasiensis</i>	10	23-41	97%	-9.92 (0.5752)	2.748 (0.1666)
<i>Variola louti</i>	13	32-53	95%	-10.91 (0.8212)	2.968 (0.2168)
<b>Scombridae</b>					
<i>Gymnosarda unicolor</i>	26	54-102	99%	-11.46 (0.3115)	3.065 (0.0729)

Table 3. The results of ANOVA on condition indices of bottom fish species landed from different geographic locations (see text for locality definitions). The dependent variable is the K statistic, an index of condition. NS indicates non-significance whereas an asterisk shows that significant differences were detected at the  $P = 0.05$  level.

Species	F	df	P	r <sup>2</sup>	Comparison of Means		
					I-II	I-III	II-III
<i>Pristipomoides zonatus</i>	15.88	2-3887	0.0001	0.81%	NS	*	*
<i>P. auricilla</i>	17.22	2-1163	0.0001	2.88%	NS	NS	*
<i>P. flavipinnis</i>	2.41	2-504	0.0912	0.95%	NS	NS	NS
<i>P. filamentosus</i>	4.67	2-189	0.0105	4.71%	NS	NS	*
<i>Etelis carbunculus</i>	1.23	2-966	0.2923	0.25%	NS	NS	NS
<i>E. coruscans</i>	0.20	2-194	0.8206	0.20%	NS	NS	NS
<i>Caranx lugubris</i>	3.95	2-317	0.0203	2.43%	NS	NS	*
<i>Selar crumenophthalmus</i>	38.96	2-744	0.0001	9.48%	*	*	NS

Length-weight regressions for each of the 23 species are presented in Table 2. The weight of fish is typically related to length by the power function, linearized by a double logarithmic transformation of the data (Ricker, 1975). Presented for each species are: 1) the sample size, 2) the FL size range over which the regression was performed (i.e., lower and upper bounds), 3) the goodness of fit as indicated by the  $r^2$  value, 4) the estimate of intercept, including standard error (S.E.), and 5) the estimate of slope and S.E. All results are given based on transformations of weight in kilograms and fork length in centimeters to natural logarithms, and all regressions are significant to at least the  $P = 0.005$  level.

During sampling it was apparent that fishes from the northern islands of the Mariana Ridge (Scott *et al.*, 1980) were differently colored than those from the more southerly islands. Those from the former region were frequently much darker than conspecifics from the latter region. Furthermore, fish sampled from the offshore seamounts of the West Mariana Ridge seemed not only more abundant, but larger and more robust than those from other sampling locations (Polovina, 1986). Differences such as these suggested that condition factors of bottom fish subpopulations might vary among geographical regions.

To test for this possibility, each specimen was assigned to one of three broad geographic areas. This classification was based on the geologic history of the Mariana Archipelago (Scott *et al.*, 1980; see Fig. 1): Area I—the southern limestone islands of the Mariana Ridge which were formed 30–40 million years ago, including Guam, Rota, Tinian, Saipan, Aguijan, and Farallon de Medinilla; Area II—the recently formed basaltic northern islands of the Mariana Ridge (formed 1 million years ago to present), including Esmeralda Bank, 38-Fathom Bank, Anatahan, Sarigan, Guguan, Alamagan, Pagan, Agrihan, Asuncion, and Maug; and Area III—the offshore seamounts of the West Mariana Ridge which arose 10–20 million years ago, including Arakane Reef, Pathfinder Reef, Bank A, Bank C, and Bank D.

Table 3 presents the results of ANOVA on the K values for each of eight species classified by geographic location. Only those species which were collected in excess of

Table 4. Comparison of mean condition indices by species and location. For each species the mean K statistic is given from each of three different geographic areas, followed by a ranking of the means by significant differences ( $P = 0.05$ ). N is the sample size for each mean. See also Table 3.

Species	Area I		Area II		Area III		Rank Order
	$\bar{K}$	N	$\bar{K}$	N	$\bar{K}$	N	
<i>Pristipomoides zonatus</i>	2.07	202	2.09	2365	2.13	1323	I & II < III
<i>P. auricilla</i>	1.61	96	1.59	574	1.64	496	II < III
<i>P. filamentosus</i>	2.61	46	2.55	90	2.64	56	II < III
<i>Caranx lugubris</i>	2.00	24	1.95	86	2.00	210	II < III
<i>Selar crumenophthalmus</i>	0.98	275	1.03	153	1.02	319	I < II & III

100 individuals were included for analysis. Five of the eight species tested (i.e., *Pristipomoides zonatus*, *P. auricilla*, *P. filamentosus*, *Caranx lugubris*, and *S. crumenophthalmus*) showed significant differences in condition among the three regions. The ANOVA  $r^2$  values, however, indicate that the treatment effect (i.e., locale) accounts for only a minor portion of the variation in K, with values ranging from 0.81 to 9.48% among these five species.

To specifically identify where treatment differences lay, *a posteriori* testing of the class means was performed using Sidak t-tests (SAS, 1982). This method controls the experiment-wide probability of committing Type I error, and is useful when multiple comparisons are performed. The data in Table 3 show that in four of the five significant cases, mean K values from Areas II and III were different from each other. Importantly, these differences were consistent in direction (Table 4). Note that for the four bottom fish species, the mean K statistic from the seamounts (Area III) was greater than that calculated from the basaltic northerly islands of the Mariana Ridge (Area II). The single other significant result, for *S. crumenophthalmus*, showed that the means of Areas II and III were greater than that from Area I. Moreover, of the three species which failed to show significant differences in condition among areas, two were rarely caught at seamount locations (*P. flavipinnis* and *E. coruscans*). When taken as a whole, these results indicate that the fishes sampled from the seamounts of the West Mariana Ridge were heavier and more robust than those from other locations.

### Discussion

A slope equal to 3 from the regression of  $\log(\text{weight})$  on  $\log(\text{FL})$  reflects isometric growth; that is, no change in either body proportion or density with changing length (Ricker, 1975; Anderson and Gutreuter 1983). Of the species listed, eight demonstrate allometry, in that the slope of the regression equation is either significantly greater or less than 3 over the ranges of lengths indicated. Of these, *P. flavipinnis*, *P. filamentosus*, and *Gymnocranius japonicus* become relatively lighter with increasing length (i.e., slope less than 3); whereas *P. auricilla*, *P. sieboldii*, *Lutjanus bohar*, *S. crumenophthalmus*, and *Epinephelus* sp. all show an increase in relative weight with increasing length (slope greater than 3). The growth pattern of the remaining 15 species could not be distinguished from isometric.

Uchiyama *et al.* (1984) provided length-weight parameter estimates for eight species of bottom fish from the Northwestern Hawaiian Islands. Six of these were also found during the present study in the Marianas, including *P. zonatus*, *P. filamentosus*, *P. sieboldii*, *Etelis carbunculus*, *E. coruscans*, and *Seriola* sp. Although no error estimates were provided for their statistics, there is generally good correspondence between their results and mine. In particular, their estimate of slope was within the 95% confidence interval of slope derived here for *P. filamentosus*, *P. sieboldii*, *E. carbunculus*, and *Seriola* sp. The same is true for the estimate of slope provided by Forster *et al.* (1970) for *E. carbunculus* from Aldabra in the western Indian Ocean, the only species they had sufficient data to analyze. These results suggest a pattern of distinct morphological similarity in bottom fish stocks from widely divergent localities, supporting the application of the parameter estimates presented in Table 2 to conspecific stocks from regions other than the Marianas.

Intraspecific variation in condition index, as demonstrated here, has been associated with a variety of factors. Foremost among these are sexual dimorphism, diel patterns in feeding activity, seasonal differences in maturational state, and gross differences in the nutritional state of fish populations from different localities or habitats (Weatherley, 1972). The first two putative explanations are unlikely because samples were obtained haphazardly with respect to sex and time of day at all three sites. Thus no systematic bias was introduced into the sampling procedure from these effects, which in turn could have affected the outcome of the ANOVA. Moreover, there is little possibility that the samples obtained within the three geographic regions were confounded by a seasonal effect (Table 1). Samples were obtained during all seasons, and visits to all three areas were accomplished during each of the six cruises. Because of this balance in sampling it is unlikely that the statistical differences in condition factors associated with the geographic classification, as slight as they are, could have been due to a disguised seasonal effect. Rather, it would seem that slight but real differences in condition exist between populations of these fishes on the seamounts and elsewhere.

Previous work has shown that seamounts can induce the formation of semi-stationary anticyclonic eddies (i.e., Taylor columns) over their summits, with associated upwelling of cold nutrient rich water (Borets, 1979; Cheney *et al.*, 1980; Roden *et al.*, 1982). Thus, depending on eddy stability and persistence, seamount communities may benefit from enhanced production (Uda and Ishino, 1958; Genin and Boehlert, 1985). Increased productivity may, in turn, enhance the condition of the resident fish fauna.

Alternatively, seamounts may entrap and accumulate vertically migrating plankton and micronekton by interfering with the diurnal descent of pelagic species horizontally advected over the summit by currents (Isaacs and Schwartzlose, 1965; Tseitlin, 1985). Such a process would augment the forage base of the resident fish community, also leading to elevation of condition indices. Without further information concerning the physical and biological oceanography of the seamounts of the West Mariana Ridge, however, any explanation of the patterns reported on here must remain speculative.

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## References Cited

- Anderson, R. O., and S. J. Gutreuter. 1983. Length, weight, and associated structural indices. In L. A. Nielsen and D. L. Johnson, (eds.), *Fisheries Techniques*, pp. 283–300. Am. Fish. Soc.
- Borets, L. A. 1979. The population structure of the boarfish, *Pentaceros richardsoni*, from the Emperor Seamounts and the Hawaiian Ridge. *J. Ichthyol.* 19: 15–20.
- Brouard, F., and R. Grandperrin. 1985. Deep-bottom fishes of the outer reef slope in Vanuatu. ORSTOM Centre, Noumea, New Caledonia.
- Cheney, R. E., P. L. Richardson, and K. Nagasaka. 1980. Tracking a Kuroshio cold ring with a free-drifting surface buoy. *Deep-Sea Res.* 27A: 641–654.
- Druzhinin, A. D. 1970. The range and biology of snappers (Fam. Lutjanidae). *J. Ichthyol.* 10: 717–736.
- Eginton, R., and P. Mead. 1978. Report on the South Pacific Commission outer reef fisheries project in Funafuti (Tuvalu), 21 September 1976–28 March 1977. S. Pac. Comm., Noumea, New Caledonia, 1164/78, 19 pp.
- Forster, G. R. 1984. The distribution of fishes on the outer reef slopes of Aldabra (Indian Ocean) in relation to bottom temperatures. *Environ. Biol. Fish.* 10(3): 129–136.
- Forster, G. R., J. R. Badcock, M. R. Longbottom, N. R. Merrett, and K. S. Thomson. 1970. Results of the Royal Society Indian Ocean deep slope fishing expedition, 1969. *Proc. R. Soc. Lond. B. Biol. Sci.* 175: 367–404.
- Genin, A., and G. W. Boehlert. 1985. Dynamics of temperature and chlorophyll structures above a seamount: An oceanic experiment. *J. Mar. Res.* 43: 907–924.
- Hume, H. 1975. Report on the South Pacific Commission outer reef fisheries project in the New Hebrides (1 August 1974–28 February 1975). S. Pac. Comm., Noumea, New Caledonia, 433/75, 13 pp.
- Hume, H. 1976. Report on the South Pacific Commission outer reef fisheries project in the Cook Islands (1 December 1975–31 May 1976). S. Pac. Comm., Noumea, New Caledonia, 597/76, 21 pp.
- Hume, H., and R. Eginton. 1976. Report on the South Pacific Commission outer reef fisheries project in Western Samoa (1 April–31 October 1975). S. Pac. Comm., Noumea, New Caledonia, 55/76, 19 pp.
- Isaacs, J. D., and R. A. Schwartzlose. 1965. Migrant sound scatterers: Interactions with the sea floor. *Science* 150: 1810–1813.
- Loubens, G. 1980. Biologie de quelques especes de poissons du lagon neo-caledonien, III. Croissance. *Cahiers de l'Indo-Pacifique*, 2(2): 101–153.
- Mead, P. 1978. Report on the South Pacific Commission deep sea fisheries development project in American Samoa (28 March–2 July 1978). S. Pac. Comm., Noumea, New Caledonia, 267/79, 13 pp.
- Munro, J. L. (ed.) 1983. Caribbean Coral Reef Fishery Resources. ICLARM Studies and Reviews 7. Int. Cent. Living Aquat. Resour. Manage., Manila, Philippines. 276 pp.
- Polovina, J. J. 1986. Variation of catch rates and species composition in handline catches of deepwater snappers and groupers in the Mariana Archipelago. Fifth International Coral Reef Symp., Papeete, Tahiti.
- Polovina, J. J., and S. Ralston. 1986. An approach to yield assessment for unexploited resources with application to the deep slope fishes of the Marianas. U.S. Natl. Mar. Fish. Serv., Fish. Bull. 84: 759–770.
- Ralston, S. 1984. Biological constraints on production and related management issues in the Hawaiian deep-sea handline fishery. In R. W. Grigg and K. Y. Tanoue, (eds.), *Proceedings of the Second Symposium on Resource Investigations in the Northwestern Hawaiian Islands, May 25–27, 1983, Vol. 1*, pp. 248–264. University of Hawaii, Honolulu, Hawaii. UNIHI-SEAGRANT-MR-84-01.
- Ralston, S., R. M. Gooding, and G. M. Ludwig. 1986. An ecological survey and comparison of bottom fish resource assessments (submersible versus handline fishing) at Johnston Atoll. U.S. Natl. Mar. Fish. Serv., Fish. Bull. 84: 141–155.
- Ralston, S., and J. J. Polovina. 1982. A multispecies analysis of the commercial deep-sea handline fishery in Hawaii. U.S. Natl. Mar. Fish. Serv., Fish. Bull. 80: 435–448.
- Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Board Can.* 191, 382 pp.
- Roden, G. I., B. A. Taft, and C. C. Ebbesmeyer. 1982. Oceanographic aspects of the Emperor Seamounts region. *J. Geophys. Res.* 87: 9537–9552.

- SAS Institute. 1982. SAS User's Guide: Statistics. SAS Institute Inc., Cary, N. C. 584 pp.
- Scott, R. B., L. Kroenke, and G. Zakariadze. 1980. Evolution of the south Philippine Sea: Deep sea drilling project leg 59 results. *In* L. Kroenke, R. Scott, *et al.* (eds.), Initial Reports of the Deep Sea Drilling Project, Vol. 59, pp. 803–815. U.S. Gov. Print. Off., Wash. D.C.
- Taumaia, P., and J. Crossland. 1980. Report on the South Pacific Commission deep sea fisheries project in Truk (1 February–13 March 1980). S. Pac. Comm., Noumea, New Caledonia, 709/80, 15 pp.
- Tseitlin, V. B. 1985. The energetics of the fish population inhabiting the underwater mountain. *Okeanologiya* 25(2): 308–311.
- Uchiyama, J. H., S. M. Kuba, and D. T. Tagami. 1984. Length-weight and standard length-fork length relationships of deepsea handline fishes of the Northwestern Hawaiian Islands. *In* R. W. Grigg and K. Y. Tanoue, (eds.), Proceedings of the Second Symposium on Research Investigations in the Northwestern Hawaiian Islands, May 25–27, 1983, pp. 209–225. University of Hawaii, Honolulu, Hawaii. UNIH-SEAGRANT-MR-84-01.
- Uda, M., and M. Ishino. 1958. Enrichment pattern resulting from eddy systems in relation to fishing grounds. *J. Tokyo Univ. Fish.* 44: 105–129.
- Weatherley, A. H. 1972. Growth and Ecology of Fish Populations. Academic Press, London, New York. 293 pp.