AN ECOLOGICAL SURVEY AND COMPARISON OF BOTTOM FISH RESOURCE ASSESSMENTS (SUBMERSIBLE VERSUS HANDLINE FISHING) AT JOHNSTON ATOLL

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ABSTRACT

The deep slope (100-365 m) environment at Johnson Atoll in the central Pacific was surveyed with a submersible and the standing crop of commercially important bottom fishes (i.e., lutjanids, serranids, and carangids) estimated by visual quadrat censusing. Results are compared with an assessment made by hook-and-line fishing.

Overall, 69 species of fish were recorded from the submersible and 10 from fishing. Well over half of the sightings from the submersible were new locality records. Bottom fish abundance estimates (fish/hectare and fish/line-hour) varied by site but agreed broadly with one another. Together they are used to estimate catchability (0.0215 hectare/line-hour), which is shown to vary through the day.

Bottom fish were contagiously dispersed along both vertical and horizontal dimensions, with increased numbers of the snapper *Pristipomoides filamentosus* in upcurrent localities. On a finer scale this species and *Etelis corruscans* were aggregated near underwater promontories and headlands, but at different depths.

Numerous observations concerning the deep slope environment of this central Pacific Ocean atoll are included.

Perhaps the most widespread precept in fisheries today is the supposition that catch rate is proportional to stock abundance (Gulland 1974; Ricker 1975; Pitcher and Hart 1982). Even so, there are numerous studies which demonstrate exceptions to this assumption (see for example MacCall 1976: Bannerot and Austin 1983). A departure from linearity in the relationship of these two variables reflects varying catchability. This variation may be due to schooling behavior, gear saturation, or any number of other factors which affect catch per unit effort (CPUE) in addition to stock abundance (Rothschild 1977). It is often difficult, if not impossible, to evaluate the validity of the linearity assumption in most practical situations. A multiple approach to stock assessment has often been suggested as a means of circumventing this problem, including the use of hydroacoustics (Barans and Holliday 1983; Thorne 1983), underwater television-diver surveys (Powles and Barans 1980), and submersibles (Uzmann et al. 1977) to corroborate CPUE data. Consistency in results among a set of independent assessment techniques is necessary for validation and verification of data.

Submersibles in particular have also proven useful in studying the distribution of fishes in various deepwater habitats (Brock and Chamberlain 1968; Strasburg et al. 1968; Colin 1974; Shipp and Hopkins 1978), in identifying nursery grounds of commercially important rockfish species (Carlson and Straty 1981), and in assessing the effectiveness of baited longline gear (High 1980; Grimes et al. 1982). In many situations submersibles provide an ideal means of independent assessment (Uzmann et al. 1977) if questions concerning bias in visual surveys can be adequately addressed (Colton and Alevizon 1981; Sale and Douglas 1981; Brock 1982).

The purpose of this study was to examine the distribution and abundance of tropical deep slope bottom fishes (i.e., lutjanids, serranids, and carangids) at Johnston Atoll in the central Pacific Ocean with a research submersible and to compare the results with an assessment made by fishing. This comparison provides not only a basis for testing the validity of a CPUE statistic, but also for estimating the catchability coefficient. Both are important issues because of the widespread use of hook-and-line catch and effort statistics in resource assessments of bottom fish stocks worldwide (Moffitt 1980; Ralston 1980; Ivo and Hanson 1982; Ralston and Polovina 1982; Munro 1983; Forster 1984). Of special interest was determining the relationship between CPUE and visual estimates of bottom fish standing stock.

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In addition, a variety of observations made from the submersible substantially improved our understanding of factors controlling the distribution and abundance of the entire deep slope fauna at Johnston Atoll.

DESCRIPTION OF THE STUDY AREA

A National Wildlife Refuge since 1926, Johnston Atoll is located 1,250 km southwest of Oahu, HI. The atoll's physical environment has been reviewed by Amerson and Shelton (1976) and is summarized here.

Located between lat. $16^{\circ}40' \cdot 16^{\circ}47'$ N and long. $169^{\circ}24' \cdot 169^{\circ}34'$ W (Fig. 1), Johnston Atoll lies in the North Pacific central water mass, where salinities range from 34.8 to $35.3'_{60}$. Surface water temperatures show little seasonality, ranging from 25° to 27° C. The atoll is directly in the path of the westerly flowing North Equatorial Current, with surface currents typically 0.5 kn (0.25 m/s). Deeper layers flow smoothly past the atoll, but an island wake

forms in lee surface waters, with effects evident up to 600 km downstream (Barkley 1972).

The atoll is composed of a coral platform, encompassing over 130 km² of reef under water <30 m deep. A narrow lagoon lies between the northwest barrier reef and Johnston and Sand Islands to the southeast (Fig. 1). The atoll is unusual in that the main outer reef extends only about one quarter of the way around its perimeter (Fig. 1). A large portion of the atoll lies exposed to prevailing easterly weather conditions without benefit of barrier reef protection. Evidence suggests that subsidence and tilting of the reef platform to the southeast created this unusual condition.

The climate is tropical marine, i.e., there is little seasonal variation in temperature and windspeed, but substantial variation in rainfall. A 4-mo "winter" season extends from December to March, when temperatures drop slightly, winds become more variable, and precipitation increases. The mean annual air temperature is 26.3° C, with a daily range of $4.0^{\circ}-4.5^{\circ}$ C. Daily maximum and minimum temper-



FIGURE 1.—Map of Johnston Atoll. The lines encircling the atoll are isobaths of constant depth (fathoms). The four shaded areas at the upper left are emergent lands (Johnston, Akau, Hikina, and Sand Islands). Letters (A-J) indicate the 10 dive sites of the *Makalii* during the study. Numbers (1-6) indicate fishing stations of the *Townsend Cromwell*.

atures vary little throughout the year, as do sea surface temperatures, which are in near equilibrium with the air. Strong easterly trade winds prevail all year but increase during the summer period. Annual mean wind speed at Johnston Island is 13 kn (7.5 m/s) and monthly means range from 11 to 14 kn (5.5-7.0 m/s).

METHODS

Makalii

The Makalii is operated by the National Undersea Research Laboratory at the University of Hawaii. It is a two-man, battery powered, 1-atmosphere submersible which is 4.8 m long, with a pressurized capsule 1.5 m in diameter. When carrying a pilot and one observer, its normal operating speeds range from 1 to 3 kn (0.5-1.5 m/s). Maximum dive duration is 4-5 h and depth capability is 365 m. Equipment carried in this study included hydraulic manipulator, internal and external color video cameras, 2 video monitors, video recorder, video flood lights, Photosea³ 35 mm still camera with strobe, current and temperature meters, and a dictaphone tape recorder. In addition, the Makalii is equipped with an environmental monitoring system for continuous recording of temperature, salinity, conductivity, oxygen, solar radiation, and depth.

All three authors participated as observers during a series of dives at Johnston Atoll over the 2-wk period between 22 September and 5 October 1983. Once on station, a launch-recovery-transport platform was submerged to 20 m and divers released the *Makalii*, usually in 120 m of water. The submersible descended until encountering the bottom and locating the atoll's shelf break. Observations made on fishes during the dives were voice and video recorded for later analysis. Slope angle was periodically measured with a hand-held inclinometer.

Visual estimates of the density of commercially important bottom fishes (sensu Ralston and Polovina 1982) were made by a series of "quadrat" samples. These fishes included Cookeolus boops, Epinephelus quernus, Aphareus furcatus, A. rutilans, Etelis carbunculus, E. coruscans, Pristipomoides auricilla, P. filamentosus, P. zonatus, Carangoides orthogrammus, Caranx lugubris, Seriola dumerili, and Pontinus macrocephalus.

During quadrat sampling the observer would look out his port and count the total number of bottom fish, without regard to species, over an area of the bottom judged to be 30 m². Quadrat areas always lay on the oblique planar surface of the slope face and were away from the immediate vicinity of the submersible. A sampling period consisted of four counts systematically performed, one every 15 s. To the extent possible, each count was made at an instant in time. All bottom fish seen in the water column above the sample area were included in counts.

The submersible progressed stepwise down the slope (100-365 m) in a clockwise direction around the atoll, with the observer's starboard port always oriented to the slope face. Upon reaching the *Makalii*'s depth limit, a slow stepwise ascent would begin to 100 m, where the dive would end. Descents generally lasted 2.5 h and ascents 1.5 h. Thus the entire vertical distribution of the deep slope was sampled more or less equally (i.e., observations were not concentrated in any particular depth zone).

Townsend Cromwell

The National Oceanic and Atmospheric Administration's (NOAA) RV *Townsend Cromwell* is 50 m long and when rigged for bottom handline fishing carries four hydraulic fishing gurdies (Charlin motors and Pacific King fishing reels), each with 365 m of braided prestretched 90 kg Dacron line. The terminal rig is composed of four No. 28 Tonkichi round fishing hooks and a 2 kg weight. Stripped squid was used for bait and fishing was conducted only during the day.

The vessel spent 3 d (3-5 November 1983) at Johnston Atoll sampling deep slope bottom fish by drift fishing. After wind and current directions had been determined, the vessel was positioned over the desired depth and fishing lines were dropped. Fishing continued until the vessel drifted over an unsuitable water depth, when lines were retrieved and the *Townsend Cromwell* repositioned. Single drifts were the fundamental sampling unit by which catch and effort statistics were summarized. Six fishing stations were occupied (Fig. 1), one during the morning and afternoon of each day. Fork length to the nearest millimeter and depth of capture were recorded for all fish landed.

RESULTS

Makalii

Ten dives were completed at Johnston Atoll (Fig. 1). Due to precipitous dropoffs which occur through-

³Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

out the study area (100-365 m), the length of the atoll's 183 m (100 fathom) isobath (64 km) provides a convenient measure of total deep slope habitat (Ralston and Polovina 1982). The average point-topoint distance covered by the submersible during one 4-h dive was 2.27 km (s = 0.56 km). An aggregate 22.7 km were thus surveyed during this study, comprising 35% of the deep slope habitat at the atoll.

Temperature

Ambient temperature and depth were recorded often during dives, from which temperature-depth profiles were later constructed. The results are summarized in Figure 2. The solid line represents median temperatures at depth, with the shaded area encompassing the range of temperatures observed among all 10 dives. Surface water temperature was typically 27°C and the mixed layer 100 m deep. A second weak thermocline was found around 240 m. Although its depth varied somewhat (220-245 m), it was present around the entire atoll, i.e., both windward and leeward exposures, and was observed as a shimmering layer below the submersible as it descended. This effect is believed due to refraction of light passing through variable density water, a result of the thermocline in association with a decrease in salinity.4 Ambient water temperature usually had dropped to 8.5°C at a depth of 350 m.

Slope Angle

The relationship between the bottom's slope and depth was also measured. These data were summarized after each dive and bottom contours plotted. Overall, there was little variation in slope angle around the atoll, i.e., the general pattern was one of uniformity at all sites visited. Figure 3 presents pooled results for all slope angle-depth determinations. In the figure, horizontal and vertical scales are equal and the composite contour of the bottom (100-365 m) at Johnston Atoll is shown in profile. The slope was stratified into three 50-fathom depth zones for later analysis.⁵ The slope angle between 50 and 100 fathoms averages $\Theta_1 = 25^{\circ}$ (Table 1). Similarly, $\Theta_2 = 47^{\circ}$ and $\Theta_3 = 59^{\circ}$. There is a definite trend at Johnston Atoll for the slope to steepen with in-



FIGURE 2.—The pooled relationship (n = 10) between temperature and water depth at Johnston Atoll. Solid line = median values; shaded area = range of values.

TABLE 1.—Total habitat areas stratified by depth zones at Johnston Atoll.

Depth stratum (fathoms)	Digitized horizontal planar areas (ha)	Slope angle	Oblique planar habitat areas (ha)
Emergent lands	305 (1%)	_	-
0-10	15,012 (60%)	_	_
10-50	6,123 (24%)	_	_
50-100	1,624 (7%)	25°	1,785
100-150	964 (4%)	47°	1,418
150-200	1,020 (4%)	59°	1,962
Total	25,048 (100%)	_	5,165

creasing depth, at least between 100 and 365 m.

In the shallowest regions surveyed (<125 m) the bottom was a monotonous sandy plain in the shoreward direction, but at 125 m it began to slope steeply

⁴E. Chave, Hawaii Undersea Research Laboratory, University of Hawaii, Honolulu, HI 96822, pers. commun. June 1984.

⁵Stratification of depth into zones was performed using units of fathoms (1 fathom = 1.83 m) because nautical charts, hydrographic surveys, and fathometers are so measured. For the sake of brevity and clarity, isobaths and depth strata will henceforth be given only in this unit of measure.

downward. Although not easily seen in the figure, a small but prominant ledge 5-10 m high encircled the atoll between 130 and 140 m. Somewhat deeper, between 180 and 275 m, the bottom was uniform in slope and its surface relatively smooth and devoid of features. Slope angles approached the vertical at most sites in the 300-350 m depth range, with overhanging caves formed by subaerial dissolution.⁶ At the deepest points visited (360 m) the bottom became less precipitous, and in some areas a sediment-laden terrace had formed along the base of the deep dropoff.

Based on estimates of slope angle, existing charts, and a hydrographic survey by the *Townsend Cromwell*, habitat areas for the three depth zones were determined. The positions of the 10 and 100-fathom isobaths were already known, but they were refined and the locations of the 50-, 150-, and 200-fathom isobaths estimated. Figure 1 is a simplified representation of a much larger chart which was digitally analyzed to determine the horizontal (i.e., level) areas bounded by isobaths (Table 1). The results show that emergent lands (Johnston, Akau, Hikina, and Sand Islands) account for only 1% (305 ha) of the level planar area of the atoll. The largest area (60%) lies between sea level and 10 fathoms. The

⁶Keating, B. H. Geologic history and evolution of Johnston Island: Submersible dive results. Manuscr. in prep. University of Hawaii, Honolulu, HI 96822.

total horizontal extent of the atoll is about 25,000 ha.

These results can be misleading, however, because a vertical slope provides no horizontal habitat area. and yet both reef fish diversity and standing crop are known to be positively correlated with topographic relief (Luckhurst and Luckhurst 1978: Gladfelter et al. 1980; Carpenter et al. 1981). At Johnston Atoll the structural complexity of the substratum frequently increased with slope angle. A better estimate of total habitat is the area of bottom irrespective of slope angle, estimated by dividing the horizontal planar area of a depth stratum by the cosine of the slope angle within it. This adjustment almost doubles the estimate of total habitat area in the 150-200 fathom zone, simply due to the precipitous dropoff found there. A composite 5.165 ha of habitat occurs between 50 and 200 fathoms.

General Observations

While this study focused primarily on the deepwater ichthyofauna of Johnston Atoll, many observations were made on the oceanographic, geologic, and biotic characteristics of the study area. These are briefly recounted here.

Currents running in directions parallel to the slope were frequently encountered. They were generally weak and did not exceed 0.3 kn (0.15 m/s). They sometimes exhibited reversals with depth. During



FIGURE 3.—Composite reconstruction of the deep slope at Johnston Atoll. Horizontal and vertical scales equal. Average slope angles (θ) were measured for each of three 50-fathom depth strata.

dive F, for example (Fig. 1), a 0.2 kn (0.10 m/s) current was observed at 125 m running south (i.e., counterclockwise when viewed from above). There was no current between 180 and 275 m. At 300 m, however, a 0.1 kn (0.05 m/s) current was observed, traveling in a northerly direction (i.e., clockwise). A similar depth-related current reversal was observed during dive C, although on this occasion the shallower current (170 m) ran clockwise and the deeper one (290 m) counterclockwise. In contrast, a weak downslope current (0.1 kn or 0.05 m/s) was observed but once (dive E at 305 m). No upwelling currents were encountered.

Geologically, the deep slope of Johnston Atoll was grossly similar at all points visited. The low escarpment at 130 m was most likely due to erosion of an ancient limestone reef. This feature was characterized by mounds of coral rubble, boulders, small undercut caves, and a profusion of fishes. Below it the slope angle was remarkably uniform, with low topographic relief. The bottom was still composed of limestone and showed severe biological and chemical weathering (i.e., dissolution) along the slope gradient, being pitted and striated with numerous shallow depressions. Few sediments or boulders were observed. At a depth of 240 m topographic relief increased, as large slab boulders became increasingly prominent. Subaerial dissolution had produced low shallow limestone caves, and fine sediments were more common. Between 290 and 335 m the slope was very steep, with a well-developed system of sharp ridges and deep erosional channels. The substratum had the superficial appearance of dark basalt but was composed of thin manganese crusts overlying ancient limestone reef materials (Keating see footnote 6). Fine sediments spilled down the channels in the slope and piled up at the base of the deep dropoff (350 m). More limestone boulders were arrayed along this deep terrace and fine sediments covered the bottom.

As expected, few fleshy macroalgae were seen. The only algae encountered regularly were two corallines, *Halimeda* sp. and an unidentified crustose species. The former occurred in small scattered clumps between 100 and 200 m, with loose remnant exoskeletal "sands" found in sediment pockets as deep as 290 m. The crustose form was abundant between 150 and 250 m where it covered much of the slope face. Otherwise, an unidentified species of brown algae seen on dive H between 150 and 250 m was the only other algae seen. A more detailed description of the algal biota at Johnston Atoll is in preparation.⁷

In contrast to the depauperate flora, the inverte-

brate fauna was rich. Listed here are those forms seen often enough to constitute indicator species for particular depth strata. In addition to these a great many others were observed and photographed. In the Cnidaria, three stoney corals were especially plentiful: Leptoseris hawaiiensis (115-165 m), Stylaster sp. (135-245 m), and Madracis sp. (140-200 m). Several species of black corals (Order Antipatharia) were also common. Of the crustaceans, a single large Panulirus marginatus, previously known only from one specimen (Brock 1973), was observed in a small hole during dive A at 122 m, and at least two types of galatheid crab were very abundant in small holes pitting the reef slope between 230 and 350 m. In deep water the remaining attached valves of dead rock oysters were seen in patches along the base of the deep dropoff (350 m), as was an unidentified species of solitary tunicate (335-365 m). Echinoids were particularly abundant immediately below the shelf break; e.g., Diadema cf. savignyi (110-170 m), Chondrocidaris gigantea (120-160 m), and heart urchins (Brissidae, 130-200 m). Other than galatheid crabs, the 220-310 m zone was largely barren and devoid of megabenthos.

Ichthyofauna

A total of 69 fish species in 29 families were observed during *Makalii* dives (Table 2). Overall, the proportional representation of different families was similar to that of the shallow water community (Gosline 1955; Randall et al. in press), although the representation of genera was grossly different. Serranid species were most numerous with nine species observed (eight in the anthiine subfamily). Lutjanids were also abundant (eight species), but no members of the ubiquitous genus *Lutjanus* were seen. Forty of the species listed in Table 2 (58%) are new records for Johnston Atoll (Randall et al. in press). Photographs of several fishes observed during dives are presented in Figure 4.

An indication of species' depth distributions is given in Table 2. Because no observations were made in <100 m, upper limits can be misleading. This is particularly true of shallow-water species which penetrated to the 135 m escarpment but not beyond, including: Triaenodon obesus, Parapercis schauinslandi, Aphareus furcatus, Chromis verater, Parupeneus cyclostomus, P. multifasciatus, Forcipiger flavissimus, Holacanthus arcuatus, Bodianus bilu-

⁷C. Agegian, University of Hawaii, Honolulu, HI 96822, pers. commun. June 1984.

TABLE 2.—Fishes encountered during dives (100-365 m) of the *Makalii* at Johnston Atoll. Included for each species are the minimum and maximum depths (m) of observation as well as the median and range of the depth distribution. Under the sighting column a value of 1 indicates a species was seen repeatedly (>5 times) during each dive of the submersible, 2 means the species was occasionally seen on each dive (<5 times), 3 signifies sightings on most dives but not all (i.e., species seen on several occasions), and 4 indicates rarity (see only once or twice during all dives). An asterisk to the left of a species name signifies a new record for Johnston Atoll (Randall et al, in press).

Family-species	Min-max	Median (range)	Sighting	Family-species	Min-max	Median (range)	Sighting
Carcharhinidae				Carangidae			
Carcharhinus amblyrhynchos	90-275	185(185)	1	Carangoides orthogrammus	105-170	135(65)	2
Carcharhinus sp.				Caranx lugubris	105-355	190(250)	1
(probably galapagensis)	225-250	225(25)	3	C. melampygus	130-230		2
Triaenodon obesus		120	4	Decapterus sp.		100	4
Mobulidae			•	*Elagatis bipinnulata	90-150	120(60)	3
Manta sp.		120	4	*Seriola dumerili	120-335		1
Muraenidae			•	Apogonidae		,	•
*Gymnothorax berndti	220-260	260(40)	3	*Epigonus sp.	330-365	355(35)	2
*G. nudivomer		179(85)	2	Pomacentridae	000 000	000(00)	-
*G. nuttingi	185-300		3	Chromis verater	120-140	130(20)	3
Ophichthidae	100-000	200(110)	U	Mullidae	120-140	100(20)	U
Myrichthys maculosus	150-215	185(65)	4	Parupeneus cyclostomus		125	4
Synodontidae	150-215	100(00)	-	P. multifasciatus		125	4
Unidentified synodontid		240	4	Chaetodontidae		125	-
Holocentridae		240	4	*Chaetodon modestus	125-255	190(130)	2
	105 040	155/105)	2	*C. tinkeri			2
*Myripristis chryseres	135-240	155(105)	4		105-160		-
*Neoniphon aurolineatus	405 045	150	-	Forcipiger flavissimus	125-145		4
*Pristilepis oligolepis	165-345	230(180)	3	*Heniochus diphreutes	120-215	135(95)	2
Ophidiidae				Pomacanthidae			_
Brotula sp.			_	Geniacanthus sp.		150	4
(multibarbata or townsendi)		230	4	*Holacanthus arcuatus	130-150	135(20)	3
Priacanthidae				Labridae			
*Cookeolus boops	165-260	220(95)	1	Bodianus bilunulatus	130-135	130(5)	3
Serranidae				Cheilinus unifasciatus		120	4
*Anthias fuscinus	135-280	215(145)	1	*Polylepion russelli	245-280	275(35)	3
*A. ventralis		105	4	Acanthuridae			
Callanthias sp.	240-330	285(90)	4	*Acanthurus dussumieri		130	4
*Epinephelus quernus	135-350	230(215)		*Naso hexacanthus	120-165	150(45)	2
*Grammatonotus laysanus	310-350	335(40)	3	*Naso sp.	120-175	135(55)	1
*Holanthias elizabethae	155-260	230(105)	1	Zanclidae			
*H. fuscipinnis	160-215	170(55)	1	Zanclus cornutus		125	4
Luzonichthys sp.		• •		Scorpaenidae			
(perhaps earlei)		105	4	*Pontinus macrocephalus	200-365	305(165)	2
*Plectranthias helenae	215-220	215(5)	3	*Scorpaena colorata		272	4
Muqiloididae		.,		Scorpaena sp.	225-355	290(130)	2
*Parapercis roseoviridis	215-270	245(55)	2	Triglidae			
*P. schauinslandi	105-170	145(65)	1	*Satyrichthys engyceros	355-365	365(10)	4
Lutianidae			-	Bothidae		,	•
Aphareus furcatus	105-145	135(40)	2	Bothus mancus	270-350	310(80)	4
*A. rutilans	190-250		3	Balistidae		(00)	
*Etelis carbunculus	245-365		3	*Sufflamen fraenatus	105-170	140(65)	1
*E. coruscans	250-355		3	Xanthichthys auromarginatus		135(40)	i
*Pristipomoides auricilla	215-250		3	Monacanthidae	110-100	100(40)	1
*P. filamentosus	120-260			Unidentified monacanthid		125	4
*P. zonatus	205-295	240(90)	1	Tetraodontidae		120	
*Symphysanodon maunaloae			-	*Canthigaster sp.			
Emmelichthyidae	230-365	300(135)	1	(likely inframacula)	260-270	265(10)	4
*Ervthrocles scintillans	295-320	200/25)	4	Unidentified tetraodontid		/	4
Eryunooles solnunans	290-320	300(25)	4		135-150	145(15)	4
				Ostraciidae			
				Ostracion sp.		135	4
				Diodontidae			
				Diodon hystrix		135	4

nulatus, Acanthurus dussumieri, Zanclus cornutus, Xanthichthys auromarginatus, and Diodon hystrix. These fishes accounted for an increase in diversity at the 135 m dropoff. Similarly, due to the submersible's 365 m depth limit, lower bounds for some species are likely in error (eg., Symphysanodon maunaloae, Epigonus sp., Pontinus macrocephalus, and Satyrichthys engyceros). Nonetheless, due to the large depth range sampled (100-365 m), the data still provide useful estimates of the depth distributions for most of the species listed.

The data suggest that large species have great

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depth ranges. For example, all species with depth ranges exceeding 200 m are large (i.e., Caranx lugubris, Epinephelus quernus, and Seriola dumerili). Moreover, among extensively observed species, a significant Spearman correlation exists between ranked average weight and depth range ($r_s = 0.52$, df = 25, P < 0.01). This finding should be viewed with caution because of potential biases in depth distributions (see above).

The last column in Table 2 gives sighting scores for all species. Those assigned a value of 1 indicate species dominating the deep slope fish community in terms of species sightings. Note that some species were seen infrequently, but when encountered they were observed in large numbers (e.g., *Elagatis bipinnulata*, Fig. 4). Similarly, *Pristipomoides filamentosus* was not seen on every dive and was thus assigned an abundance score of 3. In spite of this, when seen, it was abundant and it was the most frequently caught while fishing (see next section). Sighting scores therefore do not indicate relative species' contributions to total standing crop biomass of the deep slope fish fauna.

Quadrat Sampling

A total of 974 quadrat sample counts were made during the 10 submersible dives. No attempt was made to estimate abundance separately for each species. Rather, the total number of bottom fish was recorded, regardless of species composition. Although severely reducing the detail of the data base, this did have the desirable effect of averaging biases due to attraction or repulsion of fishes to and from the Makalii. It was evident, for example, that some species were attracted to the submersible and followed it about (e.g., Seriola dumerili and Caranx lugubris), whereas others were repelled and actively avoided the submersible's lights (e.g., Pristipomoides filamentosus and Etelis coruscans). Still others did not seem to be greatly influenced (e.g., Cookeolus boops, Epinephelus quernus, Pristipomoides zonatus, and Pontinus macrocephalus). By pooling species quadrat counts, the abundance of some species was overestimated, some underestimated, and some estimated without bias. Due to averaging, we believe that pooled counts provide the best available estimates of total bottom fish density along the deep slope of Johnston Atoll.

Some 367 bottom fish were counted in quadrat samples, resulting in a mean encounter rate of 0.38 fish/quadrat. The data were fitted to the Poisson distribution to ascertain the dispersion pattern. A chi-square goodness of fit test yielded $\chi^2 = 325.32$, df = 3, $P \ll 0.005$, demonstrating nonrandom dispersion. The variance to mean ratio calculated from the frequency distribution of bottom fish/quadrat observations was 4.64 and was significantly greater than 1 ($P \ll 0.005$), indicating strong contagion.

One of the principal explanations for this result is shoaling by *Pristipomoides filamentosus* and *Etelis coruscans*. Both are large species, which formed aggregations of up to 100 individuals well off the bottom (20 m) in the vicinity of underwater headlands and promontories. These monospecific groups appeared to feed in open water on plankton, consistent with previous dietary studies of *P. filamentosus* (Kami 1973; Ralston⁸). When either was observed, there was an increased likelihood of encountering conspecifics. As a consequence 10 or more *P. filamentosus* were seen in one quadrat on 7 occasions.

Another factor contributing to clumping was nonrandom distribution with depth (Fig. 5). This figure presents the relationship between mean number of bottom fish per count and depth (vertical bars = standard errors). Note the two abundance peaks, the first at about 170 m and the second at 250 m. The former was due primarily to large numbers of *Caranx lugubris* and *P. filamentosus*. The location of the second peak was just below the second thermocline and was largely the result of local increases in numbers of *Epinephelus quernus* and *P. zonatus*.

The mean numbers of bottom fish per quadrat, stratified into 50-fathom depth intervals, are also shown in Figure 5 (i.e., 0.57, 0.47, and 0.06 fish/count). These data were converted to densities (1 quadrat = 0.003 ha) such that from 50 to 100 fathoms an average of 190 bottom fish are estimated to occur per hectare of habitat. Similarly, in the two deeper strata, estimated densities of 156 and 20 bottom fish/ha occur.

Given estimates of bottom fish density and depthspecific estimates of total available habitat (Table 1), estimates of the total standing crop of bottom fishes at Johnston Atoll indicate that about 339,000 fish occurred in the 50-100 fathom zone, 221,000 between

FIGURE 4.—Johnston Atoll deep slope fishes. A. Caranx lugubris with wire coral: B. Epinephelus quernus peering out of cave; C. Seriola dumerili (foreground) and Caranx lugubris (background); D. school of Elagatis bipinnulata with Carangoides orthogrammus (above); E. Henviochus diphreutes with black coral; and F. aggregation of Myripristis chryseres and Neoniphon aurolineatus.

⁸Ralston, S. Unpubl. data. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96812.



FIGURE 5.—The abundance of bottom fish (see text) in relation to depth. Solid line represents fish densities with changing depth (measured in meters or fathoms). Error bars are standard errors of means. Three 50-fathom depth zones are indicated, and mean fish densities within these are shown as circled points.

100 and 150 fathoms, and only 39,000 in the deepest (150-200 fathom) zone. Roughly 600,000 commercially exploitable bottom fish are estimated to comprise the deep-sea hook-and-line resource at Johnston Atoll. Because the fish are spread over a total habitat of 5,165 ha (Table 1), this corresponds to average densities of 118 bottom fish/ha.

Townsend Cromwell

Anywhere from 2 to 4 lines were deployed while fishing, resulting in an aggregate 41.8 line-h of fishing effort spread over 23 vessel drifts. A catch of 133 fishes (Table 3) produced an overall CPUE of 3.18 fish/line-h. Another 12 fish were hooked but lost to sharks before landing. All species caught while fishing were observed from the submersible with the exception of the bramid, *Eumegistus illustris*. Deepwater lutjanids predominated (69%), but substantial numbers of serranids (22%) and carangids (8%) were caught, a composition typical of tropical deep slope fisheries worldwide (Talbot 1960; Ralston and Polovina 1982; Munro 1983; Forster 1984).

Species Composition By Location

Examination of catch data suggested a difference in species composition between upcurrent (sites 5

TABLE 3.—Species composition	of the bottom fish catch from the
Townsend Cromwe	ell at Johnston Atoll.

Family-species	Catch (n)	Percent	Average size (cm FL)
Lutjanidae (snappers)			
Pristipomoides filamentosus	43	32	54.4
P. zonatus	35	26	40.8
P. auricilla	5	4	34.6
Etelis carbunculus	5	4	51.2
E, coruscans	4	3	72.7
Subtotal	92	69	
Serranidae (groupers) Epinephelus quernus	29	22	69.8
Carangidae (jacks)			
Caranx lugubris	7	5	48.1
Carangoides orthogrammus	2	2	43.5
Seriola dumerili	2	2	79.5
Subtotal	11	9	
Bramidae (pomfrets)			
Eumegistus illustris	1	1	70.3
Grand total	133	101	

and 6) and downcurrent (sites 1-4) locations (Fig. 1). Landings were pooled into these two classes, and also by species category into *Pristipomoides filamentosus*, *P. zonatus*, *Epinephelus quernus*, and "others". The resulting 2 × 4 contingency table showed a lack of statistical independence between locations and species ($\chi^2 = 22.36$, df = 3, *P* << 0.005). Examining individual contingency table cells showed that the greatest contribution to the total chi-square was for P. filamentosus (58% of total). Specifically, under the hypothesis of independence, 16.5 were expected downcurrent but only 5 were caught, while 26.5 were expected upcurrent where 38 were landed. The apparent surplus of P. filamentosus along the eastern exposure, where trade winds prevail and oceanic currents first impact the atoll (Barkley 1972), may relate to this fish's habit of feeding on large deepwater plankton, especially salps (genus Pyrosoma). Bray (1981) has shown that small resident planktivores will travel to the upcurrent edge of a reef to access pelagic plankton. The distribution of P. filamentosus at Johnston Atoll may represent a similar situation on a much larger scale.

Bottom Fish Catch Rate

One-way analysis of variance (ANOVA) of CPUE data was used to examine whether geographical differences exist in bottom fish abundance, i.e., the two treatment classes were upcurrent and downcurrent regions (see above). The ANOVA was insignificant (F = 1.62, df = 1, 21, P = 0.21), although the mean catch rate along the eastern exposure (5.6 bottom fish/line-h) was 60% greater than downcurrent (3.5 bottom fish/line-h). This result suggests the lack of significance may have been due to small sample size.

The CPUE data were analyzed by time of day to determine if catchability fluctuates through the day. The results in Figure 6 show that fishing was distinctly better during the morning than afternoon. In this figure individual values of drift CPUE (n =23) have been plotted against the midpoint of the drift time interval. The solid line represents aggregate catch rates, calculated by pooling both catch and effort statistics from all areas into 1-h intervals and then forming CPUE ratios. Different symbols represent each of six separate fishing locations (Fig. 1). Note that catch rates were highest when fishing began each day and consistently declined to a low during the midafternoon. The data further indicate that catch rates may increase again with the onset of the evening crepuscular period, although the data are meager. This pattern was evident both within and among the six sites fished and, when averaged out, resulted in morning catch rates 2.07 times greater than afternoon rates.

Catchability

Having the Makalii and Townsend Cromwell at Johnston Atoll at similar times prompts comparison



FIGURE 6.—The effect of time of day on the catch rate of bottom fish at Johnston Atoll. Catch rates calculated for each drift of the vessel and presented for each of six different fishing stations (see Figure 1).

of the assessment techniques. We assume that in the 1-mo interim between visits no changes occurred in overall levels of abundance, because Johnston Atoll is a National Wildlife Refuge where no fishing is permitted and the fishes are typically long lived (Ralston and Miyamoto 1983; Ralston see footnote 8). Any differences in assessment are then likely due to differences in method.

To compare surface estimates of bottom fish abundance with those derived from submersible surveys, we matched fishing stations (numbers) with submersible dives (letters) which occurred nearby (Fig. 1). Specific pairings were F-1, E-2, B-3, H-4, I-5, and D-6. For each dive the overall abundance of bottom fish was estimated by forming the ratio of total fish counted to total number of quadrat counts, and then converting to density measured in bottom fish/ha. The CPUE statistics were used to estimate abundance for each fishing station, after correcting for fluctuating catchability (Fig. 6). The result is presented in Figure 7. There is a positive correlation between CPUE and bottom fish density (r = 0.54), although it is insignificant.

One means of estimating catchability, q, is to determine the slope of the regression of CPUE on stock density. We estimated the functional regression (Ricker 1973) of the data presented in Figure 7 (solid line) and determined that q = 0.0215 ha/line-h. A second estimate of q is obtained by forming the ratio of the average catch rate of bottom fish at the atoll



FIGURE 7.—The relationship between *Townsend Cromwell* CPUE and *Makalii* abundance estimates. Line fitted by functional regression. See text for further discussion.

(3.18 fish/line-h) to the average density of bottom fish viewed from the submersible (118 bottom fish/ha). The resulting estimate of q is 0.0269 ha/line-h.

DISCUSSION

The most enlightening aspect of this study was our ability to perform an in situ assessment of factors controlling the distribution and abundance of the deep slope biota at Johnston Atoll. Organisms showed not only distinct zonational patterns with depth but clumped dispersion along horizontal gradients as well.

The fish fauna of Johnston Atoll is often considered a depauperate outlier of the Hawaiian fauna (Gosline 1955; Randall et al. in press). In a later paper, Gosline (1965) examined vertical zonation in Hawaiian fishes, arguing that depth zonation patterns are often sharply demarcated in intertidal and shallow-water habitats, but these become increasingly attenuated with depth. The results of our study and Randall et al. (in press) support his conclusion (see also Forster 1984). Some deep slope species have extremely broad depth ranges (exceeding 200 m), vet few representatives of the shallow-water community extend appreciably beyond the 130 m escarpment encircling the atoll. Other investigators have noted that many Hawaiian species, which are commonly thought of as strictly associated with coral reefs. penetrate to depths well in excess of those favoring the growth of scleractinian corals (Brock and Chamberlain 1968; Strasburg et al. 1968; Clarke 1972). Yet the distributions of these fishes are limited largely to areas near the shelf break or shallower, while a true deep slope ichthyofauna, comprised largely of anthiids and lutjanids, exists along outer reef dropoffs at both Johnston Atoll and in the Hawaiian Islands.

Distributional patterns of fishes were nonrandom along horizontal gradients as well, as was readily apparent in the atoll-wide distribution of *Pristipomoides filamentosus*. Based simply on catch totals, 60% more *P. filamentosus* were expected to occur on the upcurrent exposure of the atoll than downcurrent, although 760% more were observed there, illustrating the clumped dispersion pattern which characterized this species during fishing surveys. Contagion was also evident in quadrat samples. Future studies would be well advised to incorporate statistical models consistent with these findings, including use of the negative binomial distribution to describe spatial patterns.

On a more local scale, it was clear from submersible observations that P. filamentosus and Etelis coruscans were concentrated near underwater headlands. Brock and Chamberlain (1968) made similar observations on deepwater populations of Chaetodon miliaris, attributing the very localized distribution of this species to increased accessibility of its food (plankton) in the vertical turbulence plumes formed by the impact of currents on underwater promontories. Because of its known planktivorous food habits, this hypothesis could explain abundance patterns of P. filamentosus. Moreover, fishermen emphasize the importance of currents in locating feeding aggregations of both P. filamentosus and E. coruscans. These two species taken together comprise the most important species landed in the Hawaiian deep-sea hook-and-line fishery, both in terms of yield and economic value. The relative abundance of these species in the deepwater bottom fish community may be due to their utilization of an allochthonous plankton resource transported to neritic waters from the open sea.

Bottom Fish Abundance

Certain methodological problems hindered this study and should be reviewed before comparing the abundance estimates from the two surveys. Any technique, including those used here, has its own specific combination of advantages and disadvantages.

There is ample reason to suspect bias in assessments based on underwater visual surveys. Sale and Douglas (1981) have shown that a single visual fish

census seldom records all individuals present at the time of the census. Similarly, Colton and Alevizon (1981) showed that a guarter of the community they studied was characterized by significant diurnal changes in abundance. They concluded that unless sampling time is carefully controlled and standardized, results from visual abundance surveys may be seriously biased. Standardization was achieved in this study because all 10 dives started between 0840 and 0950 in the morning and each lasted 4 h. Furthermore, Brock (1982) showed that large, conspicuous, diurnally active species are accurately censused with visual assessment techniques, although the most abundant are often underestimated. With the exception of Cookeolus boops, which, although nocturnal, shelters in the open along the slope face, all of the species included in the quadrat sampling fit these criteria. Biases which frequently accompany visual assessments have thus been considered and minimized here.

Another factor which may have affected the results of Makalii surveys is attraction and repulsion of certain species to and from the submersible. Previous investigators have typically ignored this problem (Uzmann et al. 1977; High 1980; Powles and Barans 1980; Carlson and Straty 1981), while at the same time acknowledging that some species are attracted (e.g., black sea bass, southern porgy, Pacific halibut, sculpin, and yelloweve rockfish) or repelled (e.g., squid, herring, mackerel, butterfish, and wolf eel) to submersibles and divers. Nevertheless, as pointed out by Uzmann et al. (1977), one can at least observe the reactions of species to the submersible's presence, giving the viewer the opportunity to evaluate potential sources of error. We have attempted to address this problem by pooling counts for all species. While admittedly this procedure may not remove all bias, it is our feeling that in the absence of more quantitative information, little else can be done to improve the data. Studies are now being implemented to specifically evaluate the degree of attraction or repulsion of different species to the Makalii.

Provided an awareness of these concerns, the results presented here support the contention that the catch of bottom fish/line-h is a suitable CPUE statistic. This conclusion is based on the data presented in Figure 7, where CPUE generally increases with fish density and the regression intercept passes close to the origin. Although the relationship is statistically insignificant, this is likely due to small sample size (n = 6). Moreover, differences in bottom fish abundance between upcurrent and downcurrent locations were shown to result largely from the contagious dispersion of *Pristipomoides filamentosus*

along the eastern side of the atoll, where its primary food resource first becomes available for consumption.

The estimation of catchability for deep-sea hookand-line gear is a useful application of the dual sampling program presented here. The results suggest relatively great sensitivity of bottom fish stocks to exploitation pressure, a finding consistent with previous and ongoing studies (Ralston 1984). If we use q = 0.0215 ha/line-h as an estimate of catchability, we conclude that 1 line-h of Tounsend Cromwell fishing effort removes about 2.2% of the bottom fish inhabiting 1 ha of habitat. A similar finding was reported by Polovina⁹, who estimated q from the same vessel for a Mariana stock of bottom fish. Removals such as this are not insubstantial and underscore the importance of developing methods of stock assessment which can be used early in the development of a fishery and in the absence of conventional data sources. A combination of surface platform surveys with submersible ground-truthing is certainly a promising assessment technique to pursue (Uzmann et al. 1977).

ACKNOWLEDGMENTS

We would like to thank the U.S. Army Corps of Engineers Pacific Ocean Division, the U.S. Army Toxic and Hazardous Materials Agency, and the National Undersea Research Program at the University of Hawaii for making this study possible Special thanks go to the staff of the Hawaii Undersea Research Laboratory Program and the *Makalii* operations crew for help in coordinating the dive program and in meeting our needs for logistical support.

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