# The Summer Standing Crop of Fish on a Shallow Bermuda Reef[1]

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ABSTRACT

Repeated estimates of reef fishes by visual counts were made on a shallow isolated Bermuda reef with a surface of approximately one hectare (2.5 acres). A standing crop of 490 kg was found in midsummer.

Comparisons between the fish fauna of this reef and more extended reef areas indicate that carnivorous reef fishes predominate on isolated reefs, while herbivores become more prevalent on large browsing areas. Available information on the yearly growth rates of Bermuda reef fishes suggests a relatively high overall efficiency of utilization of incident solar energy (*ca.* 0.0014%). The similarity of isolated reefs to ponds is discussed.

Estimates of standing fish crops have been used as indices of fertility of aquatic environments (Carlander 1955). From them alone, unfortunately, one can obtain only fragmentary information on the productivity of an area, but studies of rates of production may not be feasible especially if the region involved is poorly accessible. For this reason biological investigations of reef fishes are, as yet, mostly confined to the realm of taxonomy; reefs, after all, are in the tropics, fairly remote from the concentrations of aquatic biologists in America and Europe. The study of Odum and Odum (1955) is one notable exception; here the entire trophic structure of a Pacific reef was investigated, albeit in a relatively short time.

The aims of the present study were to make repeated estimates of the standing fish crop on a shallow Bermuda reef and to compare this isolated reef with more extended reef areas. Growth studies on certain species of reef fishes and observations on their movements were made in the same reef area (Bardach and Menzel 1957, Bardach 1958). Though these have been reported elsewhere they will be drawn upon in the discussion.

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## MATERIALS AND METHODS

The study reef is located in Bermuda's northern reef chain, about 8 miles from the islands and almost 2 miles in a landward direction from the drop-off into the Atlantic Ocean (Fig. 1). It is part of a group of isolated reefs, rising from the lagoon floor at 40–50 feet almost to the water level. Waves do not break over it, but at low tide some of its coral heads are only two feet below the surface. It is irregularly oval, and dotted with smaller and larger sandholes which are between 15 and 20 feet deep and make up about one-third of its surface area (Fig. 2). The surface and the fairly vertical walls comprise roughly 2.5 acres (close to one hectare). This reef was not fished by commercial fishermen.

The predominant corals are: *Porites astroides*, *Diploria labyrinthiformes*, *Millepora alcicornis*, and some *Agaricia* sp. Staghorn coral (*Acropora* sp.) is absent from the Bermuda reefs, where one of the most striking features is the profusion of sea rods and sea fans with *Rhipidogorgia flatbellum*, *Pleuxaura flexuosa*, and *Eunicea grandis* as the most prominent. Algae such as *Dictyota* sp., *Zonaria zonalis*, and *Sargassum* sp. are the predominant plants which grow in profusion on dead coral.

The method of estimating the numbers of fish resident on this reef was to count them with the help of SCUBA equipment, along the lines reported by Brock (1954). Counts were made in August of 1955, 1956, and 1957.

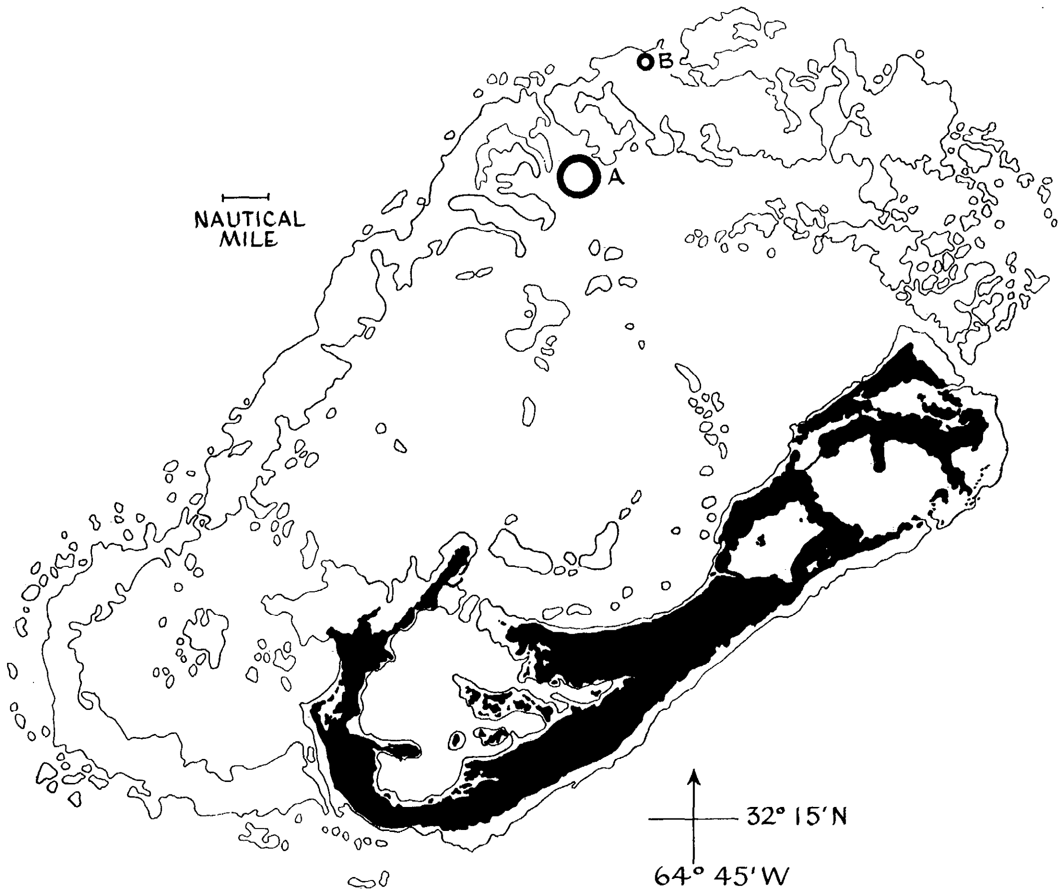


FIG. 1. Map of Bermuda islands and surrounding reefs. *A*. Location of one hectare study reef. *B*. Location of study area on extended reef surface.

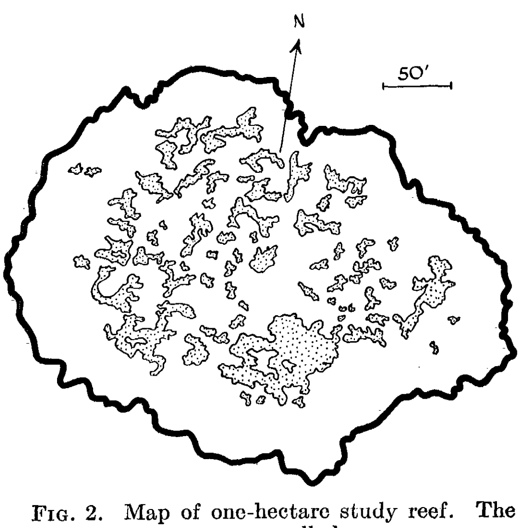


FIG. 2. Map of one-hectare study reef. The dotted areas represent sandholes.

The reef surface was divided into six to eight lanes by means of discarded telephone cable laid from a boat. The 1955 count was made on half the reef on each of two successive days; in 1956 eight divers were available and the entire reef was covered; in 1957 a scarcity of divers restricted the count to somewhat less than half the reef surface. All divers knew the local fauna. They were given opaque plastic slates with lists of the species they might expect to encounter so that they only had to make one pencil stroke for each fish. They started simultaneously and tried to keep abreast of one another. The counts on the vertical walls were made by two divers in all 3 years. They started from the same place and circled the reef in opposite directions. Thus, they checked each other's counts, as much as possible.

Tagging and recapture data for several species are available but were not included in the tabulation of the counts (Table 1) for reasons which will be given in the discussion. An estimate of nocturnal and crepuscular fish was made by rotenone treatment of a smaller area on an adjacent, very similar reef. Small fishes were counted on 100-m$^2$ quadrats, representing coral as well as sandy substrates.

In 1957 four lanes similar to those described above were laid on an extensive reef area near the edge of the reef barrier (Fig. 1); they comprised somewhat less than half an acre. Between June 14 and July 16 four counts were made by two divers at irregular intervals. Two additional counts by one diver extended the period of observation in this area to September 6, 1957. The two divers started at opposite corners of this area and each covered the entire four lanes after meeting the other in the middle. They thus arrived at two independent tallies of the representatives of certain selected species (Table 2). It was hoped that this additional survey might serve 1) to check on the reliability of the census method, 2) to yield some data to compare extended with isolated reefs, and 3) to indicate what day-to-day differences one might expect in the numbers of certain fish on the reef. The days on which these counts were made were largely determined by the weather.

Diving observations were also made during the winter of 1956 but no counts were attempted then. Average weights of the various fishes (Table 1) were based on length/weight tabulations from specimens secured by trapping and angling on surrounding reefs; several hundred fish were tabulated for some species, but at least 20 individuals were available for the rarer kinds. The modes in length-frequency distribution were used to determine average weights.

## RESULTS AND DISCUSSION

Before discussing the results of the counts and their implications, an examination of the method and its reliability may be in order. Estimates of mixed marine fish populations by any method are difficult, and visual counts are possible only in clear tropical waters. It is of additional advantage for counting that most coral reef fishes are demersal.

Netting is not possible because of the irregularities of the substrate; baited traps may attract fish which do not "belong" on the reef, and on most days baited and unbaited traps failed entirely to catch certain species, or if an occasional catch was made, it was found unrepresentative of the numbers assessed by underwater counts (*e.g.*, grey snappers and grunts). Conversely it is possible that certain fish such as angelfish and groupers select a trap for their home (Bardach 1958), and this somewhat complicates the use of the marking and recapture method for population estimates on reefs. For these reasons trapping data have been omitted from the tables.

The use of fish poisons was found difficult on areas larger than half an acre, and even there many fish were known to have escaped in spite of previously set surrounding seines. Other fish were affected by the poison and were later found dead on the sandy bottom 500 yards or further from the poisoning site. Obviously, they could not all be collected by skin divers even with SCUBA equipment. In spite of these shortcomings there was no other method to estimate nocturnally active species which were hiding during the day. This estimate is suspected to be low unless one can assume that all nocturnal fishes left their hiding places under rotenone stress.

Dynamiting a portion of a reef might be another method to obtain a fairly complete sample. This, again was not a satisfactory method for several reasons: 1) the charge required for about half an acre of reef would have been awkward to handle adequately from the boat with shallow draft which we had to use, 2) it was not advisable for reasons of public relations, and 3) when dynamiting was tried on a small scale the sharks which were attracted made the collection of dead fish by swimmers and divers hazardous, if not impossible.

This clearly indicates that visual counts were, under the prevailing conditions, the least biased and best census method. It

TABLE 1. *Summer standing fish crop on a 1-hectare reef near Bermuda*

| Fishes[1] | Numbers of individuals (and their estimated total weight, in kg) | | | | | | Av. wt. kg/ha |
|---|---|---|---|---|---|---|---|
| | 1955 | | 1956 | | 1957 | | |
| | No. | Wt. | No. | Wt. | No. | Wt. | |
| **Omnivores (mostly herbivorous)** | | | | | | | |
| Angelfish *Holacanthus bermudensis* (250) | 82 | 20.5 | 47 | 11.8 | 45 | 11.3 | 14.5 |
| Surgeonfish *Acanthurus* sp. (200) | 150 | 30.8 | 27 | 5.4 | 18 | 3.6 | 13.3 |
| Parrotfishes Adult *Scarus* and *Sparisoma* sp. (1000) | 46 | 46.0 | 46 | 46.0 | 50 | 50.0 | 47.3 |
| Subtotals, omnivores[2] | | 97.3 | | 63.2 | | 64.9 | |
| Juvenile *Scarus* and *Sparisoma* (350) | 70 | 24.5 | — | — | — | — | 24.5 |
| Misc. small fish Young surgeon and parrotfish pomacentrids, etc. (10) | 7000 | 70.0 | 4200 | 42.0 | — | — | 56.0 |
| Total weight, omnivores | | | | | | | 155.6 |
| **Carnivores** | | | | | | | |
| Red hind *Epinephelus guttatus* (600) | 63 | 37.8 | 24 | 14.4 | 42 | 25.2 | 25.8 |
| Nassau grouper *Epinephelus striatus* (1115) | 9 | 10.0 | 9 | 10.0 | 12 | 13.4 | 11.3 |
| Other groupers *Mycteroperca* sp. (1500) | 12 | 18.0 | 10 | 15.0 | 12 | 18.0 | 16.0 |
| Coney *Cephalopholis fulvus* (400) | 15 | 6.0 | 3 | 1.2 | 3 | 1.2 | 2.8 |
| Grey snapper *Lutjanus griseus* (1000) | 82 | 82.0 | 78 | 78.0 | 81 | 81.0 | 80.3 |
| Bluestriped grunt *Haemulon sciurus* (400) | 226 | 90.4 | 353 | 141.2 | 250 | 100.0 | 110.5 |
| Porgy *Calamus* sp. (750) | 3 | 2.3 | 1 | 0.8 | 6 | 4.5 | 2.5 |
| Puddingwife *Halichoeres radiatus* (300) | 4 | 1.2 | 2 | 0.6 | 1 | 0.3 | 0.7 |
| Spanish hogfish *Bodianus rufus* (200) | 24 | 4.8 | 15 | 3.0 | 25 | 5.0 | 4.3 |
| Hogfish *Lachnolaimus maximus* (3000) | 6 | 18.0 | 3 | 9.0 | 2 | 6.0 | 11.0 |
| Subtotals, carnivores[2] | | 270.5 | | 273.2 | | 254.6 | |
| Subtotals, omnivores and carnivores[3] | | 367.8 | | 336.4 | | 318.5 | |
| Moray *Gymnothorax* sp. (400) | — | — | 24 | 9.6 | — | — | 9.6 |
| Small wrasses *Thalassoma bifasciatum* and *Halichoeres* sp. (10) | 3200 | 32.0 | 4000 | 40.0 | — | — | 36.0 |

TABLE 1—*Concluded*

| Fishes[1] | Numbers of individuals (and their estimated total weight, in kg) 1955 No. | 1955 Wt. | 1956 No. | 1956 Wt. | 1957 No. | 1957 Wt. | Av. wt. kg/ha |
|---|---|---|---|---|---|---|---|
| Small nocturnal and crepuscular fishes *Holocentrus* sp., *Apogon* sp. *Blenniidae* etc. (20) | — | — | 1200 | 24.0 | — | — | 24.0 |
| Total weight carnivores | | | | | | | 334.8 |
| Grand total weight | | | | | | | 490.4 |

[1] Figures in brackets under species names give average individual weights of fish in grams.
[2] Subtotals of omnivore or carnivore species respectively for which three separate counts were made.
[3] Subtotals of all species for which three separate counts were made.

TABLE 2. *Occurrence of certain species of reef fishes on an extended reef near Bermuda, summer 1957, as counted by two divers, M and B*

| Fishes | June 14 M | June 14 B | June 20 M | June 20 B | June 26 M | June 26 B | July 16 M | July 16 B | Aug. 19 M | Sept. 6 M |
|---|---|---|---|---|---|---|---|---|---|---|
| **Omnivores** | | | | | | | | | | |
| Parrotfishes | | | | | | | | | | |
| *Scarus* | 9 | 9 | 13 | 15 | 23 | 23 | 29 | 35 | 47 | 39 |
| *Sparisoma* | 9 | 6 | 27 | 12 | 33 | 19 | 28 | 20 | 27 | 22 |
| Angelfish | | | | | | | | | | |
| *Holacanthus* | — | — | 14 | 15 | 14 | 14 | 18 | 19 | 25 | 20 |
| Surgeon fish | | | | | | | | | | |
| *Acanthurus* | 11 | 4 | 30 | 21 | 20 | 14 | 21 | 18 | 33 | 28 |
| **Carnivores** | | | | | | | | | | |
| Red Hind | | | | | | | | | | |
| *Epinephelus guttatus* | — | — | — | 1 | 2 | 2 | 1 | 1 | — | 1 |
| Groupers | | | | | | | | | | |
| *Mycteroperca* sp. | — | — | — | 1 | — | 1 | — | 1 | — | — |
| Coney | | | | | | | | | | |
| *Cephalopholis fulvus* | — | — | 2 | — | — | 5 | 1 | 1 | 3 | 2 |
| Grunts | | | | | | | | | | |
| *Haemulon* sp. | 3 | 3 | 1 | 2 | 4 | 2 | 5 | 5 | 2 | 4 |
| Grey snappers | | | | | | | | | | |
| *Lutjanus griseus* | 3 | — | — | 1 | — | — | — | — | — | — |
| Puddingwife | | | | | | | | | | |
| *Halichoeres radiatus* | 2 | — | 2 | 2 | 2 | 2 | 2 | 3 | — | — |
| Others | — | — | 9 | 7 | 5 (Barracuda) | 4 | 3 (School of jacks, 50+, seen by both) | 3 | 3 | 9 |

is quite likely that some fish were counted twice, in spite of instructions to divers only to count the fish in their own lane, but on the other hand it is equally likely that a fair number of fish escaped detection altogether.

On adding the weight of all species for which estimates were made in three successive years, though this does not represent the total weight of fish present, we find the three subtotals to be 368, 336, and 319 kg/ha, respectively (Table 1). The difference between the highest and lowest of these is 50 kg or 13.4% of the largest subtotal. It is likely that the highest estimate of 368 kg in 1955 is the least representative because more baited traps were set on the study reef during this year than during the following two. Some of the groupers, especially (*Epinephelus guttatus*), have been found to remain on the same reef for one or even two to three years, while others of the same species move from reef to reef (Bardach 1958). It is these roaming, larger fish which would stay on a reef as long as they find well baited traps as an inducement. In 1955 there was also an unexpectedly high count of surgeonfish (*Acanthurus* sp.), which is discussed below.

Table 2 contains independent counts by two divers on a larger reef. Among the 28 paired observations of fish seen by both divers, the same numbers were counted on 11 occasions. In 11 other counts diver M saw more fish than diver B, while B observed more fish than M in the remaining 6 of the 28 paired counts. Nine other times only one diver saw the fish of a certain species. Mostly there were only one or two animals involved here, but once one diver missed 5 coneys. This particular discrepancy is easily explained because the fish in question habitually hide in crevices. On the whole individual differences in counts may well compensate one another if the divers are all equally proficient in the use of their gear.

There is some indication in Table 2 that the numbers of omnivores increased from June to September. The counts are spaced too far apart to rule out chance or hydrographic conditions as the causes for this increase, but it seems equally likely that it is due to recruitment, since June to September represents the most favorable period for fish reproduction and growth in Bermuda.

A total standing crop of nearly 500 kg/ha (Table 1) is high compared to demersal fish populations in more northern latitudes (Merriman and Warfel 1947, Harvey 1950). This is to be expected in view of the great sculpturing of the reef which extends the surface area, the inclusion of vertical walls in the counts, the great variety of species, and the high average temperatures (the winter low for one or, at best, two months is 18°C, the summer high 28°C). On the other hand the standing crop estimate of this shallow Bermuda reef is of very similar magnitude to that from Eniwetok Atoll (Odum and Odum 1955), the only other comparable study in the coral reef environment. Values from their "zone D; complex larger heads" (considered similar to the Bermuda study area in the general configuration of corals and types of fish) showed that 93 kg/ha of the population was made up of herbivorous and 18.4 kg/ha of carnivorous fishes. These values are in terms of dry biomass. Assuming that water makes up 75% of the weight of fish (Vinogradov 1953) it is estimated that the total standing crop was 446 kg/ha. The Bermuda figure including the grunts and snappers, two species to be discussed later, is 490 kg/ha, a close correspondence indeed.

For purpose of analysis the fish listed in Table 1 were divided into omnivorous and carnivorous species. Those classified as omnivorous include some which are predominantly herbivorous such as the parrotfishes and the surgeonfishes. These contribute the largest weight of omnivores. Diving in February 1956 established that most large parrotfish were then absent from shallow reefs. It is presumed that they migrated into deeper water with the onset of winter conditions. A summer census may, therefore, give a misleading index of their true place in the annual economy of the reef. Surgeonfish and angelfish on the other hand are permanent residents of the shallow areas. The greatest discrepancy in the numbers of a single species occurred among the surgeonfish: 154 adult surgeonfish were counted in 1955, while only 27 and 18, respectively, were seen in the two subsequent years. Surgeonfish travel in schools of varying sizes, schools of 50 or more having been observed on large unbroken reefs. Large schools occasionally also cover greater distances than the largest extent of the study reef, possibly in consequence of their browsing habits. The high incidence of surgeonfish in 1955 is probably due to the visit of one or two large travelling schools, and the lower numbers of subsequent years come closer to the reef's carrying capacity for this species.

A comparison between larger reef areas and the study reef (Omnivores in Tables 1 and 2) suggests that the largely herbivorous omnivores are abundant on extended reefs and poorly represented on isolated ones. On the large reef they outweigh the carnivores about nine to one, while in the isolated area the weight of the carnivores is slightly less than twice that of the omnivores. This, at first glance, contradicts the classical concept of biomass pyramids, but there are several explanations for this discrepancy. 1) The numbers and the weight only of fishes were estimated. The largest fraction of herbivorous reef animals is probably mollusks, crustaceans, and annelids. These organisms are also the greatest source of food for carnivorous fishes. Carnivorous fish rarely feed upon omnivorous ones: no angelfish or surgeonfish were found in the stomachs of carnivores, and young parrotfish were only rarely ingested. 2) The largest numbers per species and also the largest weight was found among the grunts and snappers. These two species appear to feed only rarely during the day while they remain on the reef. They are reported to disperse at night and feed in the surrounding sandy area (Longley and Hildebrand 1941). The populations of these two species, characteristic as they are of the several isolated reefs which were checked, consisted entirely of adults and were present throughout the year. It seems likely that these species live on isolated reefs because they find many excellent hiding places on the vertical reef walls. Small grunts and snappers are very abundant in inshore waters but were seldom seen on the study reef. These observations suggest that it might be misleading to consider an isolated reef without, to some extent, also including the surrounding sandy areas. 3) Parrotfish swim over larger areas than that of the study reef and may require larger feeding ranges than can be provided by a one-hectare reef.

It is difficult to subdivide carnivores on the basis of predominant organisms in their stomachs, but some food analyses and a look at the dentition of certain fishes suggest, for instance, that the groupers, with a subtotal weight of approximately 50 kg/hectare, feed predominantly on crustacea and fish. The large wrasses and porgies (*Halichoeres radiatus*, *Bodianus rufus*, *Lachnolaimus maximus*, and *Calamus* sp.), representing ca. 20 kg/ha, feed mostly on mollusks.

Among the smaller fishes—excluding the young parrot and surgeonfish which are herbivorous—the ubiquitous pomacentrids, small wrasses, and butterflyfish feed on all kinds of invertebrates. Plant material is also often eaten, but it is not known whether this is accidentally or purposely ingested. The study of Menzel[2] on the Bermuda angelfish, a member of the butterflyfish family, suggests that these fishes cannot grow on plant material alone.

Pomacentrids are highly territorial animals which defend the areas around their attached eggs. They are the only fish on the reef that show these behavior traits to a marked extent. They are also the only reef fishes that are definitely known to have demersal eggs. Grouper and parrotfish eggs were found to be minute, present in large numbers per female, and to bear oil inclusions, which are some clues to a pelagic larval period. In the case of two species of groupers planktonic larvae have developed into juvenile stages in laboratory tanks. While pelagic eggs and larvae are common to many reef animals (Boden 1952), finding them among non-territorial reef fishes and not among territorial ones suggests that reproductive morphology and physiology had influenced the evolution of the inherited behavior pattern of territoriality, which in turn has been postulated to serve as regulator of population density.

The absence of an active defense pattern against intruders among the larger reef fishes such as the groupers suggests further that their numbers may be limited directly by the food supply. This is, to some extent, borne out by feeding experiments which were undertaken in a study of the growth of certain commercially important reef fishes (Bardach and Menzel 1957). Adult red hinds (*Epinephelus guttatus*), the most frequently found groupers on the shallow reef, increased to 300 % of their initial weight

[2] Menzel, D. W. 1958. Utilization of algae for growth by the angelfish (*Holacanthus bermudensis*). MS.

per year when fed to satiation in laboratory holding tanks. The feeding periods from which these figures were prorated lasted only 20 days, and one could expect the food intake to level off if the experiments had been prolonged. The fish also certainly moved less in the tanks than in the natural environment. In spite of these cautions, some reef fishes seem to possess an unrealized growth potential which may, in part, be explained by a limitation of the natural food supply.

The yearly growth rates of some species on the reef were determined by recaptures of tagged fish (Bardach and Menzel 1957). Juvenile and adult carnivorous groupers added between 30 and 40% of their body weight per year allowing for slower growth during the winter; the figure for the omnivorous adult angelfish is 32%. The growth rates of the other species—grunts, snappers, and parrotfishes as well as all young of the year—are not known. It is also not known what percentage of the larger parrotfishes spend the winter in deeper water.

No commercial fishing occurred on the reef where three independent yearly estimates of the summer standing crop gave consistent results. We may, therefore, assume that growth and immigration roughly balanced natural mortality and emigration. With these cautions in mind certain speculations may now be advanced.

It is in keeping with the assumptions of similar studies and the indications gained from our own to estimate that the reef fish biota grew in weight at a rate of about 35% per year, although this value seems low when compared to the growth rates of fish in Block Island Sound (Riley 1955) and the English Channel (Harvey 1950). The absence of commercial fishing on the reef might counteract the effect of long seasonal growth favored by Bermuda's water temperatures, and a greater proportion of large, slowly growing individuals might, therefore, have occurred here than in areas of intensive commercial fisheries. Also certain fish are not on the study reef during the winter months. Their weight increment while absent would tend to lower the yearly overall growth figures. On the other hand, almost a fourth of the standing crop is made up of small, presumably shortlived fishes which do not leave the reef (Bardach 1958) and of young of the year. They can be expected to grow by more than 35% per annum. However, in the absence of more detailed growth data a 35% yearly overall growth is suggested as a first approximation.

At this rate the total yearly growth amounts to 172 kg/ha (35% of 490 kg). Homogenized whole reef fish have an energy value of 1.3 Cal/g, (determined by calorimetric procedure) and the assumed growth, therefore, represents the fixation of $2.2 \times 10^5$ Cal/ha/year. The average incident radiation in Bermuda has been estimated at $1.6 \times 10^{10}$ Cal/ha/year (U. S. Weather Bureau 1954). The overall efficiency with which fish (mostly tertiary consumers) utilized solar energy on Bermuda reefs therefore approximated 0.0014 per cent. Inaccurate as this estimate may be because of the cautions advanced above, this figure is considerably higher than the efficiency estimates (0.00005 to 0.00025 per cent) for George's Bank obtained by Clarke in 1946. His values were based on commercial landings and not on growth, and it was estimated that these landings may represent the removal of 50% of the yearly production of marketable fish. But even on doubling Clarke's upper figure the overall efficiency of conversion of solar energy into fish flesh still appears to be about three times that of George's Bank.

Hayne and Ball (1956) in comparing solar radiation with fish production in a shallow pond in Michigan (average depth 3 feet) arrived at an overall efficiency value of 0.0014 per cent. Bennett (1943) and Carlander (1953) quote standing crop estimates of 400 to 500 pounds per acre as common in Illinois and Iowa ponds with mixed fish populations; much of this weight is made up of young of the year, and overall efficiency values of utilization of incident energy are probably also high. These bodies of water are freshwater environments, more self-contained than the reef, but they are also shallow. The close correspondence between efficiency estimates from pond and reef suggests that high utilization of incident radiation by tertiary consumers may be typical of shallow waters where a substantial amount of solar energy reaches the bottom.

Silver Springs, Florida, is another example of a shallow aquatic environment with high plant productivity (Odum 1957). While it is not possible to make numerical comparisons on the fish level, the ratio between incident radiation and fish productivity indicates a high overall efficiency here also.

The Bermuda coral reefs are located in the Sargasso Sea which is renowned for its infertility, but the relative fertility of the reefs themselves is high. Reefs are littoral areas where attached primary producers abound. Nutrients may be retained there for at least part of the year (Boden 1952), and the utilization of solar energy by attached and symbiotic reef algae is as high as 3 per cent (Odum and Odum 1955). Sargent and Austin (1954) showed that Rongelap atoll was a self-sufficient community with a productivity per unit area that was considerably higher than that of the adjacent waters. This supports the belief that a high overall productivity is also a characteristic of Bermuda reef areas.

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