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REPORT

An adaptive management approach to an octocoral fishery based on the Beverton-Holt model

S. Goffredo · H. R. Lasker

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Abstract Coral reef species are frequently the focus of bio-prospecting, and when promising bioactive compounds are identified there is often a need for the development of responsible harvesting based on relatively limited data. The Caribbean gorgonian *Pseudopterogorgia elisabethae* has been harvested in the Bahamas for over a decade. Data on population age structure and growth rates in conjunction with harvest data provide an opportunity to compare fishery practices and outcomes to those suggested by a Beverton-Holt fishery model. The model suggests a minimum colony size limit of 7–9 years of age (21–28 cm height), which would allow each colony 2–4 years of reproduction prior to harvesting. The Beverton-Holt model assumes that colonies at or above the minimum size limit are completely removed. In the *P. elisabethae* fishery, colonies are partially clipped and can be repeatedly harvested. Linear growth of surviving colonies was up to 3 times that predicted for colonies that were not harvested and biomass increase was up to 9 times greater than that predicted for undisturbed colonies. The survival of harvested colonies and compensatory growth increases yield, and yields at sites that had previously been harvested were generally greater than predicted by the Beverton-Holt model. The model also assumes recruitment is independent

of fishing intensity, but lower numbers of young colonies in the fished populations, compared to unfished populations, suggest possible negative effects of the harvest on reproduction. This suggests the need for longer intervals between harvests. Because it can be developed from data that can be collected at a single time, the Beverton-Holt model provides a rational starting point for regulating new fisheries where long-term characterizations of population dynamics are rarely available. However, an adaptive approach to the fishery requires the incorporation of reproductive data.

Keywords Coral reef · *Pseudopterogorgia elisabethae* · Natural products · Population age structure · Maximum sustainable yield · Compensatory growth

Introduction

One of the arguments often advanced for the conservation of coral reef ecosystems is the extraordinary diversity of these communities and the potentially useful bioactive compounds that reef species may produce (Bruckner 2002). That potential creates a paradox, in that the discovery of compounds with potentially valuable properties generates the need to harvest that material. Even when laboratory syntheses of the compounds are possible it is often the case that the amounts of material needed for exploratory research will necessitate extensive collections. Bruckner (2002) for instance notes cases in which thousands of kilograms of tissue are needed to generate milligrams of the target compound. The need for extensive harvests, even in exploratory research, suggests a need for protocols that can be developed with a minimum of data in order to regulate these fisheries and prevent overexploitation.

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S. Goffredo
Department of Evolutionary and Experimental Biology, Alma Mater Studiorum-University of Bologna, via F. Selmi 3, I-40126 Bologna, Italy

H. R. Lasker (✉)
Department of Geology, State University of New York at Buffalo, 637 Hochstetter Hall, Buffalo, NY 14260, USA
e-mail: hlasker@buffalo.edu

While the exploitation of benthic invertebrates for natural products is still in its infancy, fisheries for precious corals have been in existence for decades, and in some areas for centuries. The black coral, *Antipathes* spp., fishery in Hawaii has been developed in the past 50 years and has been the focus of extensive studies by Grigg and co-workers for much of that time. Grigg (1976) used a Beverton-Holt fishery model to identify the minimum age/size at which black coral colonies should be harvested and the maintenance of similar population structure over a 23-year period suggests that the effort has been generally successful (Grigg 2001).

The use of red coral, *Corallium rubrum*, for jewelry dates back thousands of years, and organized harvesting in the Mediterranean is known for hundreds of years (Tsounis et al. 2007). Regulations that have been developed in the past 50 year have been based for the most part on general ecological studies that have characterized changes in population structure and have tried to integrate information on reproduction, growth, and survival into considerations of the fishery. Recently, Tsounis et al. (2007) applied a Beverton-Holt fishery model to abundance, growth, and survival data and determined that yields could be enhanced dramatically were the age at harvest increased a minimum of 3-fold (11–33 years).

To date, pseudopterosins from the Caribbean octocoral *Pseudopteroorgia elisabethae* are the only compounds from a reef species that have made their way to commercial use. Pseudopterosins exhibit anti-inflammatory and analgesic properties and are used by the cosmetics industry (Look et al. 1986). Over the last 12 years *P. elisabethae* has been harvested from the Little Bahama Bank in the Bahamas. The fishery is regulated through an export limit set by the Bahamas Department of Marine Resources. Annual harvest data are not publicly available, but Bruckner (2002) placed the value of the fishery at \$3–\$4 million and Puyana et al. (2004) notes that estimated demand for the pseudopterosins is 13–20 tonnes per year. The collection protocols in the fishery have been developed by the collectors. Colonies are collected by divers using either scuba or surface supplied air. The collectors clip the colony, removing most of the colony but with the goal of leaving at least one central branch, typically 5–15 cm in height, that contains 5–10 branchlets. The remaining tissue survives and regenerates new branches (Castanaro and Lasker 2003). Colonies develop sufficient tissue for re-harvesting in as little as 2 years (T. Higgs, Personal communication). Initially populations were allowed to recover for 2–3 years, which was the time generally required for new and recovering colonies to reach a size at which a harvest would be profitable. Additional input from more recent scientific studies (i.e., Lasker et al. 2003; Gutiérrez-Rodríguez and Lasker 2004a) has led the

collectors to extend the recovery time to allow colonies to reach reproductive size and reproduce prior to a second harvest. Some of the sites have been harvested 3 times which is suggestive of sustainability, but the fishery has not been the subject of a quantitative analysis.

The *P. elisabethae* fishery would appear to be a success story which, if correct, is due in large part to the conscientious approach of the local collectors. However, it is desirable to have a systematic approach to the development of a fishery for species like *P. elisabethae* that can provide a framework for the development of similar fisheries in the future. In this report, measures of abundance and growth of *P. elisabethae* are used to develop a Beverton-Holt fishery model and compare the fishery practices and yields suggested by that model to current practices and to harvest data provided by T. Higgs, one of the collectors in the *P. elisabethae* fishery. The utility of the Beverton-Holt fishery model is explored and its utility in an adaptive management approach to developing similar fisheries is discussed.

The Beverton-Holt fishery model (Beverton and Holt 1957) is best described as a yield per recruit model. It has been used in studying the population dynamics of vertebrates and invertebrates, including both colonial and solitary corals (e.g., Jensen 2000; Barrowman et al. 2003; Goffredo et al. 2004; Siddeek et al. 2004; Tsounis et al. 2007). The model assumes steady state and balanced recruitment and mortality. A population with those traits should have a stable age distribution, characterized by an exponential decrease in the frequency of individuals with increasing age (Grigg 1975, 1977; Mistri 1995; Chadwick-Furman et al. 2000; Goffredo et al. 2004; Santangelo et al. 2007). Given individual growth rates and natural mortality, the age-specific biomass of a cohort, i.e., its productivity, can be calculated. Growth of individuals adds to productivity, while the loss of individuals due to mortality reduces productivity. Characteristically, productivity increases until an age is reached at which growth gains to individuals no longer exceed the loss of biomass from mortality. That point represents the age of the cohort's maximum production. As the cohort ages and more individuals die, production declines to zero. Assuming a continuous supply of recruits, the age at which the cohort reaches maximum productivity corresponds to the age for harvesting that will generate the maximum sustainable yield (Grigg 1976, 1984; Pauly 1984).

Materials and methods

Population age structure

Data on colony size were used to estimate the age structure of *P. elisabethae* in two “natural populations” (i.e., not previously fished) and three fished populations in the Bahamas

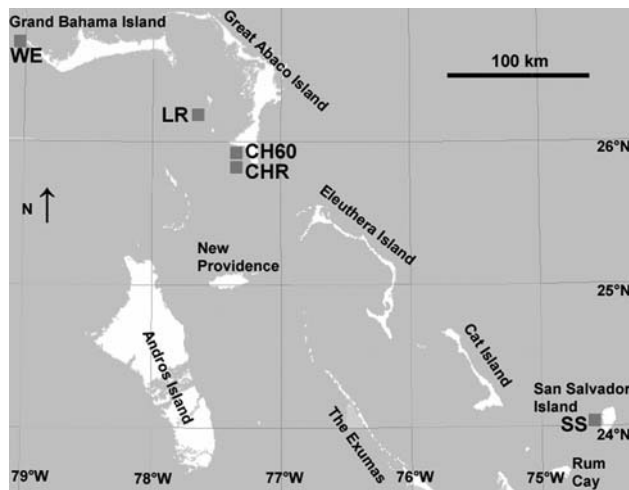


Fig. 1 *Pseudopterogorgia elisabethae*. Sampled sites and year of sampling (coordinates and abbreviations of sites in decreasing order of latitude): WE, West End (Natural Population), 26 29' N, 78 38' W, 2007; LR, Long Rock (Fished Population), 26 10' N, 77 35' W, 2007; CH60, Cross Harbour 60 (Fished Population), 25 58' N, 77 20' W, 2007; CHR, Cross Harbour Ridge (Fished Population), 25 57' N, 77 21' W, 2007; SS, San Salvador (Natural Population), 24 4' N, 74 33' W, 1999

(Fig. 1). Four of the surveys were conducted in 2006 along the Little Bahama Banks. The fifth population was surveyed on San Salvador in 1999 and has been discussed in Lasker et al. (2003) and Goffredo and Lasker (2006). Of the 4 Little Bahama Bank sites, West End had never been harvested while the other three were previously harvested (T. Higgs, personal communication). At each of the Little Bahama Bank locations, four 1-m-wide belt transects were randomly placed within 50 m of an arbitrarily chosen starting point. Colony height and the diameter of the base of all the colonies found along each transect was measured. The lengths of the transects and thus number of colonies measured varied depending on density of the population and the amount of time available at the site. The mean area surveyed at each site was 110 m² (SD = 65). The San Salvador population data were based on surveys of colony heights from colonies located on 3 arbitrarily placed 2-m-wide belt transects totaling 70 m² (Lasker et al. 2003).

Colony height and basal diameter exhibit predictable relationships with colony age (Goffredo and Lasker 2006) and can be used to estimate age. However, once a colony has been harvested the height of the colony is no longer correlated to its age. Basal diameter, being unchanged, still allows an estimate of age and was used to estimate the age of harvested colonies. Basal diameter of *P. elisabethae* colonies is related to age following the function $y = 2.5705x^{1.4493}$ ($r = 0.839$), where y is the number of annual growth rings and x is the basal diameter in millimeters (Goffredo and Lasker 2006). Assuming that there is little variability in growth rate within the bathymetric band

and the surveyed geographical area (Goffredo and Lasker 2006), the age of each colony in the four Little Bahama Bank populations was estimated from its basal diameter. *P. elisabethae* colony growth rate follows a Von Bertalanffy growth curve (Von Bertalanffy 1938; Goffredo and Lasker 2006). Colony height and the Von Bertalanffy growth function was used to estimate the age structure of the San Salvador population as diameter data were not available for those colonies.

Beverton-Holt resource management model

The Beverton-Holt age-specific curve expressing cohort yield in dry mass was generated using the growth curve of colony dry mass and the survivorship curve (i.e., cohort yield = individual colony dry mass at age $t \times$ survivorship at age t ; after Grigg 1984; Ross 1984; Chadwick-Furman et al. 2000; Goffredo and Chadwick-Furman 2003; Tsounis et al. 2007). For the 2 sites that had not been fished, West End and San Salvador, the dry weight was estimated from colony height using the equation $y = 0.002x^{2.075}$ ($r = 0.968$), where y is the dry mass of the colony in grams and x it is the height of the colony in cm (Goffredo and Lasker 2006).

Survivorship curves were calculated from the age structure of the populations at West End and San Salvador. M , the instantaneous natural mortality rate, was calculated as the exponential rate of decline in the number of individuals within each age class (i.e., $N_t = N_0 e^{-Mt}$) (after Grigg 1984; Pauly 1984; Ross 1984; Sparre et al. 1989; Babcock 1991; Chadwick-Furman et al. 2000; Goffredo and Chadwick-Furman 2003; Tsounis et al. 2007). The youngest age class (0–1 year) was excluded from the mortality-rate analysis because small, young colonies are usually under-represented in field samples (Grigg 1976, 1984; Pauly 1984; Babcock 1991; Chadwick-Furman et al. 2000; Goffredo and Chadwick-Furman 2003; Tsounis et al. 2007). Among *P. elisabethae*, the smallest (<5 cm height) colonies are both more difficult to locate and when observed can be difficult to identify to species. Colonies that are >5 cm in height are readily identified to species in the field. The inverse of M is equal to the mean age of the individuals in a population, and hence is equal to their turnover rate, or annual production:biomass ratio (P/B) (Pauly 1984; Clasing et al. 1994; Chadwick-Furman et al. 2000; Goffredo and Chadwick-Furman 2003). Maximum colony lifespan was calculated as the age at which <0.5% of the population was still surviving, based on survival curves (after Sparre et al. 1989; Chadwick-Furman et al. 2000; Goffredo and Chadwick-Furman 2003).

Growth rates of colonies after harvesting were quantified for colonies from Cross Harbor Ridge, Great Abaco. In 2006 the site, which had been harvested both in 2002 and 2005, was carefully surveyed for colonies that had been

previously harvested. The surveys were conducted with the assistance of T. Higgs, the collector who had conducted the harvests at the site. Colonies that had been harvested are readily identified in the field as clipping leads to redirected growth in which one or more of the side branches becomes the dominant axis of growth (Castanaro and Lasker 2003). The time since the harvest was also apparent as the more recently harvested colonies exhibited far less regrowth. Twenty-four colonies that had been harvested in 2005 and 32 colonies that had been harvested in 2002 were identified and collected. The portion of regenerated colony was identified by the cut scar; the length and dry mass of the regenerated portion was measured and the rate of regrowth quantified. An estimate of the expected growth rate for a colony of that age and size was calculated using the Von Bertalanffy growth model that had been derived for undisturbed colonies (Goffredo and Lasker 2006). A subsample of the collected colonies was also inspected under the binocular microscope to determine if the colonies were sexually mature.

Harvest data

Harvest yields from collections made throughout the Little Bahama Bank between 1999 and 2002 were developed from collection data made available by T. Higgs. While Higgs was not the only collector harvesting during that time period, the collectors avoid freshly harvested areas. Thus Higgs' data are representative of daily and per unit area yields in the fishery. At that time, collections were made using surface supplied compressed air and thus the diver was limited to an area defined by the water depth and the 91 m of the supply hose. Assuming a depth of 15 m, which is characteristic of most of the harvest sites, a diver would be restricted to an area no greater than 2 ha. When the collectors encountered dense beds, the boat was moved a short distance between dives. When that distance was less than the maximum extension of the air supply hose the distance between anchorages was used to calculate the collection radius. Higgs recorded the weight of air-dried tissue collected each day, and collections were made from as many as 3 locations each day. Areal estimates of yield were calculated from the mass of the collected colonies divided by the cumulative area worked on that day.

Results

Population age structure and survivorship of natural populations

Both natural populations had age structures characterized by exponentially decreasing abundance with increasing age

(Fig. 2), which is consistent with a stable age structure. The assumption that the two populations were in steady state, which is necessary for the calculation of the instantaneous rate of natural mortality, appeared therefore to be reasonable. The percentage of young, sexually immature individuals (age <5 years) was relatively high in the two observed samples, being 69.9% at West End and 61.3% at San Salvador. At West End, the mean age of the individual colonies was 3.6 year (SD = 3.2), and the oldest colony observed was estimated to be 31 year old; at San Salvador the mean age of the colonies observed was 5.1 years (SD = 4.4) and the oldest colony observed was estimated to be 21 years old. Plots of the natural logarithm of the numbers of colonies (frequency) in each age class (N_t) against their corresponding age (t) produced estimates of mortality of 0.246 at West End and 0.179 at San Salvador. Turnover and maximum longevity were 4.1 years and 22 years at West End and 5.6 years and 30 years at San Salvador.

Population biomass and yield of natural populations

The observed age-specific yield for both natural populations was somewhat bell-shaped but exhibited substantial year to year variability, reflecting variation in both the number and sizes of individuals in the different age classes

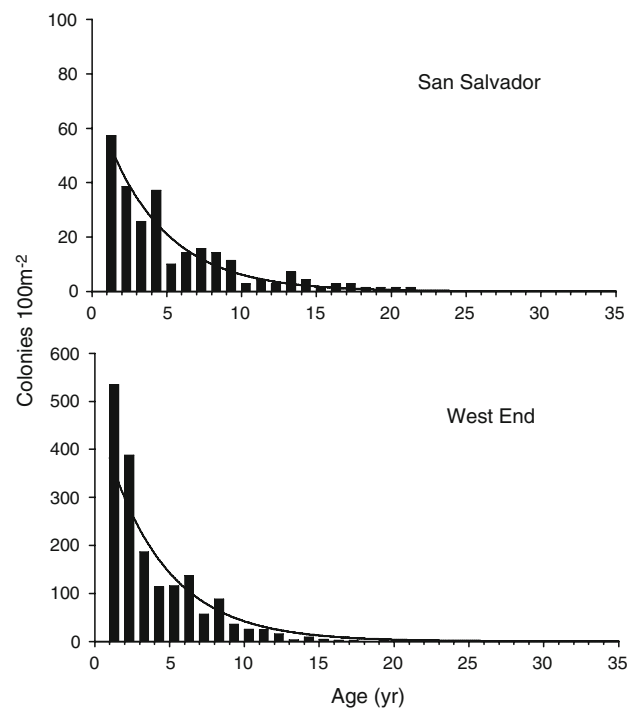


Fig. 2 *Pseudopterogorgia elisabethae*. Age class distribution of populations, at West End, Grand Bahama Island 2007, and San Salvador Island 1999. Neither population has been commercially harvested. Line represents expected abundances for a population with a stationary age distribution

at the two sites (Fig. 3). The distribution for the San Salvador population was flatter ($SD = 5.2$) than that of West End ($SD = 4.9$), and the two curves exhibited peaks at 8 and 13 years, respectively. The distribution at West End exhibited strikingly low biomass at 7 years, which was a function of there being fewer 7 years colonies than either 6 or 8 year old colonies. The young, sexually immature individuals (age <5 years), represented 16.3% of the biomass at West End and 12.2% of the biomass at San Salvador (Fig. 3).

The age-specific curves of colony growth and survival were used to calculate yield, in terms of dry mass per recruit, of *P. elisabethae* colonies at West End and San Salvador. Calculated yield, which was based on the predicted age class distribution and age-specific colony biomass, increased rapidly when the colonies were young, due to their rapid increase in size. Yield was maximal at 7 years of age in West End (maximum yield per recruit = $0.189 \text{ g recruit}^{-1}$) and at 9 years in San Salvador (maximum yield per recruit = $0.416 \text{ g recruit}^{-1}$), after which losses due to mortality overtook gains due to individual growth. The age at maximum yield occurred 2–4 years after the age at sexual maturity (Fig. 3).

Using the data from the natural populations, a steady state was assumed (i.e., recruitment equaled mortality) and the rate of natural mortality was multiplied times the standing crop, to obtain an estimate of the total number of recruits entering the population each year. This number multiplied by the maximum yield per recruit provides an estimate of the maximum sustainable yield for the population (Table 1). For production to be sustained at these levels, it is necessary to impose minimum size limits corresponding to 7 years of age (21 cm colony height) at West End, and 9 years of age (28 cm colony height) at San

Salvador (Fig. 3; Table 1). Considering that the age of reproductive maturity of *P. elisabethae* is 5 years, the above-mentioned size limits would allow 2 years at West End and 4 years at San Salvador in which reproduction would occur. It is important to note, however, that this characterization of the harvest assumes that each year members at or above the age/size at maximum sustainable yield are completely removed. In the *P. elisabethae* fishery, harvests at any site were originally limited to collections once every 3 year and the harvests included branches collected from older colonies that had regenerated following earlier harvests.

Population structure of harvested populations

If populations on the Little Bahama Bank met the assumptions of the Beverton-Holt model and if the fishery were fished as suggested by the model, then the distribution of the fished populations would be similar to the natural populations, but would be depressed above the age of maximum sustainable yield. As is apparent in Fig. 4, that is not the case. In comparison with the natural populations of West End and San Salvador (Fig. 2), the three harvested populations had fewer numbers of young colonies than expected, especially at Long Rock, where the population appeared to be particularly depressed and skewed toward older colonies (Fig. 4). Although sexually immature individuals (age <5 years) constituted the majority of the sample observed (>60%) in the natural populations, in all three harvested populations they were a minority of the sample: 45.9% at Cross Harbour 60, 44.1% at Cross Harbour Ridge, and only 21.8% at Long Rock. At Cross Harbour 60 the mean age of the individual colonies observed was 5.9 years ($SD = 4.6$), and the oldest colony observed was 24 years old; at Cross Harbour Ridge the mean age was 6 years ($SD = 4.6$), and the oldest colony observed was 23 years old; at Long Rock the mean age was 11.7 years ($SD = 7.4$), and the oldest colony observed was 37 years old.

Regrowth and reproduction of colonies after harvesting

After clipping, colonies had a higher growth rate than expected for undisturbed colonies of the same size or age (Table 2). As is evident in Figs. 5 and 6 all but 7 of the colonies had linear growth rates that exceeded predicted growth, and all the colonies had mass growth rates that exceeded predicted growth. Linear extension of the colonies cut 4 years prior to collection was greater than that of colonies clipped 1 year prior to collection (ANOVA, $F_{1,52} = 13.79$, $P < 0.001$). Linear growth of the clipped colonies was not related to age at the time of cutting ($F_{1,52} = 1.99$, $P = 0.165$), nor to the height of the colony

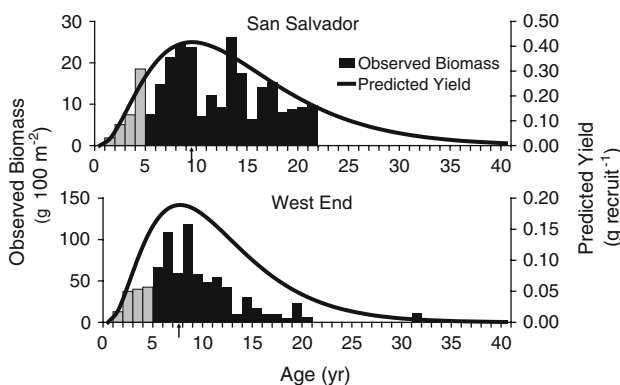


Fig. 3 *Pseudopterogorgia elisabethae*. Age class distribution of colonies' dry biomass, and Beverton-Holt population yield curve in unfished populations at West End, Grand Bahama Island (2006), and San Salvador Island (1999). Observed biomass bars shaded gray are for colonies that have not reached reproductive size. Arrow denotes age at which the harvest will yield the maximum yield

Table 1 Parameters of the Beverton-Holt fishery management model, calculated for two natural populations of *Pseudopterogorgia elisabethae* in the Bahamas

Natural population	Standing crop: # colonies ha ⁻¹	Standing crop: kg of dry mass ha ⁻¹	<i>M</i>	Recruitment: # recruits year ⁻¹ ha ⁻¹	MYR: g recruit ⁻¹	MSY: kg of dry mass year ⁻¹ ha ⁻¹	MSL: colony age (year)	MSL: colony height (cm)	MSY _(colonies) : # colonies year ⁻¹ ha ⁻¹
West end	175,000	81.5	0.246	43,000	0.19	8.1	7	21	4,414
San Salvador	26,000	27.0	0.179	4,600	0.42	1.9	9	28	523

M is the instantaneous rate of natural mortality (year-based analysis); MYR is the maximum yield per recruit; MSY is the maximum sustainable yield; MSL is the minimum size limit; MSY_(colonies) is the number of colonies at or above the minimum size limit that can be removed per year per hectare

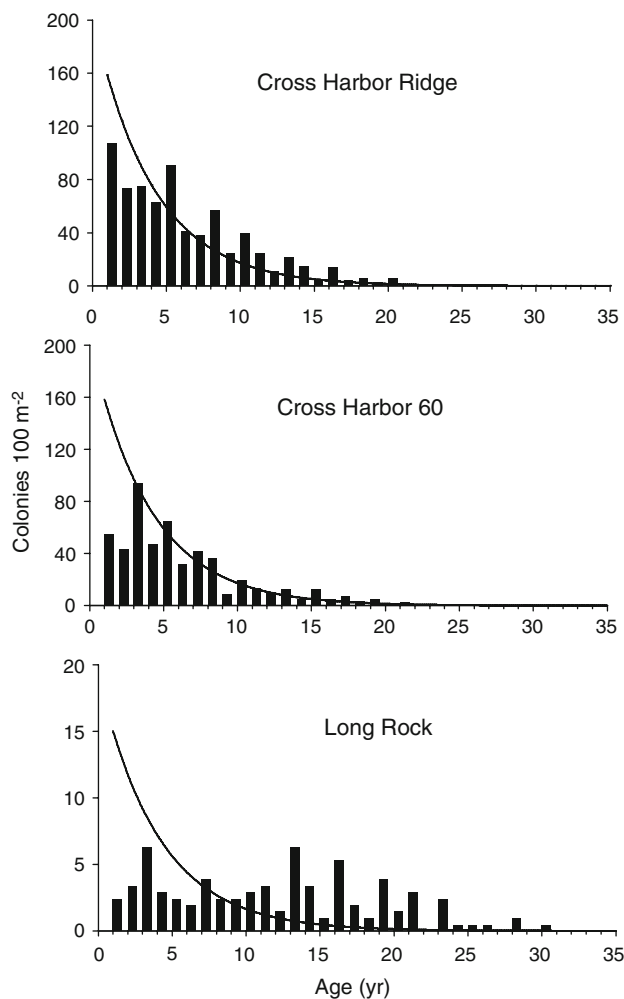


Fig. 4 *Pseudopterogorgia elisabethae*. Age class distribution of harvested populations in 2006 at Cross Harbour Ridge, Cross Harbour 60, and Long Rock. Line indicates the predicted stable age distribution assuming mortality and recruitment are equal. Line represents expected abundances for a population with a stationary age distribution

immediately after cutting ($B = -0.25$, $F_{1,52} = 4.01$, $P = 0.051$). Mass growth rates also were greater than predicted and also differed between the two harvest events with the 4-year-old colonies again exhibiting significantly greater growth than those rates measured a year after

harvest ($F_{1,52} = 4.10$, $P = 0.048$). Mass growth rates did not covary with either height of the colony after harvest or age at the time of clipping. Some of the colonies that had been harvested previously were sexually mature at the time of collection. One year after clipping 3–9 had visible gonad, and 4 years after clipping 5–8 colonies were sexually mature.

Harvest yields

Data from the 1999–2001 harvests indicate that a pair of collectors working with surface supplied air collected a mean of 24.4 kg d⁻¹ (SD = 11.4 kg d⁻¹). As is evident in Fig. 7a, there was a range of collection rates over the three years including a number of days with exceptionally high yields. The median collection of 23.9 kg d⁻¹ closely matched the mean. Detailed location data were not available for the 1999 and early 2000 collections. Converting the remaining data to areal measurements had the effect of condensing most of the data points into an even narrower range, but also led to a great number of points falling well outside that cluster. Thus the yield estimated as kg-ha⁻¹ was more variable than the raw collection data, with mean of 17.0 kg ha⁻¹ and a standard deviation of 25.5 kg ha⁻¹. The median of 9.0 kg ha⁻¹ was almost half that of the arithmetic mean. The kg ha⁻¹ estimate of yield was dependent on extrapolation of the harvesters' data on boat positioning and the area that could be sampled using a 91 m supply line from their boat. It was not possible to determine whether some of the exceptionally large values reflect differences in population density among the collection sites or inaccurate estimates of the area actually sampled. For instance, the procedure would have underestimated the collection area for harvests made in shallower depths or on days in which the harvesters did not collect throughout the entire area they could reach.

Discussion

The Beverton-Holt fishery model has been successfully employed in the Hawaiian *Antipathes* fishery for decades

Table 2 Growth of *Pseudopterogorgia elisabethae* colonies at Cross Harbour, Bahamas, that had previously been harvested

Years since harvest	Linear growth (cm year ⁻¹)		Predicted linear growth (cm year ⁻¹) based on age/height at the time of harvest		Mass growth (g year ⁻¹)		Predicted mass growth (g year ⁻¹) based on age/height at the time of harvest		N
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	
1.0	4.5	2.5	2.5/3.1	0.3/0.1	0.78	0.48	0.26/0.09	0.06/0.03	24
4.0	6.5	2.0	2.4/2.9	0.3/0.1	1.10	0.77	0.28/0.16	0.06/0.03	32

Predicted growth rates are based on the age/size of the colony after cutting and assumes growth follows a von Bertalanffy growth curve. N is number of colonies

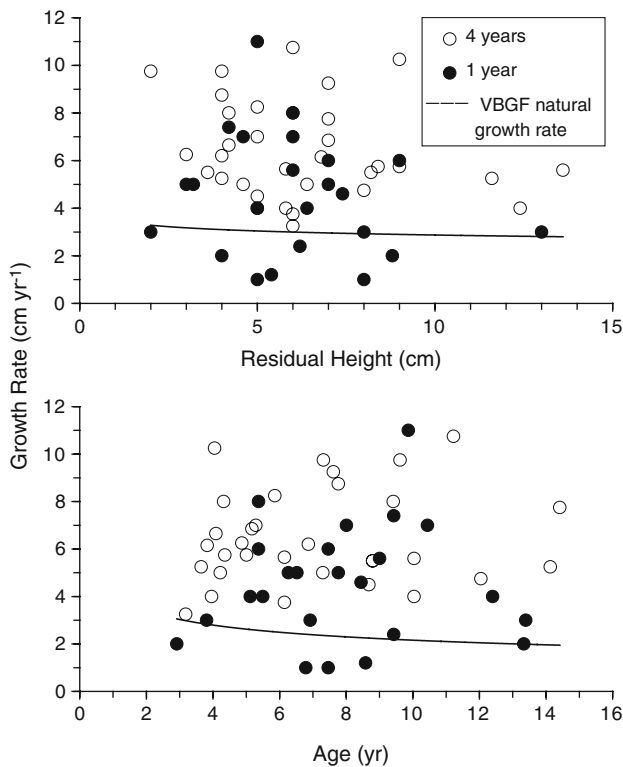


Fig. 5 *Pseudopterogorgia elisabethae*. Linear growth rates of clipped colonies 1 and 4 years after clipping are compared with natural growth rates expected for unclipped colonies of same age or size. VBGF, is the Von Bertalanffy growth function obtained from microscopic analysis of growth rings, described in Goffredo and Lasker (2006)

(Grigg 2001), and given the ability to develop the model with data that can be generated in the early stages of a fishery, it provides a simple model on which to initiate a harvest regime. However, the model makes numerous assumptions, some of which do not apply to the *P. elisabethae* fishery, and those have and may continue to produce modifications in the fishery.

The most obvious difference between the fishery modeled in the Beverton-Holt model and the *P. elisabethae* fishery is the fact that harvested colonies survive and given sufficient recovery time can be harvested multiple times. The effects of those colonies on the harvest is further

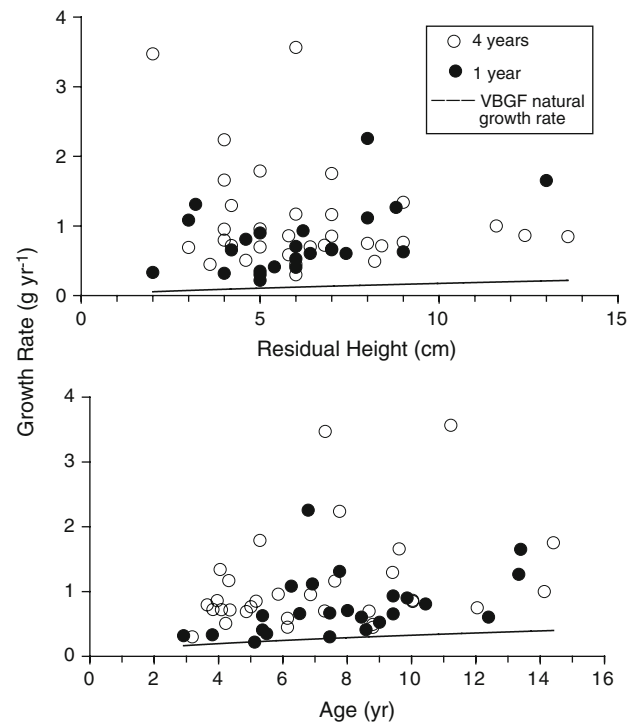


Fig. 6 *Pseudopterogorgia elisabethae*. Dry mass growth rates of clipped colonies 1 and 4 years after clipping are compared with natural growth rates expected for unclipped colonies of same age or size. VBGF is the Von Bertalanffy growth function obtained from microscopic analysis of growth rings, described in Goffredo and Lasker (2006)

compounded by the accelerated growth rates of harvested colonies. Measured as either height or biomass, the growth rates of colonies that had been clipped for harvest show markedly greater growth rates than similar size and age colonies. Compensatory growth is commonly observed among plants (Tiffin 2000) and has also been reported in *Pseudopterogorgia bipinnata* (Sánchez and Lasker 2004). Castanaro and Lasker (2003) did not find compensatory growth in clipped colonies of *P. elisabethae*, but that conclusion was based on mean rates of branch extension across all the colonies’ branches. *P. elisabethae* colonies have two classes of branches, branchlets that extend and then cease growth and “mother” branches, which give rise

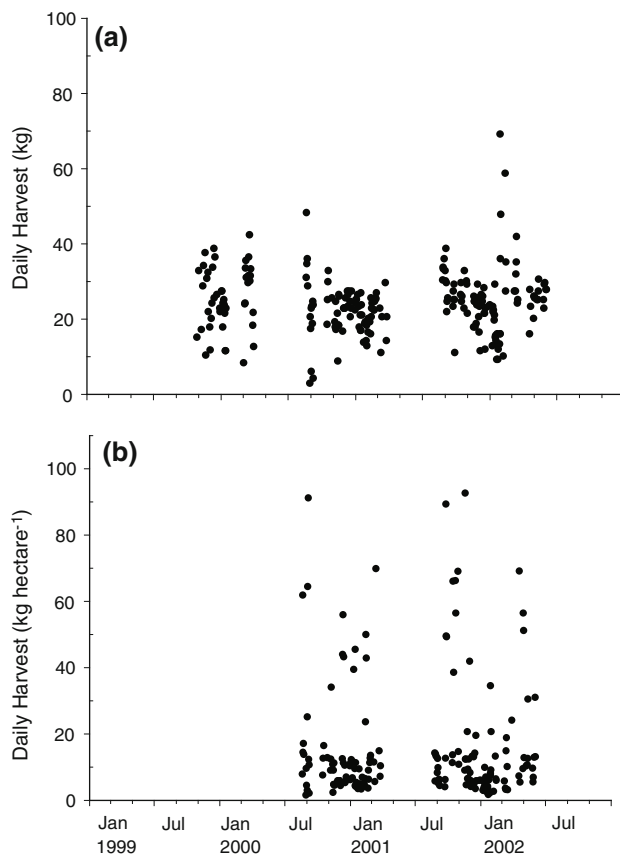


Fig. 7 *Pseudopterogorgia elisabethae* harvest yields generated by one boat working along the southern edge of the Little Bahama Bank, 1999–2002

to other side branches and which have greater growth rates than adjacent branches (Lasker et al. 2003). When a colony is clipped it is often the case that one of the branchlets transforms into a mother branch and exhibits increased growth. A reanalysis of the data from Castanaro and Lasker (2003) shows that the maximal growth rates on the clipped colonies exceeded that of the controls and that the maximum growth rates on colonies reduced to 12 branches exceeded that of colonies reduced to 4 branches (ANOVA, $F_{2,52.7} = 7.16$, $P = 0.002$, SNK post-hoc comparisons, $P < 0.05$). Compensatory growth is clearly a key component in maintaining the populations of *P. elisabethae* at the harvested sites. The differences in maximal growth between the severely cut colonies and those left with 12 branches also fits the pattern where colonies that were harvested 1 year before measurements had lower growth than those harvested 4 years before measurement. As is evident from Fig. 5, the amount of tissue left on a branch is highly variable and growth was probably retarded on some of the most severely clipped branches and would remain so until the system of “mother and daughter” branches was reorganized. An alternative explanation for the difference

in growth rates between the two harvests is that colonies with low growth rates do not survive and only the faster growing colonies are present among the colonies that survived 4 year after their initial harvest. Although the mechanism mediating the compensatory growth is unknown, its relevance to the fishery is that not only will clipped colonies recover but they also do so at an accelerated rate. The dramatic regrowth depicted in Fig. 8 represents an extreme example of how robust that growth can be.

The effect of repeated harvests of the same colonies is illustrated in Fig. 9 which shows the yield per recruit as a function of age for a population in which colonies are re-harvested once they grow back to the minimum size for harvesting. At the first harvest, collectors harvest the entire population over the age of 9 years. Assuming harvests every 3 years, the steady state harvest will include the 3 cohorts that reach harvestable size plus the older cohorts that have regrown to a size large enough for harvesting. The surviving older colonies whose regrowth was assumed to be twice the non-clipped rate dramatically increase the total yield compared to the 3 cohorts that reached



Fig. 8 *Pseudopterogorgia elisabethae* colony that was initially harvested 12 Sept 1997 and was then collected in March 1999. Lines near base indicate points at which the colony branches were cut in the original harvest. Grid lines are 10 cm apart

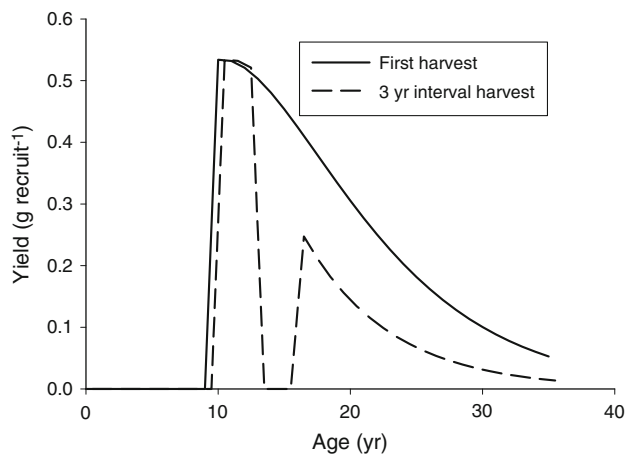


Fig. 9 Harvest yields for a *Pseudopterogorgia elisabethae* population during an initial harvest when all colonies older than 9 years are collected and then when subsequent harvests are conducted at 3 years intervals and only colonies equal in height or taller than a 9-year-old colony are collected. (The line for the 3 years interval harvest has been displaced by 0.5 year for illustrative purposes.)

harvestable size during the 3 years between harvests. While this additional, harvestable, growth is extremely important to the overall yield, it does not change the basic conclusion of the Beverton-Holt analysis that the optimal age/size at which to begin harvesting occurs at the age at which colony growth no longer can keep up with the decrease in survivorship due to mortality.

The population density of the San Salvador population is probably more similar to the regularly harvested sites than that at West End, and the Beverton-Holt analysis of that population (Fig. 3, Table 1) suggests that colonies should be harvested when they are 9 years old and have attained a height of 28 cm. Harvesting in that manner would generate an annual yield of 1.9 kg ha⁻¹. The collection data presented in Fig. 7 are primarily second or third harvests of sites that had been harvested 3 years earlier. Thus the harvest would include the three cohorts that had reached harvestable size plus previously harvested colonies that had recovered sufficiently. The observed median yield of 9 kg ha⁻¹ is not markedly different than that expected from the collection of 3 cohorts (6 kg) plus additional yield from colonies that were harvested for a second (or third) time. This similarity suggests that the Beverton-Holt model provides a conservative estimate of the yield that the fishery can generate.

A more critical assumption of the Beverton-Holt model is a constant supply of recruits that is independent of population density. Such a pattern would generate age distributions like those of West End and San Salvador. The harvested populations from Cross Harbour 60, Cross Harbour Ridge, and Long Rock (Fig. 4) all exhibit markedly lower numbers of young colonies than would be expected given the survivorship curves derived for the natural

populations. Those results may reflect natural variation in recruitment between years or alternatively an effect from harvesting. The Cross Harbour populations appear to be missing recruits in the last 5 years and the deficit at Long Rock may be as great as the 12 years over which populations have been harvested. *P. elisabethae* planulae may not disperse great distances (Gutiérrez-Rodríguez and Lasker 2004b). Even if some of the colonies are mature after clipping, harvested colonies are dramatically smaller and populations should generate far fewer zygotes after being harvested. Thus reduced recruitment at the 3 harvested sites may be a consequence of reduced fecundity and settlement caused by the harvest. This possibility has led the collectors to switch to harvesting on a longer, 5 years time interval, in an effort to give colonies greater time to reproduce before they are next used.

The goal of all fisheries is to maximize yield while minimizing risk to the populations that sustain the fishery. In the *P. elisabethae* fishery, the basic protocol had been to identify sites with dense populations (approximately >1 colony m⁻²), harvest the branches of large and medium size colonies, leaving 5–10 branches for regrowth, and then waiting 2–3 years until the density of harvest size colonies was great enough to make a return profitable. That has led to median yields for a typical collector of 24 kg d⁻¹ or 9 kg ha⁻¹ d⁻¹. Those protocols and yields are generally consistent with the recommendations and predicted yields generated by the Beverton-Holt model. However, the Beverton-Holt model alone cannot be used to regulate the fishery and the reproductive biology of the species has necessitated adjustments to the fishery. It probably will take several harvest cycles to fully characterize the success of those adjustments.

In the more general case, the Beverton-Holt model provides a rational starting point for regulating fisheries for taxa like *P. elisabethae*. In new fisheries where long-term characterizations of population dynamics are seldom available the Beverton-Holt model can be developed from data that can be collected at a single time (i.e., this study and Goffredo and Lasker 2006). The Beverton-Holt model provides a useful estimator of the age/size at which colonies should be harvested, and in fisheries in which individuals are cropped the model provides a conservative estimate of harvest yields. However, as the model assumes a continuous supply of recruits regardless of harvesting, data on the reproductive biology of the species must be evaluated to either verify that assumption or modify the harvest frequency and intensity. As those data become available the harvest regime can be modified. In similar fashion, the model assumes age/size independent mortality, and future assessments should test that somewhat unlikely assumption. More detailed survivorship data can be explicitly included in a refined Beverton-Holt model. The

more detailed data on size specific growth and survival also can be used to parameterize stage structured (c.f., Hughes and Jackson 1985; Lasker 1990) or individual based models (c.f., Butler 2003). These alternative approaches may provide the most accurate models of the species' population dynamics.

The decision to harvest any organism, especially long lived taxa, from coral reefs must always weigh the potential societal benefits and potential ecological costs of the fishery. In those cases in which harvesting is deemed appropriate, it is important to have approaches to the harvest that maximize the likelihood of developing a sustainable fishery. The Beverton-Holt model can be developed from data that can be collected in a single field season and thus can provide a starting point for an adaptive management approach for a new fishery.

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