Recruitment limitation of a deep benthic hard-bottom octocoral population in the Hawaiian Islands

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ABSTRACT: Recruitment appears to be the major determinant of abundance and structure of an isolated, spatially confined deep-water rocky bottom octocoral community in the Hawaiian Islands. As opposed to some rocky intertidal communities, post-settlement factors such as competition for space, predation and physical disturbance are of less importance. Recruitment and mortality of the primary species studied, *Corallium secundum* Dana (pink coral), was found to be low, relatively constant and independent of population density. Constant recruitment in isolated habitats could be a consequence of long-lived larvae with good capability to postpone settlement. Recovery of species from man-induced disturbance in such environments may be a direct function of recruitment and year-class infilling.

INTRODUCTION

Larval recruitment is a subject of renewed interest as a major determinant of community structure in marine benthic ecology (Underwood & Denley 1984, Connell 1985, Gaines & Roughgarden 1985). For the past several decades, much ecological work on benthic community structure has stressed the significance of post-settlement factors such as competition, predation and physical disturbance (Connell 1961a, b, Dayton 1971, Levin & Paine 1974, Paine 1974). The lack of attention in this work to larval recruitment is somewhat surprising in view of earlier studies in benthic ecology (Coe 1956, Wilson 1958), and many years of research in fisheries biology in which recruitment has been viewed as a major controlling factor (Hjort 1914, Thorson 1966, Jones 1982). Indeed, the novelty of 'supply side ecology' (recruitment) has recently been questioned (Young 1987).

Nevertheless, it is important to mention reasons for the past emphasis on post-settlement factors. Partially due to historical accident and logistic access, many sites selected for studies of benthic community structure have been intertidal habitats in which recruitment is a non-limiting factor. Such environments are frequently saturated by recruits such that seasonal variations in the supply of planktonic larvae are damped by limitations in space. Hence ecological models based on the results of these studies did not include a 'supply

side factor' (Connell 1961a, b). In fact the renewed attention to recruitment has come about largely by research conducted in habitats where space is under-utilized, or at least not the major limiting factor (Gaines & Roughgarden 1985, Genin et al. 1986, Lewin 1986).

In this paper, a deep-water rocky-bottom community apparently not controlled by space limitations is described. The study site is located at depths between 375 and 450 m in the Hawaiian Archipelago, in the channel between the islands of Oahu and Molokai. This habitat is characterized by extremely strong bottom currents (0 to 3 knots) and dominated by large octocorals some of which are commercially harvested for the manufacture of coral jewelry. The study site is often referred to as the 'Makapuu coral bed', and comprises an area of about 3.6 km² (Fig. 1). The existence of precious pink (*Corallium*) and gold (*Gerardia*) corals in the bed have stimulated various research activities from 1970 to the present. Also, a commercial fishery for pink and gold coral existed in the Makapuu bed for 6 yr between 1974 and 1979. These circumstances have produced a long-term data base (14 yr) on a significant but poorly understood deep water ecosystem as well as a unique 'experiment' consisting of a 6 yr disturbance (harvesting). Data on recruitment and mortality of a community dominant species (*Corallium secundum*) were collected *before* and several times *after* the harvesting period.

Except for hydrothermal vent communities and sev-

Fig. 1. Location of Makapuu coral bed off Oahu, Hawaii (hatched), and area within the bed where transect data were collected (black). Depth contours in fathoms (1 fathom = 1.83 m)

eral deep seamounts, very little is known about the benthic ecology of deep hard-bottom communities (Genin et al. 1986). The results of this study are therefore important both from the standpoint of better understanding factors which regulate the population dynamics of hard bottom benthos in general as well as developing models or strategies of fisheries management for the rational exploitation of longevous species characterized by low rates of recruitment, mortality and slow growth.

MATERIALS AND METHODS

Corallium secundum (pink coral) was selected for study because it is (1) abundant throughout the bed, (2) commercially important, and (3) because its pattern of life history (*K*-selected) is representative of 38 other octocorals which exist in this habitat (Grigg 1976, Grigg & Bayer 1976). Transect surveys of the population density and size frequency of *C. secundum* were conducted with the use of a manned submersible in 1971, early 1983 and late 1985. Surveys were carried out in the same area, by the same individual (the author), with the same submersible ('Star II', presently renamed 'Makalii'). The 1971 survey was done before any commercial harvesting had taken place. In contrast, the 1983 and 1985 surveys were completed about 3 and 6 yr, respectively, after harvesting had ceased. During the period of harvest about 17 500 kg of *C. secundum* were selectively collected from the Makapuu coral bed with the use of a manned submersible (Maui Divers of Hawaii, Ltd, pers. comm.). This represents about 40 % (by weight) of the estimated standing crop of this species in the entire bed (Grigg 1976).

The 3 transects were located in approximately the

same area of the bed at depths between 365 and 400 m (Fig. 1). Each transect consisted of a line of observation approximately 1000 m in length. All colonies observed along the transect were counted and measured (height only). A calibrated rod (Fig. 2) was used to measure the height of all colonies. Size frequency data were converted to age frequency with the use of a linear growth measure (0.9 cm yr^{-1}) relating size to age (Grigg 1976). Size is a good measure of age in *Corallium secundum* because the fan-shaped growth form is regular and even; colonies which have undergone partial mortality are irregular in growth form and were considered only in calculations of density, not age frequency. Density was approximated by counting all colonies within 3.0 m either side of the observation port. Each transect thus covered approximately 6000 m^2 of bottom area. The first 2 transects were continuous while the third was broken into 3 replicates. For this reason, estimates of variance were calculated only for the third transect (Fig. 3). The densities of other large and abundant octocorals were recorded but no attempt was made to measure their size frequency. All counts and measurements were recorded on audiotape. The 1985 transects were also recorded on color videotape and are permanently archived at the Hawaii Undersea Research Laboratory at the University of Hawaii. Numerous still photographs were taken with both internal and externally mounted cameras on all 3 transects. Samples of the substrata and various other species were collected with the use of a hydraulic cutter, robotic arm and basket assembly (Grigg et al. 1973).

Estimates of instantaneous natural mortality of *Corallium secundum* were obtained by the regression of the natural logarithm of age frequency versus time (age) (Deevey 1964, Grigg 1976). This method relies on assumptions of steady state recruitment and samples being representative of the age composition of the whole population. While recruitment is not absolutely constant, the relatively stable age structure of the population suggests this assumption is not badly violated. The first 5 yr of age classes were not included in the calculation because they appear to be significantly under-represented. This is probably an artifact due to the difficulty in seeing small colonies from a submersible and their tendency to settle in cracks and declivities on the bottom. Year-classes beyond Age 5 were lumped into 5-yr groups because estimates of height converted to age were not considered more accurate than at least 2 year-classes in either direction. This procedure helps to reduce variability due to measurement error because (assuming no systematic bias) errors within groups should be off-setting. In the case of year-classes divisible by 5, equal numbers were assigned to younger and older groups (Fig. 3). Fishing mortality was calculated as the difference in slope of

Fig. 2. Within transects in the Makapuu bed, a 1 m long rod, calibrated in intervals of 10 cm, was used to measure the height of all undamaged colonies of the pink coral *Corallium secundum*

the equation $\ln N_t = a - mt$ between virgin and fished populations (the difference in mortality between the 1971 and 1983 transects) (Beverton & Holt 1957) (N_t = age frequency percent at time t ; a = the y intercept; m = the coefficient of mortality; t = time).

RESULTS

The combined mean density of all megafaunal species present in the Makapuu bed did not change greatly between 1971 and 1985 and is approximately 0.1 colonies per m^2 (Table 1). Increases in *Lepidisis olapa*, *Narella* sp. and *Pseudotothesea* sp. in 1985 over 1971 appear to be caused by patchiness rather than real differences in view of their standard deviations of abundance. Since the largest holdfasts for any species occupy only about 0.1 m^2 or less in bottom area, the mean area occupied by megafauna in the Makapuu bed is less than 1 % of the available space. Careful examination of the substrata on numerous dives failed to indicate the presence of a significant microfauna. The substrata in the Makapuu bed consists primarily of indurated limestone although, in some areas, shallow

lenses of sand and coarse calcareous rubble consisting of broken fragments of calcitic gorgonian skeletons cover the bottom (Fig. 2). In general, sediments are concentrated in pits, holes and low-lying areas.

Samples of limestone substrata collected from the bottom in the Makapuu bed were examined in the laboratory. The upper surfaces of all of the samples were heavily pitted and supported few micro-organisms. The undersurfaces were covered by some serpulid polychaetes and other encrusting species but in low abundance. The low density of all species suggests that space is not a limiting factor for these populations in the Makapuu bed.

Examination of the age frequency distribution of *Corallium secundum* both before and after the harvesting period reveals a pattern of life history characterized by low recruitment, low mortality and slow growth (Fig. 3). As mentioned above, recruitment of Year-Classes 1 to 5 is probably significantly underestimated, and therefore was excluded from the calculation of the coefficient of mortality. Recruitment was calculated as the intercept of the y -axis of the regression of the natural logarithm of age frequency against time for the virgin population. This turned out to be 8 ($39 \div 5$) age-

Fig. 3. *Corallium secundum*. Age frequency distribution for colonies in the Makapuu bed in (A) 1971, (B) 1983 and (C) 1985. Natural mortality (before harvest) is depicted in (A) by the curve $\ln Y = 3.65 - 0.06X$. The line is dashed for the first 5 yr because data for this year-class group was excluded from the calculation. The coefficient of natural mortality is -0.06 . In (B), downward pointing arrows depict decreases in relative age frequency within year groups between 1971 and 1983. In (C), upward pointing arrows depict increases in relative age frequency within year groups between early 1983 and late 1985; error bars represent 1 standard deviation. Short horizontal bars in (B) and (C) serve as reference marks for the population structure in 1971 and 1983

frequency % (Fig. 3). By comparison, recruitment (the first year class) in many intertidal invertebrates often makes up 90 % or more of populations numerically (Coe 1956).

Turning to natural mortality, this rate for *Corallium secundum* in the virgin population was 0.06 (or about 6 % yr^{-1}) which is also low. Given this mortality rate, the oldest colonies should be about 60 yr in age, which is in fair agreement with observation. The largest and oldest colonies observed in the bed are about 0.7 m in height and approximately 80 yr old. Causes of natural mortality for *C. secundum* include, in order of observed frequency, (1) toppling caused by organisms which bore into basal holdfasts (primarily sponges and polychaetes; toppled colonies do not fragment and very rarely reattach to the substratum), (2) smothering by shifting deposits of sand and other coarse-grained sediment, and (3) encrustation by hexactenellid sponges. The rate of natural mortality appears to be relatively constant and there is no indication of age-specific

differences. There is no evidence of even partial predation and all observations of epi-bionts suggest they are symbiotic (mutualistic, commensalistic or parasitic). Inter- and intraspecific competition for space is rarely observed.

Changes in the age-frequency distribution brought about by 6 yr of coral harvesting provide additional information about the population dynamics of *Corallium secundum* (Fig. 3). Cumulative fishing mortality (altered by 3 yr of recovery), integrated over the period of harvest, was 0.07 %. Even so, there was no significant change in recruitment between 1971, 1983 and 1985. This suggests that mortality caused by harvesting did not affect the rate of recruitment, i.e. recruitment is density independent (at least for this level of fishing mortality recognizing there might be an effect at some threshold level).

The age frequency distributions in 1983 and 1985, relative to the virgin population, provide a measure of impact caused by harvesting as well as a measure of

Table 1 Mean density of dominant benthic macrofauna in Makapuu bed, Hawaii Islands (colonies $\text{m}^{-2} \pm \text{SD}$)

Species	Year	
	1971	1985
<i>Corallium secundum</i> (pink coral)	0.020	0.022 $\pm$ 0.01
<i>Lepidolapa</i> (bamboo coral, unbranched)	0.025	0.041 $\pm$ 0.02
<i>Gerardia</i> sp. (gold coral)	0.001	0.0005 $\pm$ 0.001
<i>Narella</i> sp. (gorgonian)	0.010	0.030 $\pm$ 0.06
<i>Pseudothesea</i> sp. (gorgonian)	0.005	0.020 $\pm$ 0.05
<i>Stylatula</i> sp. (sea pen)	0.010	0.010 $\pm$ 0.01
<i>Callorgorgia gilberti</i> (gorgonian)	0.002	0.001 $\pm$ 0.002
<i>Acanella</i> sp. (bamboo coral, branched)	0.002	0.001 $\pm$ 0.002
<i>Leiopathes glaberrima</i> (black coral)	0.003	0.002 $\pm$ 0.002
Total colonies m^{-2}	0.077	0.127

the potential of the species to recover (Fig. 3). In 1983, all age groups between 15 and 55 had declined in relative abundance by 2 to 9 %, shifting the age frequency distribution to the left. In 1983 all age groups older than 35 yr were absent, suggesting complete removal of this segment of the population. The largest relative decrease in abundance was for 20 to 25-yr-old colonies. The declines in year-classes between 1971 and 1983 for Classes 15 to 55 are slightly conservative because they 'contain' 3 yr of recovery.

The changes in age frequency between 1983 and 1985 can be viewed as measures of recovery (assuming no differences in natural mortality between the 2 periods). During this time (1983 to 1985) all age class groups between 15 and 40 yr showed increases in relative abundance ranging from 12 % for the 20 to 25 yr group to 1 % for the 30 to 35 and 35 to 40 yr groups. In 1985, at least 15 more yr would be required to *partially* infill the older age classes. However, if the age frequency distribution in 1985 is compared to 1971, it can be seen that in 1985, *full* recovery has occurred only up to age 30, suggesting that full recovery will require at least 25 yr.

These results are in close agreement with a model developed by the Western Pacific Fisheries Management Council in 1977, which predicted nearly full recovery in 23 yr (Anonymous 1979). The good agreement may be in part due to 2 factors; first, in the model, recruitment was assumed to be unaffected by harvesting and this turned out to be true, and second, both model and field age data (size frequency conversions) were based on the same estimate of growth (0.9 cm yr^{-1}). It is reassuring that field results provide verification of these assumptions. With respect to resource management, the results demonstrate the utility of using a yield-production population model for the management of a slow-growing longevous benthic invertebrate such as precious coral. Recovery appears to be a simple function of *growth infilling* of year classes that have been removed by harvesting.

DISCUSSION

Larval recruitment appears to be the most important factor determining the abundance of megafauna in the Makapuu coral bed. Post-settlement effects are of lesser importance. Competition for space rarely occurs and predation does not appear to contribute to the mortality of octocorals. Physical disturbance from sediment build-up is limited to pits, holes and other low-lying areas of the bottom. The age frequency distribution of *Corallium secundum* suggests that the rate of mortality is low and relatively constant. These observations indicate that larval recruitment is the major determinant of abundance of many species which occupy

the Makapuu coral bed. This conclusion is supported by the harvesting 'experiment' with *C. secundum* which verified that a change in population abundance did not affect the recruitment process for this species. If recruitment is density independent, larval settlement must depend on population sources outside the Makapuu Bed. Because the Makapuu coral bed is spatially confined and a geographically isolated habitat, low rates of recruitment would be expected. If so, this would explain the low population abundance of many species.

The Makapuu bed is an unusual environment because of (1) the presence of a channel, (2) strong bottom currents, and (3) the presence of a hard limestone substratum. The coral bed is geographically isolated because these oceanographic features of the habitat do not often combine in the main Hawaiian Islands. Of 31 other locales at 400 m depth in the major Hawaiian Islands surveyed by the investigator in a submersible between 1971 and 1975, only one other site (off Kauai) was characterized by comparable bottom currents and a sediment-free substratum (Grigg 1974). Bottom currents in the Makapuu coral bed commonly range between 0 and 3 knots, compared to 0 to 0.50 knots for the 29 other sites.

If isolation is the primary reason for low recruitment, it is surprising that recruitment is so constant (as indicated by the relative stable age distribution of *Corallium secundum*). Perhaps the larvae of *C. secundum* and other species with a similar life history have extremely long-lived larvae with good capability of postponing settlement until suitable environmental conditions are encountered (Wilson 1958, Thorson 1966, Sheltema & Williams 1983, Grigg et al. 1985). This behavior should increase the probability of some larvae always 'locating' and settling within isolated environments and could explain the pattern of low but relatively constant recruitment.

Research on other spatially confined and isolated ecosystems in the world such as high peaks in mountain ranges or on isolated tropical islands (MacArthur 1972), discontinuous hydrothermal vent systems (Lutz et al. 1984, Hessler et al. 1985), communities dependent on oil and gas seeps (Brooks et al. 1987), shelf base escarpment communities (Paull et al. 1984), and isolated seamounts (Grigg et al. 1985) indicates that many species which occupy isolated habitats may have longevous (teleplanic) larvae. On the other hand, some species which are highly patchy and locally abundant in isolated ecosystems may reproduce vegetatively or have adapted to producing extremely short-lived larvae (Lutz et al. 1984). In isolated environments natural selection may operate on life history characteristics in a bimodal fashion, favoring species at both ends of the spectrum with regard to larval longevity.

In summary, the Makapuu coral bed would appear to represent another benthic marine habitat in which recruitment may be more important in determining abundance and community structure than post-settlement factors such as predation, competition and physical disturbance. Forces of natural mortality appear to be low, relatively constant and independent of age. As further varied and exotic benthic communities are studied, many more seem to be characterized by *recruitment limitation*.

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