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Are large colonies a "key factor" in the dynamics of gorgonian populations?

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Abstract: Life cycle stages responsible for fluctuations in population sizes have often been described as "key factors". In this study, a key factor approach was used to examine the dynamics of a shallow-water gorgonian population from 1983-1996 near La Parguera on the southwest coast of Puerto Rico. Gorgonian abundances increased from 8.1 to 99.6 colonies/m^2 between 1983 to 1985 and gradually declined to 57.3 colonies/ m^2 in 1996. These variations in population size are largely attributable to recruitment, which increased from 2.1 to 44.9 colonies/ m^2 between 1983 to 1985, and declined thereafter. Survival of recruit colonies which was generally higher after periods of high recruitment also played a contributing role in these population fluctuations. In contrast, survival of large colonies ($\geq$10 cm in height) was essentially constant (about 94.1%/yr), and consequently had negligible effects on variations in abundances. These results demonstrate that large colonies are not a key factor underlying fluctuations in gorgonian populations. However, this assessment of large colonies differs if the results are examined in a different conceptual context. The combination of high and constant large colony survival, and variable "reproductive success" (recruitment and recruit survival) conforms to the "bet-hedging" interpretation of life history pattern. According to bet-hedging theory, large colonies are essential to the persistence of populations.

Key words: Key factor analysis, gorgonian, recruitment, bet-hedging, population fluctuations, population persistence, coral reef.

"Seek simplicity, but distrust it"

Natural populations are almost never constant in size (Williamson 1972). Instead, populations fluctuate in size, with the degree of fluctuation highly dependent upon the species involved. For example, marine ecologists have long recognized that some species as the beach clam *Donax gouldi* Dall exhibits largescale (20 000fold) fluctuations in abundance (Coe 1953). Alternatively, abundances of another mollusc species *Macoma calcarea* (Gmelin, 1791) varies only about 2fold (Thorson 1950).

The examination of population fluctuations can be important in several respects. Fluctuations in abundances are obviously relevant to ecological studies on the control and regulation of natural populations. Economic considerations can also be involved because largescale population fluctuations may affect commercially important marine species (Burkenroad 1946). Environmental issues may also be concerned because the effects of pollution and other human-related activities must be separated from the "noise" of natural fluctuations in population size for the development of effective policies.

Quantitative analyses of population fluctuations have traditionally employed "key factor" approachs, and have been largely limited to terrestial organisms with complex life cycles. In fact, the term "key factor analysis" originated with Morris (1963) from his study of the outbreaks of an insect pest, the spruce budworm, in Canada. Mathematical procedures used in key factor analyses are described by Varley et al. (1973) among others. In brief, a central goal of key factor analysis is the identification of life history stages responsible for fluctuations in population size.

To my knowledge key factor analyses have not been applied to marine populations. This is somewhat surprising because fluctuations of marine populations have been recognized for several decades (note above references), and the complex life cycles of many marine organisms make key factor analysis directly applicable. However, the lack of quantitative life cycle data (especially for the planktonic larval stage) is often a major obstacle for such analyses (but see Yoshioka, in press). Nevertheless, as with key factor analysis, studies of marine populations often attempt to identify critical life history stages. Suggestions that recruitment (e.g., "supply-side" ecology; see Young 1987) and fertilization rates (e.g., Petersen et al. 1992) are important factors in the dynamics of marine populations are recent examples in this regard.

In this report I employ an approach analogous to key factor analysis to examine fluctuations in colony abundances in a shallow-water gorgonian community on the southwest coast of Puerto Rico. In this preliminary and largely descriptive examination I pool gorgonians of all taxa into a single "population", and only examine colony recruitment and the survival of newly-recruited and large (adult) colonies as possible key factors. Throughout this examination I restrict the term "key factor" to its original context, namely fluctuations in population size. In the discussion I examine more general issues by evaluating key factor approaches relative to the broader perspectives of population dynamics. In this evaluation, I pay special attention to the role of large (adult) colonies in gorgonian populations and other coral reef assemblages.

In brief, the species composition at the study site is highly typical of gorgonian communities in Puerto Rico (Yoshioka & Yoshioka 1989a; Yoshioka 1991) with *Pseudopterogorgia americana* (Gmelin), 1791; *Pseudopterogorgia acerosa* (Pallas), 1766; *Pseudoplexaura wagenaari* (Stiasny), 1941; *Pseudoplexaura porosa* (Houttuyn), 1772; *Gorgonia ventalina* Linnaeus, 1758; and *Plexaura flexuosa* Lamouroux, 1821. being some of the more common species. Other aspects of the gorgonian community examined in this study (recruitment, growth, survival, spatial dispersion, life history pattern) are described elsewhere (Yoshioka & Yoshioka 1989b; Yoshioka 1994, 1996).

MATERIALS AND METHODS

The study site (17°56.2'N, 67°3.2'W) occurs at a depth of 6.7 m and is located near La Parguera, on the southwest coast of Puerto Rico about 0.5 km south of a reef locally known as Media Luna reef. The study site is unprotected by emergent reefs, and is fully exposed to wave action generated by the easterly tradewinds. Topographic relief is relatively low, and only about 8% of the substrate is covered by sponges, corals and other macrobiota (V. Vicente, pers. comm.). These habitat characteristics are fairly typical of shallow-water gorgonian communities of Puerto Rico (Yoshioka & Yoshioka 1989b).

Colony recruitment, survival and growth have been monitored in a 1 X 32 m belt transect at Media Luna from 1983 to the present. Gorgonians were monitored semi-annually from 1983 to 1991 and annually thereafter. Individual colonies were located by placing a 0.5 m^2 (0.5 X 1.0 m) quadrat subdivided into 1/16 m^2 (25 X 25 cm) subsections along the transect. A chain laid in the center of the transect and nails placed at 0.5 m intervals in the center and along the edges of the transect were used to reposition quadrats between surveys.

A gorgonian recruit was defined as a colony which was observed for the first time on a given survey (excluding the initial survey). Recruit colonies generally resulted from sexual reproduction (planulation); recruitment by asexual fragmentation was relatively uncom-

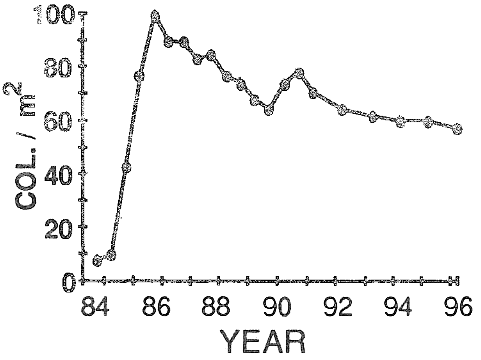

Fig. 1. Gorgonian colony abundances in the 32 m^2 transect during the study period.

mon (<5%) and limited to a few species [e.g., *Briareum asbestinum* (Pallas), 1766]. The majority (90%) of recruit colonies were only a few (<5) cm tall when first observed.

RESULTS

Colony Densities: Colony densities varied over 12fold during the study period (Fig. 1). The most prominent fluctuation in abundances was a dramatic variation in colony density from autumn 1983 and autumn 1985 when densities increased from 8.1 to 99.6 colonies/ m^2. A less dramatic increase in densities also occurred in 1989-90. In general densities declined after 1986 to about 57.3 colonies/ m^2 in 1996. The fluctuations in abundances at the study site are very large for gorgonians and essentially span the entire range of colony densities observed in 26 gorgonian communities in various areas around Puerto Rico (Yoshioka & Yoshioka 1989b).

Because variations in abundances represent the net effect of increases and decreases in colony densities, an examination of colony recruitment and survival rates should provide insights into key factors underlying changes in population size.

Recruitment: Recruitment was highly variable at the study site, ranging 22fold from 2.1 to 44.9 colonies/ m^2 (Fig. 2). Not suprisingly, temporal variation in colony recruitment was a major factor underlying fluctuations in colony densities. For example, the large increase in colony densities in 1985 is closely paralleled by an increase in recruitment during this period. Decreased grazing pressure due to the mass mortality of the urchin *Diadema antillarum* Philippi, 1845 in January, 1984 was evidently responsible for high recruitment during this period (Yoshioka 1996). A moderate increase in recruitment in 1989-90 was evidently also responsible for the less dramatic increase in colony abundances during this period. Finally, the gradual decline in colony densities after 1986 is at least partially attributable to decreased recruitment during the latter part of this study. These results clearly indicate that recruitment is an important key factor underlying fluctuations in this gorgonian population.

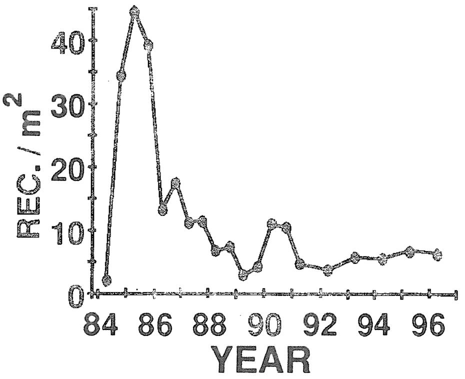

Fig.2. Recruitment of gorgonian colonies at the study site. Note that recruitment was measured on an semi-annual and annual basis before and after 1991 respectively.

Because the monitoring interval was changed from a semi-annual to annual basis in 1991, estimates of recruitment are not strictly comparable over the entire study period. However, this change in methodology does not alter the conclusions reached above.

Recruit Colony Survivorships: Annual survivorships of recruit colonies varied about 1.6fold, or from 44-72% (Fig. 3). Some similarities between the temporal patterns of recruit survival and recruitment are evident. For

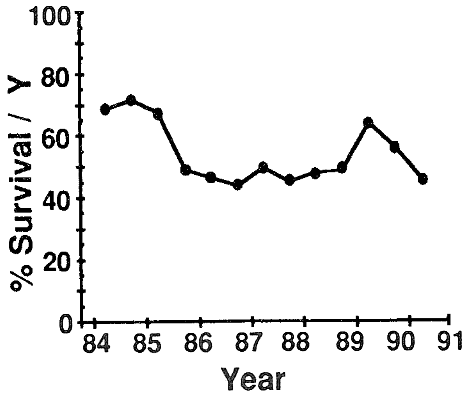

Fig. 3. Annual survivorships of recruit colonies.

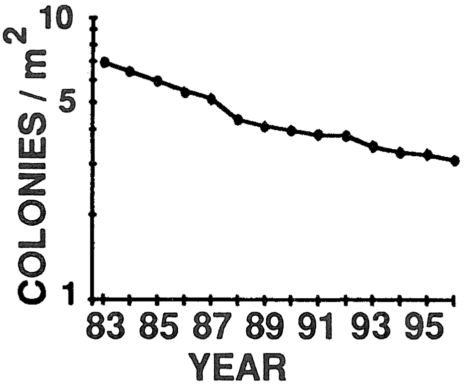

Fig. 4. Decreases in abundances of colonies that were >10 cm tall (i.e., "large colonies") at the beginning of the study Note that abundances are plotted on a logarithmic scale.

instance, the high recruitment of 1984-85 coincided with relatively high recruit survivals. As an example, the high recruitment of autumn 1984 (34.7 recruit colonies/ m^2) was followed by relatively high survival (72%) of that recruit cohort. Relatively high recruitment and recruit survival was also evident in 1989-90. Alternatively, relatively low survivorship coincided with low recruitment. As an example, the few recruits of spring 1988 (6.8 recruits/ m^2) experienced relatively low (48%) survivorships. The positive correlation bewteen recruitment and recruit survivorship would accentuate the effects of recruitment on population fluctuations (i.e., 0.72 X 34.7, compared to 0.48 X 6.8). Thus, colony abundances increased in 1984 and remained high thereafter because of high recruitment combined with high recruit colony survival during this period. In this respect recruit survival plays a contributing role as a key factor underlying variations in gorgonian abundances. Yoshioka (in press) presents a more detailed examination of the relationship between recruitment and recruit survival for some gorgonian taxa.

Large Colony Survivorships: To exemplify survivorship patterns of large gorgonians, I examined colonies $\geq$10cm tall that were present at the beginning of this study. In contrast to the variable survivorships of recruit colonies, survivorships of these colonies were high and relatively constant. Annual survivorships of over the study period varied only 1.17fold, from a maximum of 99.2% in 1991-92 to a minimum of 85% in 1987-88. In addition, the comparatively low survival of large colonies in 1987-88 may be somewhat atypical because of most of the mortality during this interval can be attributed to the passage of Tropical Storm Gilbert in September 1988 (pers. obs.)

The effect of high and constant survivorships on fluctuations in colony densities can be inferred from Fig. 4 which shows the decline in abundances of these colonies over the study period. As can be seen, the decrease in colony densities is approximately linear (even with the inclusion of 1987-88 value). Because abundances are plotted logarithmically, a linear decrease indicates that survivorships are nearly constant. This survivorship pattern is consistent with the contention that the major causes of large colony mortalities, detachment and basal fracture, are essentially random in nature (Yoshioka & Yoshioka 1991). In terms of a key factor assessment, high and constant survivorships indicate that large colonies have negligible effects on variations in abundances.

DISCUSSION

This descriptive study clearly indicates that recruitment is a key factor underlying popula-

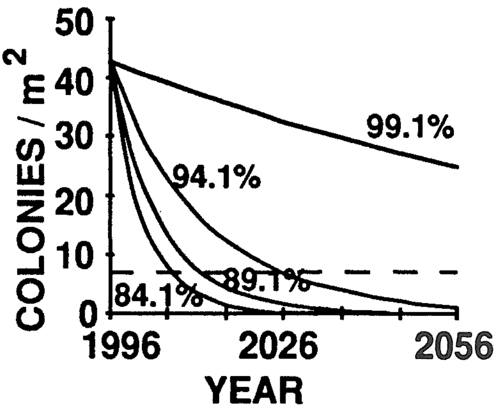

Fig. 5. Projections of large colony abundances with no recruitment and with various levels of annual survivorships (84.1%, 89.1%, 94.1%, 99.1%). The abundance of large colonies in 1996 was used as the initial point in all projections. The dotted line represents the abundance of large colonies originally observed in1983.

tion fluctuations of gorgonians. The 12fold (8.1 to 99.6 colonies/ m^2) variation in gorgonian abundances observed during the study period are largely attributable to the 22 fold (2.1 to 44.9 colonies/ m^2) fluctuation in recruitment. The 1.6 fold (44-72%) variation in recruit colony survival, as well as the coupling between recruitment and recruit colony survivorships also play contributing roles as key factors. In contrast, nearly constant survivorships (from 85-99%, or a 1.17fold variation) indicate that large gorgonian colonies have a negligible effect on variations in colony abundances.

However, this evaluation does not mean that large colonies are unimportant in the population dynamics of gorgonians. A drastically different conclusion is reached if the same results reviewed above are examined from another perspective. Stearns (1976) describes the relatively high and constant survival of large colonies and variable recruitment and recruit survivorship (i.e., variable "reproductive success") as a "bet-hedging" life history strategy. Some population consequences of bet-hedging are easily illustrated by a simple model. Using the density of large colonies in 1996 (43 colonies/ m^2) as the starting point for all calculations, Fig. 5 shows projections of colony densities with no recruitment (i.e., the extreme case of low reproductive success) and various levels of large colony survivorships. For example, given the average annual survivorships observed in this study (94.1%), colony densities will not decline to levels observed in 1983 (7 large colonies/ m^2) until the year 2026. Alternatively however, this colony density will be reached in only 10 years (2006) if survivorships are decreased by 10% (to 84.1%). At the other extreme, it will take about 200 years for colony densities to decline to this level if survival is increased by 5% (to 99.1%). This model (which is only a simple exercise in exponential decrease) clearly illustrates that large colonies probably play a critical role in the persistence of gorgonian populations. Longterm survival allows large (adult) colonies to compensate for years of poor reproductive success by taking advantage of infrequent periods of successful reproduction. Gorgonian populations could probably persist if successful reproduction occurs only a few times per century with the observed survivorship rates. Murphy (1968) provides a more detailed examination of the population consequences of bet-hedging. Because the bet-hedging life history pattern is evidently also shared by many sponges and scleractinian corals (Hughes & Jackson 1985), this conclusion is probably also applicable to many of the major components of Caribbean reefs.

In terms of practical environmental concerns, the results of the population model indicate that transient episodes of pollution (or other human-related effects) that negatively affect reproductive success (gamete production, fertilization, larval survival and dispersal, recruitment, and recruit survival) may have relatively little impact on bet-hedging populations because life history patterns are, in a sense, "pre-adapted" for reproductive failures. Alternatively however, if such effects increase adult colony mortalities only slightly (i.e., 5-10%), the longterm well-being of coral reef populations could be seriously jeoparidized. Management policies should therefore pay special attention to survivorship patterns of large colonies.

In terms of basic scientific issues, the preceding discussions indicate that the dynamics of natural populations encompass a variety of different features (i.e., the fluctuations and persistence of populations). In turn, each feature may present complexities. Royama (1996) contends that key factor analysis is too simplistic for analyses of population fluctuations. Similarly, mechanisms for population persistence extend well beyond the bet-hedging stratègy examined in this study. Population persistence resulting from long lifespans could be described as population "inertia" (Murdoch 1970), and differs from persistence resulting from the negative feedback properties of density dependence.

The multi-faceted and complex nature of population dynamics means that "key factor" questions must be formulated with extreme caution. The search for critical (key) factors is appropriate only for highly specific topics within the broader scope of population dynamics. In other words, the fault is not with key factor analysis *per se* or its goal of determining life cycle stages underlying fluctuations in population size, but the tendency to extrapolate the results to all aspects of population dynamics. To underscore this point, it should be noted that the title of this study, "Are large colonies a 'key factor' in the dynamics of gorgonian populations?" is unanswerable and therefore invalid. Thus, despite the large research effort currently being expended on recruitment ("supply-side ecology") and fertilization rates, and despite their obvious ecological relevance, it is important to resist the bandwagon tendency to regard such research as the "key answer" to the dynamics of marine populations.

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RESUMEN

Fluctuationes en abundancia de gorgonios se relacionan a etapas específicas del ciclo de vida, consideradas como "key factors" de su dinámica poblacional. En este estudio se examinan aspectos de la dinámica poblacional de los gorgonios de aguas someras en La Parguera, al suroeste de Puerto Rico durante el período de 1983 al 1996 utilizando procedimientos de "key factor". La abndancia de gorgonios aumentó de 8.1 a 99.6 colonias/m^2 desde 1983 a 1985 y luego se redujo gradualmente hasta 57.3 colonias/m^2 en 1996. Las variaciones en abundancia estuvieron mayormente asociadas a reclutamiento, el cual aumentó de 2.1 a 44.9 colonias/ m^2 entre 1983 y 1985. Variaciones en las tasas de sobrevivencia de reclutas, que fueron mas altas durante eventos de mayor reclutamiento, juegaron un rol importante en los tamaños de las poblaciones. Por otro lado, la sobrevivencia de colonias grandes (>10 cm de alto) fue basicamente constante (aprox. 94.1%/año) y por consiguiente tuvo un efecto mínimo en las fluctuaciones de abundancia en la población. Estos resultados parecen demostrar que las colonias grandes no representan un "key factor" en la dinámica poblacional de gorgonios de aguas someras. Sin embargo, este análisis de las colonias grandes sería distinto si se examinan los resultados desde otro punto de vista conceptual. Las tasas de sorbrevivencia alta y constante de las colonias grandes, combinadas al variable éxito reproductivo (reclutamiento y sobrevivenica de reclutas) son consistentes con las estrategias de vida del tipo "bet-hedging". De acuerdo a la teoría de "bet-hedging", la persistencia de las poblaciones de gorgonios, en este caso, dependen escencialmente de las colonias de gran tamaño.

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