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Comparative demography of mushroom corals (Scleractinia: Fungiidae) at Eilat, northern Red Sea

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Abstract The population structure and growth rates of stony corals may provide important information concerning their processes of turnover and recovery on coral reefs, yet for most corals such information is lacking. We quantify here the population dynamics of solitary free-living mushroom corals on a fringing reef at Eilat, northern Red Sea. Population models were applied to estimate growth, mortality, and lifespan in members of four common taxa: *Ctenactis echinata*, *Fungia scutaria*, *F. fungites*, and the subgenus *F.* (*Danafungia*) spp. Individuals of *C. echinata* and *F. scutaria* grew allometrically: their oral disc length increased more rapidly than width, leading to an oval body shape. Individuals of *F. fungites* and *F. (Danafungia)* spp. grew isometrically, retaining a circular body shape. A population of *F. scutaria* on the intertidal reef flat was characterized by young individuals (mean age = 2 years), with high mortality and short lifespan (13 years). In contrast, populations of the other three mushroom coral taxa on the reef slope consisted of older individuals (mean age = 4–9 years), with lower mortality and longer lifespans (24–46 years). Demographic patterns appeared to vary with species characteristics, and possibly with the level of disturbance in each reef habitat. Minimum sizes at which these mushroom corals may be removed sustainably from the populations range from 7 to 22 cm polyp diameter (5–14 years of age). We conclude that

the Beverton and Holt population dynamic model is applicable to the management of stony corals with solitary or compact, upright growth forms that rarely fragment.

Introduction

Understanding the population dynamics of reef-building corals is important for the management of coral reef resources, and for assessment of reef recovery rates following disturbances (Grigg 1984; Ross 1984; Wilkinson 1993; Meesters et al. 2001). Demographic parameters also reveal relationships between organisms and their environment, and contribute to assessment of habitat stability (Grigg 1975; Bak and Meesters 1998; Meesters et al. 2001). In addition, information on population turnover in reef-building corals may contribute to techniques for the restoration of damaged or degraded coral reefs (Connell 1973; Rinkevich 1995; Chadwick-Furman et al. 2000).

Scattered information is available on the population dynamics of scleractinian corals. Connell (1973) reviewed the modest amount of data that had been collected as of 30 years ago, and described parameters such as growth and survivorship. Since then, demographic processes have been described for some coral species in the Red Sea (Loya 1976a,b; Goffredo 1995; Chadwick-Furman et al. 2000), northeastern Pacific (Gerrodette 1979; Fadlallah 1983), Caribbean Sea (Hughes and Jackson 1985; Johnson 1992; Meesters et al. 2001), Great Barrier Reef of Australia (Babcock 1988, 1991), and Mediterranean Sea (Goffredo 1999). The paucity of information on population dynamics in most species of scleractinian corals may in part be attributed to a distortion of age–size relationships in this group, resulting from processes of fragmentation, fusion, and partial colony mortality (Hughes and Jackson 1985; Hughes and Connell 1987; Babcock 1991; Hughes et al. 1992). These phenomena, characteristic of clonal modular organisms (Hughes 1989), prevent the application of traditional growth and population dynamic

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models based on organism age, and reveal highly complex demographic patterns (Hughes and Jackson 1985). A recent analysis of 13 Caribbean coral species used a size-based rather than age-based assessment of population structure, due to the above complexities of colony growth patterns (Meesters et al. 2001). In some cases, it is possible to overcome this barrier to coral age determination by selecting model species, whose individuals rarely fragment or fuse, and in which partial mortality is discernable by anomalies in the regular growth pattern (Chadwick-Furman et al. 2000). Corals that form discrete, upright branching colonies that rarely fragment in certain environments, such as *Pocillopora* and *Stylophora*, are suitable for this analysis (Grigg 1984). In addition, in some solitary corals, age estimates may be obtained from growth rings that are visible externally (Abe 1940; Chadwick-Furman et al. 2000) or detectable by x-ray analysis (Goffredo et al., unpublished data). Growth-ring analysis has been used more widely to age colonial scleractinian and gorgonian corals (Knuston et al. 1972; Buddemeir and Maragos 1974; Grigg 1974; Logan and Anderson 1991; Mistri and Ceccherelli 1993; Mitchell et al. 1993). As such, growth and population dynamic models based on age may be applied to certain growth forms of scleractinian corals to elucidate demographic characteristics (Nisbet and Gurney 1982; Grigg 1984; Ross 1984; Bak and Meesters 1998; Chadwick-Furman et al. 2000).

Solitary, free-living mushroom corals are conspicuous members of reef coral assemblages in the Indo-Pacific region (Hoeksema 1990; Goffredo and Chadwick-Furman 2000). They contribute to reef building, and in some areas build patch reefs consisting entirely of mushroom corals (Littler et al. 1997). Of particular interest are coral reefs at Eilat in the northern Red Sea, where mushroom corals are abundant on the reef flat and shallow slope (Kramarsky-Winter and Loya 1998; Goffredo and Chadwick-Furman 2000). Populations of mushroom corals at Eilat appear to meet the assumptions of standard population dynamic models, in that they occur in stable environmental conditions at the northern end of an enclosed sea, so their population structure appears to be stable, with no large recent changes in recruitment or mortality rates (Chadwick-Furman et al. 2000).

We describe here the comparative demography of mushroom corals at Eilat, by applying the population dynamic model of Beverton and Holt (1957) to four common taxa: *Ctenactis echinata* (Pallas, 1876), *Fungia scutaria* Lamarck, 1801, *F. fungites* (Linnaeus, 1758), and *F. (Danafungia)* spp. Wells, 1966. In combination with previous work on *F. granulosa* (Chadwick-Furman et al. 2000), we thus define population characteristics of the major mushroom corals in this reef area.

Materials and methods

This study was conducted during January–April 1996 at the Japanese Gardens fringing reef site at Eilat, northern Gulf of Aqaba,

Red Sea. The coral community structure and reef profile at this site have been described in detail by Loya and Slobodkin (1971) and Loya (1990). To assess mushroom coral population structure, we deployed a 1×25 m belt transect parallel to shore at each of 12 depths: 1 m (inner margin of the reef flat), 1 m (outer margin of the reef flat) and at 2, 3, 6, 9, 12, 15, 21, 27, 33, and 40 m, thus encompassing the depth range of most mushroom corals at this site. A total area of 300 m² was surveyed (i.e. 25 m² per depth×12 depths surveyed, after Hoeksema 1990, 1991a; Goffredo and Chadwick-Furman 2000). Within each transect, we identified all mushroom corals to species according to Hoeksema (1989). Individuals of *Fungia (Danafungia) horrida* and *F. (Danafungia) scruposa* were grouped under the subgenus name *F. (Danafungia)* (see Hoeksema 1989), because the only trait distinguishing them was the presence of perforations in the corallum wall, which were not discernable in live polyps in the field (after Chadwick-Furman and Loya 1992; Goffredo and Chadwick-Furman 2000). Data on population dynamics of these two species grouped together were included here, because: (1) both species appear to be abundant at Eilat based on skeletal examination of dead polyps (N.E. Chadwick-Furman, personal observations), (2) both are known to have similar distribution and abundance patterns on reef slopes (Hoeksema 1990), and (3) no discontinuities were detected in their growth patterns, including mass–length relationships (see Fig. 1). The following information was recorded for each live mushroom coral observed: life history phase (attached anthocaulus or free-living anthocyathus), length (along axis of the oral disc parallel to the stomodeum's major diameter), and width (along axis of the oral disc perpendicular to the stomodeum's major diameter, after Abe 1940; Bablet 1985). Here we present data for four of the most common taxa, *Ctenactis echinata*, *F. scutaria*, *F. fungites*, and *F. (Danafungia)* spp., because too few individuals were observed of the other mushroom coral species to assess their population dynamics (Goffredo and Chadwick-Furman 2000).

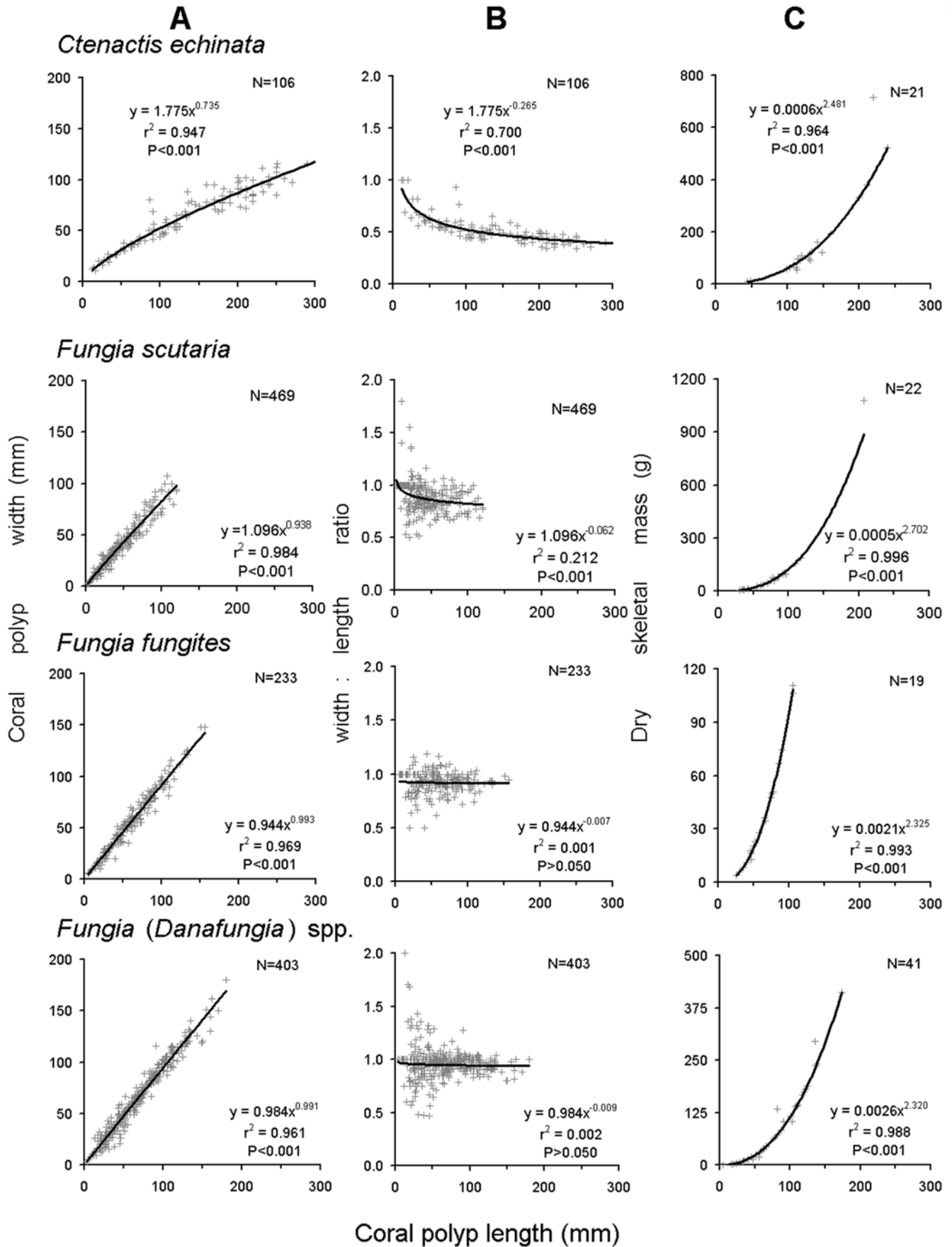
To establish the relationship between polyp length and dry skeletal mass, we used a non-destructive method (after Chadwick-Furman et al. 2000) in compliance with coral conservation regulations of the Nature and Parks Authority of Israel. Skeletons of recently dead polyps found in the field were collected, observed under a dissecting microscope to eliminate any sediments or epifauna, dried at 400°C for 24 h, and weighed. Based on growth rings visible on the external aboral surface of live polyps observed underwater, and of skeletons examined in the laboratory, we established the relationship between age and length for polyps of each taxon (after Abe 1940; Chadwick-Furman et al. 2000). The growth rings visible on each polyp were counted several times to ensure accuracy.

Growth was expressed according to the von Bertalanffy function (von Bertalanffy 1938):

$$L_t = L_m(1 - e^{-Kt})$$

where L_t is individual length at age t , L_m is asymptotic length (maximum expected length), K is a growth constant, and t is individual age. The parameters L_m and K were determined via application of a von Bertalanffy plot to age–length relationships obtained by growth-ring analysis (after Pauly 1984; Sparre et al. 1989). The Fisheries Program “Fishparm” (Prager et al. 1989) was used for parameter estimation. Maximum expected skeletal mass, expressed as asymptotic mass (W_m), or the mass corresponding to asymptotic length L_m , was calculated for each taxon based on the relationship between polyp length and dry skeletal mass.

Fig. 1A–C Patterns of individual growth in four taxa of mushroom corals at Eilat, northern Red Sea. Variation with individual length in: **A** width, **B** width:length ratio, and **C** dry skeletal mass. Relationships between linear parameters (columns A and B) were obtained from live polyps observed in the field; relationships between length and mass (column C) were obtained from recently dead polyps collected from the field. Equations are shown for the regression line in each graph



The age structure of each population was determined from the population size structure, using the above length–age function. The instantaneous rate of mortality (Z) was expressed as a numeric reduction of the corals over time (i.e. survivorship curve):

$$N_t = N_0 e^{-Zt}$$

where N_t is the number of individuals at age t , N_0 is the number of individuals at age 0, Z is the instantaneous rate of mortality, and t is individual age (after Grigg 1984; Pauly 1984; Sparre et al. 1989; Chadwick-Furman et al. 2000). The age classes of 0–2 years were excluded from mortality-rate analysis because they are known to be under-represented in field samples of corals (Grigg 1984; Babcock 1991). According to the Beverton and Holt (1957) model, an age-specific curve expressing the cohort yield in skeletal mass was generated using the growth curve of skeletal mass and the survival curve of the individuals (after Grigg 1984; Ross 1984; Chadwick-Furman et al. 2000). Maximum individual 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).

Results

Individual growth patterns

The mushroom corals grew in two distinct forms, as shown by analysis of their shape parameters (Fig. 1). The first growth form, seen in *Fungia scutaria* and *Ctenactis echinata*, was characterized by an inverse exponential relationship between individual length and width:length ratio, with this ratio changing as the coral grew (Fig. 1A, B). This changing proportion indicated allometric growth, in that oral disc length increased more rapidly than width, resulting in an oval body shape. The second growth form occurred in *F. fungites* and *F. (Danafungia) spp.*, and was characterized by a linear relationship between oral disc width and length, indicating isometric growth and the retention of a circular body shape (Fig. 1A, B). In terms of mass–length relationships, the corals characterized by allometric growth (*F. scutaria* and *C. echinata*) had higher exponent values and lower constant values than those with isometric growth [*F. fungites* and *F. (Danafungia) spp.*, Fig. 1C].

In all taxa, very few individuals (<0.5%) were observed with partial mortality of their tissues, or with distorted body shapes indicating previous skeletal fragmentation, fusion, or restriction of growth by location.

Growth curves

Members of all four mushroom coral taxa grew determinately, as revealed by analysis of their growth rings and maximum individual sizes (L_m) in field populations (Fig. 2A). It was possible to assess age from skeletal growth rings only in young corals, because the rings became too close together to distinguish in older corals, due to the slowing of coral growth rate with age (Fig. 2A). The largest corals that we were able to age using external growth rings were 220 mm polyp length for *C. echinata* (12 years old), 118 mm for *F. scutaria*

(9 years old), 77 mm for *F. fungites* (7 years old), and 66 mm for *F. (Danafungia) spp.* (6 years old) (Fig. 2A). Due to the exponential relationship between polyp length and mass (Fig. 1C), the growth curves for skeletal mass were sigmoidal (Fig. 2A).

Survivorship

Population age structure varied widely between the taxa examined (Fig. 2B). Mean coral age varied from 2 years in the population of *F. scutaria*, to 4 years in *F. fungites*, 5 years in *F. (Danafungia) spp.*, and 9 years in *C. echinata* (arrows in Fig. 2B). During the first and second years of life, most of the individuals in each taxon occurred in the attached phase, but this proportion decreased, until by 3–5 years of age, all individuals became free living (Fig. 2B).

The instantaneous rate of mortality (Z) was two to four times higher for *F. scutaria* than for the other three taxa examined (Fig. 2B). Estimated survival curves indicated individual lifespans of about 13 years for *F. scutaria*, 24 years for *F. fungites*, 30 years for *F. (Danafungia) spp.*, and 46 years for *C. echinata* (Fig. 2C).

Population yield

All taxa exhibited rapid early growth in population mass, followed by a peak as losses due to mortality overcame gains due to individual growth. Subsequently, population mass decreased for older specimens due to their low survival rate (Fig. 2C). Population yield curves for *F. fungites* and *F. (Danafungia) spp.* were similar, with peaks in population skeletal mass at 8 and 10 years, respectively. The population of *F. scutaria* peaked in mass at a much younger individual age of 5 years, and that of *C. echinata* at a much older age of 14 years (Fig. 2C).

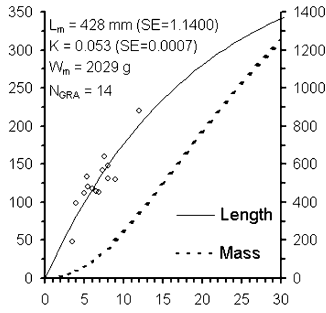
Discussion

General

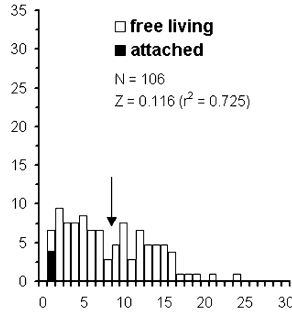
We demonstrate here that populations of mushroom corals on a coral reef at Eilat are highly dynamic: mean

►
Fig. 2A–C Population dynamic parameters of four taxa of mushroom corals at Eilat, northern Red Sea. **A** Growth curves (age–length and age–mass relationships) (*open circles* age–length data from growth rings; L_m asymptotic length; K growth constant; W_m asymptotic mass; N_{GRA} number of corals examined for growth ring analysis; SE standard error). **B** Population age structure [*arrows* indicate mean coral age in each population; N sample size; Z instantaneous rate of mortality; r^2 coefficient of determination of the semi-log regression from which the Z -value has been estimated (after Pauly 1984)]. **C** Survivorship curves and population yield in dry skeletal mass

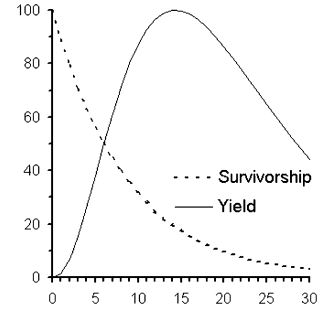
A
Ctenactis echinata



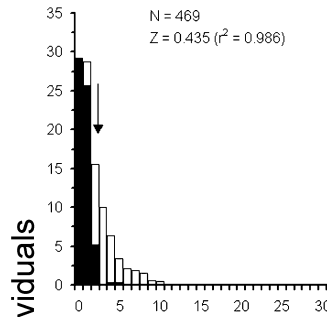
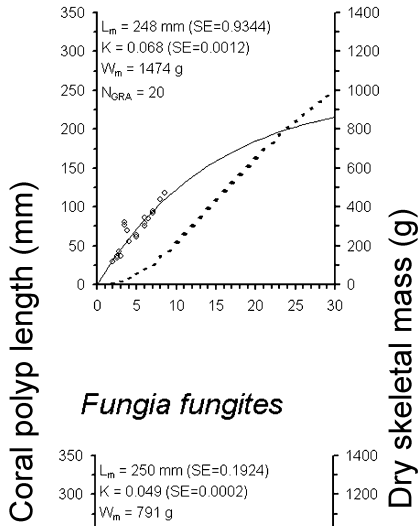
B



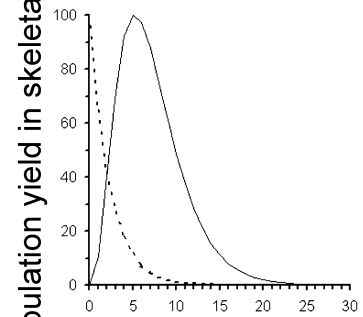
C



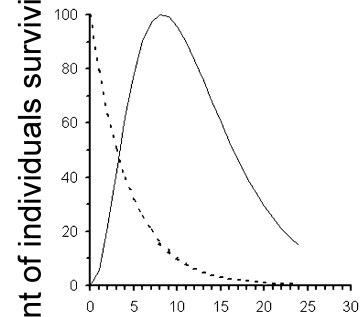
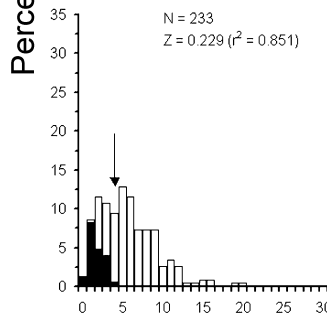
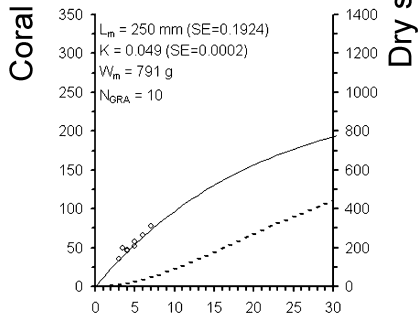
Fungia scutaria



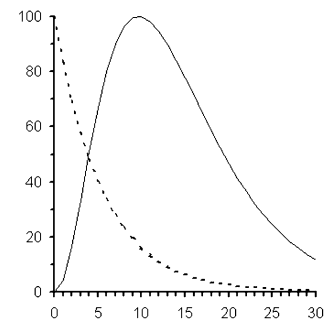
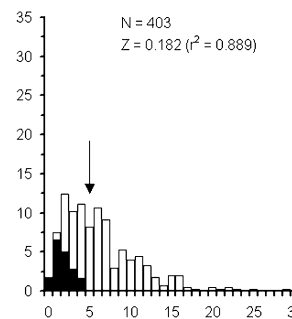
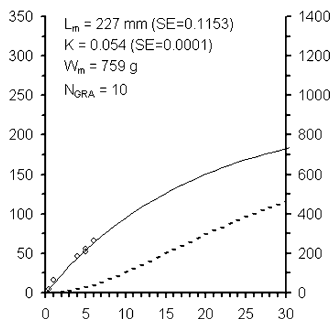
Percent of individuals surviving or population yield in skeletal mass



Fungia fungites



Fungia (Danafungia) spp.



Age (years)

coral age in all populations was estimated at < 10 years, indicating a high turnover rate among individuals. In addition, polyps of *Fungia scutaria*, which live mainly on the intertidal reef flat (Goffredo and Chadwick-Furman 2000), had much higher mortality and faster turnover than did mushroom corals living on the reef slope. Comparison of demographic traits among the four taxa reveals different potential recovery rates of each taxon from physical disturbances.

Individual growth patterns

Isometric polyp growth likely represents the ancestral growth form for scleractinian corals (Wells 1956). Isometric growth occurs in all coral polyps with a circular adult shape, and has been demonstrated among mushroom corals in *F. actiniformis* (Abe 1940), *F. fungites* (Goffredo 1995; present paper), *F. granulosa* (Chadwick-Furman et al. 2000), and *F. (Danafungia)* spp. (present paper). In contrast, allometric growth is probably a derived trait, in which circular juvenile coral polyps develop into oval or oblong adults. This process has been documented for the mushroom corals *Ctenactis echinata* (Hoeksema 1991b; Claereboudt 1993; Goffredo 1995; present paper), *F. paumotensis* (Bablet 1985), and *F. scutaria* (present paper). Allometric growth is a product of less active skeletal secretion along the width than along the length axis of the oral disc, and results in (lengths being equal) a smaller oral disc surface area than in individuals with isometric growth. The relatively small surface area of oval or elongate corals may favor the removal of sediments and the acquisition of food in unstable habitats (Foster et al. 1988; Hoeksema 1991b).

Growth curves

Among the most common mushroom coral taxa at Eilat (Goffredo and Chadwick-Furman 2000), individuals of *C. echinata* grow to become the largest ($L_m = 428$ mm; Fig. 2A). In contrast, individuals of *F. granulosa* have a growth constant (K) double that of the other fungiids examined here, indicating that they reach maximum adult size most rapidly (compare our Fig. 2 with Chadwick-Furman et al. 2000). Estimates of L_m calculated here appear to be correct, as they are similar to those obtained from direct measurements of polyps in worldwide collections of these taxa (Hoeksema 1989).

Mushroom corals in the northern Red Sea have growth constants ($K = 0.049$ – 0.109) less than half of those of mushroom corals living near the equator ($K = 0.215$ – 0.404 , reviewed in Chadwick-Furman et al. 2000). Within species, this pattern also occurs in *F. fungites*, the only mushroom coral for which growth data have been collected along a latitudinal gradient: Eilat (29°N) with $K = 0.049$ (present paper), Sharm el Sheikh (27°N) with $K = 0.088$ (Goffredo 1995), and Low Isles on the Australian Great Barrier Reef (17°S) with

$K = 0.215$ (Stephenson and Stephenson 1933). Together, these data indicate that the growth rates of mushroom corals vary widely with latitude. A negative relationship between growth rate and latitude also has been demonstrated for corals of the genus *Porites* at sites along the Great Barrier Reef of Australia (Isdale 1983; Lough and Barnes 2000) and in the Hawaiian archipelago (Grigg 1981, 1997).

Survivorship

The population age structures of mushroom corals at Eilat are characterized by an exponential decrease in the frequency of individuals with age, with the rate of this decrease varying among the taxa (Chadwick-Furman et al. 2000; Fig. 2B). This type of pattern indicates that these populations may be numerically stable over time (Grigg 1977, 1984; Ross 1984; Yablokov 1986; Santangelo et al. 1993). Eilat's location at the northern tip of an enclosed sea appears to offer a relatively stable environment for most of these corals (Kramarsky-Winter and Loya 1998; Goffredo and Chadwick-Furman 2000), and could explain the steady state of the populations observed.

Variation in survivorship among fungiid taxa at Eilat appears related in part to differences in suitability between the reef habitats examined (Grigg 1975). Polyps of *F. fungites*, *F. granulosa*, and *F. (Danafungia)* spp. occur mainly on the reef slope at wide depth ranges of 2–55 m (Goffredo and Chadwick-Furman 2000), and have similar population dynamics (our Fig. 2; Chadwick-Furman et al. 2000). Polyps of all three taxa have intermediate turnover times (4–6 years, calculated as the inverse of mortality rate Z , and also equal to mean coral age) and lifespans (24–33 years). Individuals of the two grouped species, *F. (Danafungia)* spp., may differ slightly in their population biology, but they are known to be closely related and ecologically similar species of fungiids (Hoeksema 1989, 1990). In contrast, individuals of *C. echinata* have a limited depth range on the reef slope of 2–8 m, and a longer turnover time (9 years) and lifespan (46 years) (Fig. 2). Polyps of *F. scutaria* occur almost exclusively on the reef flat at 1 m deep, and have a more rapid population turnover (2 years) and shorter polyp lifespan (13 years) than those of the fungiids on the reef slope (Fig. 2). Many small polyps of *F. scutaria* were attached to large, adult polyps, and were probably generated through asexual reproduction (Kramarsky-Winter and Loya 1998; Gilmour 2002). This reproductive strategy is observed in mushroom coral populations subjected to disturbance, and results in high mortality rates to the asexually produced young (Gilmour 2002). In contrast, mushroom corals on the reef slope likely reproduce mainly via sexual reproduction of dispersive propagules (Kramarsky-Winter and Loya 1998; Chadwick-Furman et al. 2000), which have lower rates of mortality (Gilmour 2002). We observed relatively few 1- to 2-year-old individuals of mushroom corals in the

field, except for those of *F. scutaria* (Fig. 2B). This variation appears to result from differences in reproductive patterns among these coral species (see discussion in Chadwick-Furman et al. 2000).

Population yield

We propose that the Beverton and Holt population dynamic model, which expresses a cohort's biomass curve in relation to age, be applied more widely to the management of exploited populations of certain stony corals. This model has been used to manage a handful of commercially important species of precious and hermatypic corals in both tropical and temperate ecosystems (Grigg 1984; Ross 1984; Caddy 1993). By arriving at estimates of the minimum size at which individuals may be removed sustainably from populations, wider use of this model could contribute to techniques for the transplantation of corals from "pristine" reef habitats to damaged areas in need of restoration (Rinkevich 1995; Edwards and Clark 1998; Epstein et al. 1999). Rinkevich (1995) asserts that transplantation practices aimed at the recovery of depleted coral reefs are best done by harvesting and transplanting artificially raised organisms from local mariculture instead of exporting individuals from natural populations. He terms this renewal strategy "coral reef gardening", and suggests the transplantation of individuals belonging to relatively fast-growing coral species. Among the most common mushroom corals at Eilat, the best candidate for contribution to reef restoration would be *F. granulosa*, whose growth rate constant (K) is substantially higher than those of other local fungiids (Chadwick-Furman et al. 2000; Fig. 2A). Some mushroom corals may make a unique contribution to reef restoration, because for years following initial transplantation, the stalked polyp base continues to produce multiple free-living polyps that detach and migrate downslope onto sandy areas. After the polyps die, their skeletons provide hard substrata onto which other corals may settle, thus facilitating the natural extension of reef areas onto the surrounding sand (Chadwick-Furman and Loya 1992).

The minimum size for removal of individuals from field populations of corals must be larger than the size at first reproduction, in order to allow a buffer period for the production of sexual recruits. Among the fungiids examined here, the size at first reproduction in Eilat is known only for *F. scutaria* (Kramarsky-Winter and Loya 1998). Polyps of this species begin to release sperm at 25 mm polyp length (~1.5 years old) and eggs at 50 mm length (~3.5 years old) (Kramarsky-Winter and Loya 1998), which results in a 2–4 year buffer period for sexual reproduction before these polyps reach size at maximum yield (Fig. 2). According to the Beverton and Holt model, the size at maximum yield represents the minimum size of individuals that can be removed from the population in a sustainable manner, without decimating it.

The population dynamic models employed here may be useful tools for comparative analyses of demographic traits in certain types of stony corals. Due to the increasing exploitation of corals for the jewelry and handicraft industries, and for live displays in aquariums, sustainable management programs are urgently needed for the commercial harvest of coral populations (Rinkevich 1995; Bentley 1998; Hatcher 1999). Broader application of the Beverton and Holt model to suitable coral species could help to reduce the rapid depletion of natural coral populations, as well as contribute to planning the recovery of damaged and degraded coral reefs.

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