Fractal environments select for high von Bertalanffy *K*'s in crevice-dwelling fishes

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Recent evidence shows that coral reefs and other structurally-complex marine ecosystems often correspond to a fractal expectation in crevice size availability. Growth studies show that fishes dependent on crevices in such habitats usually show high values of von Bertalanffy *K*. Given that the number of crevices declines rapidly with size in fractal habitats, crevice-dependent species often show high values of *K* and small maximum sizes (L_{∞}). A comparison of growth characteristics of reef fishes allows a distinction to be made between obligate crevice occupants, and fish that are associated with reefs but are mostly free-living. Fish with high *K*'s are less likely to be excluded from crevices since further growth in size is inhibited, and they survive for generally long life spans. Their growth strategy includes a rapid attainment of maturity in response to the severe density-dependence at size imposed by the rapid decline in crevice numbers in fractal habitats. This is consistent with the hypothesis that crevice-availability at size is a key environmental variable.

Key words: Fractal coefficient, von Bertalanffy growth, coral reefs, resident reef fish, natural mortalityat-size.

Selección de entornos fractales para altos índices K de von Bertalanffy en peces de hábitats de grietas

Reciente evidencia muestra que los arrecifes coralinos y otros ecosistemas marinos complejos en su estructura corresponden a menudo a una muestra fractal en disponibilidad de tamaño de grietas. Estudios de crecimiento muestran que los peces que dependen de grietas en dichos hábitats por lo regular presentan valores altos de la *K* de von Bertalanffy. Dado que el número de grietas disminuye con rapidez con el tamaño en hábitats fractales, especies que dependen de la grieta a menudo muestran altos valores de *K* y tamaños máximos pequeños (L_{∞}). Comparar las características de crecimiento de los peces arrecifales permite distinguir a ocupantes de grietas de peces asociados a los arrecifes, pero sobre todo de vida libre. Peces con una *K* elevada tienen menos probabilidad de ser excluidos de las grietas, ya que su crecimiento en tamaño está inhibido, y por lo general tienen larga vida. Su estrategia de crecimiento incluye alcanzar pronto la madurez en respuesta a la fuerte denso-dependencia en tamaño, impuesto por la veloz disminución de grietas en el hábitat fractal. Lo anterior es consistente con la hipótesis de que la disponibilidad de grietas por su tamaño es una variable ambiental clave.

Palabras clave: Coeficiente fractal, crecimiento de von Bertalanffy, arrecifes coralinos, peces arrecifales, mortalidad natural por talla.

Introduction

The key issue considered in this paper is how habitat characteristics can provide a clue to realistic measures of natural mortality, which are difficult to obtain from purely biological data. The choice of reef fishes as a model for exploring habitat-linked mortality rates was dictated by recent studies showing coral reefs are typified by a fractal distribution of crevice sizes which can reasonably be linked to predation risk.

Considering their growth strategies, so-called "reef fish" are of 2 main categories. The extreme

variants are that they either remain small and have high *K* values, or become larger with relatively low *K* values. An explanation of the habitat consequences of this choice are considered here. Those characterized by a moderate to high maximum size (*p.ej.* groupers, snappers) show a low coefficient of *K* which allows continuous growth, and they may be called "reef associated species" (Table 1). In contrast, "reef-dependent species" have high *K*'s, and attain a maximum size at a uniformly small L_{∞} of <100-200 mm. Not surprisingly, transitional examples between these two categories occur, but for the arguments followed here, these two extreme strategies remain the main interest.

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Fractal characteristics of marine habitats

The idea that the life histories of marine crevicedwelling organisms are constrained by the structural characteristics of a fractal habitat was first proposed by Caddy & Stamatopoulos (1991). Recent measures of the fractal coefficient D along transects have confirmed that a fractal hypothesis could apply to many structurallycomplex forms of cover - p.ej.: algae (D = 1.07 - 1.35, Davenport et al. 1999). Fractal coefficients of surfaces (D'), such as those of caves (D' < 3.0, Tercafs 1997) and pore-rock interfaces p.ej., D' = 2.27-2.89 (Krohn 1988; quoted in Schmid 2000) may lie in the range 2.01 - 2.99. This is relevant, since many motile organisms occupy fractal surfaces early in their life history. Often the early stages of motile fauna migrate subsequently to other structurally-complex habitats (see p.ej. Gillanders et al. 2003) where larger crevice sizes are presumed to be available. Although a strong density-dependence of newly-recruiting reef fishes is improbable (Doherty 2002) given the large number of small crevices available on a reef, the situation must differ for larger individuals. Small endemic coral reef fish are not typically migratory, except where they come from another habitat type (p.ej. mangrove roots), prior to arriving in their adult reef habitat (Jones et al. 2010). This may explain why the same species on adjacent reefs may have different von Bertalanffy growth parameters (Williams et al. 2003), suggesting that there is a limited mixing of adult sub-populations; each responding to a different crevice size frequency.

Reef-associated fish species found on the then-unexploited Pedro Bank off Jamaica in the 1970's were studied by Munro (1983). This data set was re-analyzed by Caddy (2011) by size frequency analysis, who found that for most resident species, the rate of change in log size frequency with size was compatible with fractal coefficients of their reef environment approximating to a limiting value of $D' \leq 3.0$. This analysis also suggested a high level of habitat occupancy for larger fishes.

Reef-dependent fish use semi-enclosed spaces to avoid predation, and for these, the critical fractal dimension is close to 3; a volume. This prediction resembles one made by Purkis & Kohler (2008) based on geomorphological analysis of coral reefs. Other authors (*p.ej.* Mark 1984) also suggested that coral reefs match a fractal expectation. The Munro data set led to the deduction that large reef fishes, once they are excluded from the reef by an absence of large crevices, risk high predation mortality.



Fig. 1. Predicted log frequency of crevices with size in two fractal environments.

Using the fractal relationship to predict an order of magnitude for M

Confirmation that the fractal function can be regarded as an index of mortality at size comes from a comparison of predicted M's-at-age using the fractal approach, with a reciprocal relationship of *M versus* age (postulated for *M* -at-age by Caddy 1991), after minimizing the difference between the two predicted vectors of *M* -at-age. Both approaches can result in similar vectors of *M* -at-age (Fig. 2).

A rapid decline in natural mortality rate occurs in the first year of life: for the example in *figure 2*, from M = 1.5 for age = 0.2 yr, to a constant mortality rate at age of 0.2-0.1 for adults, where K = 0.6; $L_{\infty} = 100$ and D = 1.15 (Fig. 2). These values are not discordant with other estimates of *M*-at-age for well-documented fish species.

Coral reefs as fractal environments

In their natural habitats, reef-dependent species often occupy broken surfaces ranging dimensionally between a surface (2) and a volume (3).



Fig. 2. Two mortality functions plotted against age: $M = 0.06 + 0.23 \text{ t}^{-1}$, and a conversion from fully-occupied fractally-distributed crevices to numbers of fish at age (K = 0.6; L_∞ = 100; D = 1.15) assuming a von Bertalanffy function (eq. 3).

Changes in holding capacity with size for crevice-dependent motile organisms must be in part a function of these fractal characteristics (*p.ej.* Fig. 1). From satellite imagery, Purkis & Kohler (2008) showed that coral reefs are fractal over scales ranging from <10 m² to >1 000 m², with coefficients along a linear transect on the Puerto Rican shelf of D = 1.2 - 1.3, and higher values of 1.4 - 1.65 in the Arabian Gulf. Mark (1984) also found fractal coefficients approximating D = 1.2 for transects across a coral reef. Other structurally-complex marine habitats are also fractal, as summarized in Caddy (2007, 2008), and are used as cover by motile demersal and benthic marine organisms at various life history stages.

Purkis & Kohler (2008) measured the fractal coefficient of the <u>surfaces</u> of coral reefs (D'), and noted that as the surface coefficient D' approaches 3, it corresponds to a surface "so rough as to fill three-dimensional space". They suggested that we should expect the demography of reef-dependent fish to reflect this habitat scaling.

Growth characteristics of reef-associated and reef-dependent species

A large sample of data on von Bertalanffy parameters for reef fishes is found in the literature, including parameters from fish taken on coral reefs throughout the tropics. Experts on reef fish have noted the plasticity in growth form between fish populations on individual reefs, even those adjacent to each other. The data for species included in the samples incorporated in *figure 4* include von Bertalanffy parameters extracted from the following references: Munro (1983), Ault*et al.* (1998), Choat & Robertson (2002), Gust *et al.* (2002), Choat *et al.* (2003), Kaunda-Arara *et al.* (2003), Williams *et al.* (2003), Kingsford & Hughes (2005) and Robertson *et al.* (2005).

Figure 3 shows a well-known phenomenon: larger fast-swimming species with generally fusiform bodies (reef-associated species), typically show a limited inflexion of the growth curve (K = 0.1-0.25), and while associated with reefs, are more free-living than "reef-dependent" fishes. At the other end of the wide growth spectrum, the small reef-dependent species are of a small maximum size; rarely exceeding 200 mm in body length, but with values of *K* extending upwards from 0.3 to 3.0 +. This implies that after a rapid juvenile increase in size, growth effectively ceases (Fig. 3).



Fig. 3. Typical growth patterns of reef-associated (K = 0.1 and $L_{\infty} \ge 1\ 000$ mm) and reef-dependent species (K = 0.8 and $L_{\infty} \le 150$ mm).

The horizontal band of small fish in *figure 4* shows progressively higher *K* values (given by Berumen 2005 as high as K = 3.0+), and limited maximum sizes. It is proposed that their growth constraint is

due to the fractal nature of coral reefs, leading to an intense competition for the few larger crevices available. Choat & Robertson (2002) noted that:

Coral reefs harbor numerous taxa of small fishes, especially in families Gobiidae, Blennidae, Apogonidae, and Pomacentridae, most of which tend towards high values of von Bertalanffy κ . In these families the maximum size rarely exceeds 100 mm standard length (SL). However, in a number of abundant but heavily exploited taxa (Acanthuridae, Haemulidae, Labridae, Lethrinidae, Lutjanidae, Scaridae, and Serranidae) the mean length for species is close to or greater than 300 mm SL the maximum size achieved by species ranges from 100 to 1 000 mm SL in many families.

At least two groups of species emerge in *fi*gure 4: one group with *K* values ranging from 0.2 - 0.4, and L_{∞} 's from 100-1000 mm; the other with *K*'s extending from 0.5 - 3.0+, and sharing a narrow range of values for L_{∞} ; predominantly between 75 and 200 mm. This second group is the one mainly focused on in the following, and the taxa selected are given in *Table 1*. Larger species (with low *K*'s), tend to swim above or around the reef; escaping predators by rapid avoidance reactions and by taking advantage of the irregular external configuration typical of coral reefs.

Both groups of species may reach an advanced age exceeding 15 yrs (*p.ej.*, Choat & Robertson 2002), implying that both reef association and reef dependence are successful survival strategies. The growth patterns of reef-dependent species show close to linear growth in the

 Table 1

 The main reef fishes for which data are included in figure 4

Species	Author
Acanthurus lineatus	Gust et al. (2002)
Chlorurus sordidus	
Scarus (two species)	
Siganus sutor	Kaunda-Arara et al.
Lethrinus mahsena (two species)	(2003)
Zebrasoma scopas	Choat & Robertson
Zebrasoma veliferum	(2002)
Bolbometopon muricatum	
Cetoscarus bicolor	
Chlorurus (two species)	
Hipposcarus longiceps	
Scarus (eight species)	
Sparisoma (six species)	
Acanthurus (13 species)	Choat & Robertson
Ctenochaetus striatus	(2002)
Naso (seven species)	
Zebrasoma (two species)	
Bolbometopon muricatum	
Cetoscarus bicolor	
Chlorurus (two species)	
Hipposcarus longiceps	
Scarus (eight species)	
Sparisoma (six species)	
Chaetodon (four species)	Berumen (2005)

initial 10-20% of the life-span (Gust *et al.* 2002), and after settlement on reefs, a high rate of increase in size to maturity occurs, leading to early sexual maturity. This is an advantage if few individuals survive to a large size. A few larger individuals of reef-dependent species may establish residence times of several years in the limited number of larger crevices.



Fig. 4. von Bertalanffy κ and L_{∞} values for a sample of reef fishes (sources in *Table 1* and references).

A wide variation in von Bertalanffy parameters occurs between different areas and between inshore/offshore reefs, even if closely situated (Choat & Robertson 2002). This implies that the critical characteristics of a reef are determined in part by the reef itself, and that shortage of large crevices for fast-growing fishes dictates their behavior patterns. Although the tendency has been to ascribe to a limited food supply the dominant constraint on population growth (Jones 1986), the need to conserve an individual residence subject to intense competition presumably requires high energy expenditures and potentially limits foraging area.

Simulations of survival rates in fractal environments

The mortality component due to predation is often assumed to be considerable (Hixon 1991) and size-specific (p.ej. Mapstone & Fowler 1988). Gust et al. (2002) noted that differences in habitat complexity can influence mortality rates, and low or reduced habitat complexity may explain the high mortality rates experienced by scarids (Gust et al. 2002). Habitat structure has been suggested to moderate the effects of predation by Caley (1993), Caley & St. John (1996), Eggleston et al. (1997) and Caddy (2007). Prey species can reduce their risk of predation in more complex habitats if fish remain in refuges where predators cannot reach them (Christensen & Persson 1993). However, a specific relationship between the geometry of the coral reef and predation probability seems not to have been suggested previously. This led to a simulation of the fractal environment using a relationship proposed by Morse et al. (1985) for terrestrial insects, namely:

$$N_{(L2)}/N_{(L1)} = L_1^{D+1}/L_2^{D+1}$$
 (Eq. 1)

Where: N_{L2} and N_{L2} are the number of crevices of width L_1 , (and larger) L_2 , in a surface with a fractal coefficient D+1.

Simulations were carried out for successive five cm size intervals, and the survivors from the first crevice size interval were used as inputs to estimate survival in the next larger crevice interval, and so on, until an arbitrary maximum size of 100 mm was reached (Fig. 4). It is important to note that equation 1, which defines the ratios of numbers of crevices of sizes l_a and l_b , resembles the equation for a mortality rate expressed as the log ratio of individuals at two different sizes, and is used as such in the following, assuming that all crevices are occupied.

Biological similarities in fractal habitats

An interesting similarity emerges from comparing the rate of decline in crevice numbers with models of juvenile fish mortality (Caddy 2013). Increasing the fractal coefficient of a surface increases the rate of decline in numbers of crevices with size, and this will increase the natural mortality rate for species dependent on coral reef refuges.

In this simulation a bias is accepted by expressing fish size as length, rather than some other measure such as maximum girth which might be a more realistic; but this is unlikely to invalidate the general argument. The drop in number of crevices with size was calculated for those fractal environments transitional between a surface and a volume, with survival rates calculated for a 'surface fractal coefficient', D'.

It has been suggested (Sale 1978) that if competition for a crevice occurs between a larger fish just fitting within it, and a smaller one, the larger fish will generally prevail. If all crevices in the reef are occupied by fish of close to maximum size for each crevice, and if excluded fish are predated, then for two sizes of crevices, L_1 and a larger one, L_2 , the natural mortality rate occurring during growth between them, could be defined by:

$$M_{1,2} = \ln(N_{L2}/N_{L1}) = \ln(L_1^{D+1}/L_2^{D+1})$$
(Eq. 2)

This mortality rate does not take into account the time taken for fish with different von Bertalanffy parameters to grow between successive sizes l_a and l_b . This interval can be defined by:

$$\Delta t_{a,b} = -(1/K).[((L_{\infty}-L_{a})/L_{\infty}) - ((L_{\infty}-L_{b})/L_{\infty})]$$
(Eq. 3)

Time intervals can be calculated for five mm crevice sizes over 20-100 mm for growth coefficients ranging from K = 0.3 - 1.5, and show that 'low *K*' species occupy crevices for a longer time than high *K* species. In both cases, older fish may occupy larger crevices for several years, which effectively blocks new recruitment and increases juvenile mortality. This effect will be more pronounced for low *K* reef residents, which are faster growing as older fish.

Knowing the time it takes to grow between any two sizes, allows an approximation to what we may call the instantaneous mortality rate (Fig. 5):

$$M_{\rm L} = M_{\rm a,b} \cdot \Delta t_{\rm a,b} \tag{Eq. 4}$$



Fig. 5. Illustrating the predicted trends in instantaneous rates of mortality ($M_{L} = M_{a,b}.\Delta t_{a,b}$) with different von Bertalanffy κ 's, over five cm size intervals (D' = 2.15).

Figure 5 shows the instantaneous rate of natural mortality at age (M_L) derived from the log ratio of numbers of individuals in two crevice sizes, multiplied by the time to grow between them. The predicted result of a change in fractal parameters is that an increase in D' leads to higher vulnerability to predation through a sharp increase in the rate of decline in the number of crevices available for further growth in size. The as-

sumption that only animals ejected from crevices die due to predation is probably an extreme one, but evidence supports the idea that when hidden in crevices, predation mortality is lower than in the open. Although not taken into account in the current simulations, it is reasonable to expect a degree of plasticity in the growth rate to occur in response to variations in reef parameters, and field data support this assertion (*p.ej.* Paddack *et al.* 2009).

Discussion

It was desirable to test the hypothesis that organisms living in fractal environments where predation is higher outside of crevices, have an advantage in following growth trajectories that result in a low maximum size. The results of this study show that the mortality rate predicted from predation on residents in a fractal habitat will drop steeply with size for juveniles, followed by a plateau; both tendencies are similar to the configuration of actual M's-at-age for juvenile finfish species shown in Caddy (1991). Under these circumstances, the rate $M_{a,b}$. $\Delta t_{a,b}$ approaches a constant value of 0.05-0.1 for intermediate sizes (corresponding to the common "constant M hypothesis" in stock assessment). Instantaneous mortalities are predicted to rise again once the residence time in larger crevices exceeds one year. Species showing high K's have the advantage of a low maximum L_{∞} before crevice sizes become rare.

This study suggests that the use of fractal habitats early in the life history of finfish and other motile organisms is quite general, but has the corollary that for low κ species, migration to adult habitats becomes inevitable as they become more visible to predators. Field data show an even higher annual mortality for older reef fishes excluded from crevices as described in Caddy (2011). This may not be typical of free-living species however.

Few studies in finfish ecology have tried to reconcile life history characteristics with evidence that complex habitats in the sea have fractal characteristics. The extreme consequences of adapting to fractal habitats during the whole life history is well illustrated by the crevicedependent species of coral reef fishes with high *K* values, and relatively constant and low values L_{∞} . This study attempts to illustrate that the mechanisms involved must to some extent be a feature of the fractal geometry of their habitat, and not solely a function of their physiology or food requirements.

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Recibido: 3 de junio de 2013. Aceptado: 24 de agosto de 2013.

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