

OPTIMAL SCALES TO OBSERVE HABITAT DYNAMICS: A CORAL REEF EXAMPLE

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Abstract. A new technique to estimate the characteristic length scales (CLSs) of real ecological systems provides an objective means to identify the optimal scale(s) of observation to best detect underlying dynamical trends. Application of the technique to natural systems has focused on identifying appropriate scales to measure the dynamics of species as descriptors of community and ecosystem dynamics. However, ecosystem monitoring is often based not on assessing single species, but on species assemblages, functional groups, or habitat types. We asked whether the concept of CLSs based on dynamic interactions among species could be extended to examine interactions among habitat types and thus to identify optimal scales for observing habitat dynamics. A time series of three spatial maps of benthic habitats on a Caribbean coral reef was constructed from aerial photographs, Compact Airborne Spectrographic Imager (CASI) images, and IKONOS satellite images, providing the short time sequence required for this technique. We estimated the CLS based on the dynamics of three distinct habitat types: dense stands of seagrass, sparse stands of seagrass, and *Montastrea* patch reefs. Despite notable differences in the areal extent of and relative change in these habitats over the 21-year observation period, analyses based on each habitat type indicated a similar CLS of ~300 m. We interpret the consistency of CLSs among habitats to indicate that the dynamics of the three habitat types are linked. The results are encouraging, and they indicate that CLS techniques can be used to identify the appropriate scale at which to monitor ecosystem trends on the basis of the dynamics of only one of a disparate suite of habitat types.

Key words: *characteristic length scale; coral reef; ecosystem trends; habitat; monitoring; remote sensing; scale; spatial; spatial and temporal dynamics.*

INTRODUCTION

The focus of ecosystem monitoring has shifted in recent years from spatial information based on individual dynamics to that based on details of dynamics at a habitat level, where the habitat is defined, at least in part, by the community of component species. This shift has been driven by the emergence of automated technologies such as remote sensing, which provide a means of discerning patterns in ecological systems with continuous data over larger areas than had previously been impractical with ground-based field work (Roughgarden et al. 1991, Green et al. 1996). Detailed classification of habitat types using remotely sensed imagery has enabled high-resolution landscape mapping, which is playing an increasingly important role in

assessment of biodiversity, reserve design, and management zoning (Loehle and Wein 1994, Green et al. 1996, Ward et al. 1999). However, the natural scale at which to analyze the maps to detect trends in habitat dynamics is ambiguous; in examining a time series of maps, a crucial question is to identify the optimum scale to distinguish real ecological trends from noise (Habeeb et al. 2005). A technique to objectively define an appropriate scale to sample habitat maps is necessary if meaningful signals in varying abundances of habitats through time are to be identified (Rouget 2003).

Identifying the level of detail or scale needed to detect the mechanisms that generate patterns has long been an important goal in ecology (Carlile et al. 1989, Wiens 1989, Levin 1992), and one that is becoming increasingly pertinent as the scale-dependence of fundamental ecological relationships is established (Chase and Leibold 2002, Chalcraft et al. 2004). The characteristic length scale (CLS; Keeling et al. 1997) is a relatively new

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concept and is a system-level property that provides an objective estimate of the optimal scales of observation to detect underlying dynamical trends in the behavior of real ecological systems, even when dynamics show complex nonlinear oscillatory behaviors (Habeeb et al. 2005). Thus, CLSs estimate the scales of observation to most clearly observe the nontrivial dynamics of a system, which are not necessarily the optimal scales to observe individual components of the system or any one of the myriad of underlying ecological processes. Sampling a system at its characteristic length scales maximizes the potential to observe the deterministic dynamic, or nontrivial trend, of the system (which might arise through interactions of processes operating at many different spatial and temporal scales) least influenced by stochastic variability. Based on nonlinear time series analysis, estimation of these ecosystem-level length scales requires only a short time series of highly resolved spatial maps. The estimates are robust to arbitrary choices about sampling patterns such as the time interval between maps (Habeeb et al., *unpublished manuscript*), and to the choice of species to be monitored (Habeeb et al. 2005), with species across several phyla indicating similar scales (Habeeb et al., *unpublished manuscript*). The suggestion that ecological systems are likely to demonstrate several length scales (Levin 1992) is supported by the analysis of several systems which reveal both primary and secondary scales (Habeeb et al. 2005). The secondary scales are typically more variable than the primary length scales and ostensibly reflect emergent dynamics of the system.

Thus far, characteristic length scales have been detected for a variety of models (Keeling et al. 1997, Pascual and Levin 1999, Habeeb et al. 2005) and, most recently, for a real marine system (Habeeb 2005), but their estimation has always been based on the dynamics of component species. Here we examine, for the first time, whether larger natural-length scales are manifest that reflect spatial dynamics of habitat types, as opposed to those of species. In the same way that system-level length scales estimated from the dynamics of different species will be similar only if those species exist within the same interactive network of species, we anticipate that estimates of length scales based on habitat dynamics will only be similar if the dynamics of the different habitats investigated are interdependent. If length scales detectable from habitat dynamics do exist, then they could be extremely valuable to monitoring programs intended to document changes in the extent and/or location of habitats. Monitoring habitat dynamics with landscape maps derived from (increasingly available) remote sensing techniques can be useful because habitats are often good proxies for more finely resolved information that is difficult to collect (Ward et al. 1999, Rouget 2003). Here, we use data from remote sensing to search for characteristic length scales at the habitat level.

Using spatial maps covering a 21 year period of a Caribbean coral reef, we attempt to determine the CLSs of the system based on the dynamics of three benthic reef habitats. While in theory only one habitat type is necessary to estimate the length scale(s), we examine the spatial dynamics of three different lagoonal habitats to determine whether they provide similar estimates, if any, of the CLSs for this reef ecosystem. If they exist, these scales will be useful only if disparate habitat types indicate similar scales (Habeeb et al. 2005).

In applying the nonlinear time-series method of Habeeb et al. (2005) to highly resolved maps of habitat distribution, the underlying assumption is that the attractor, or the shape of the multihabitat dynamic in phase space (Takens 1981), can be reconstructed from a short time series of habitat level information. This assumption is reasonable provided that there is no ambiguity in defining habitat types, that distant locations in space within the system under consideration are at different points on the system's attractor, and that changes in the spatial pattern of habitat types reflect the deterministic dynamics of the system. In using this method, we also assume that the dynamics of the different habitat types are part of a single system and are therefore not independent of one another (otherwise they may indicate dissimilar length scales), and that successive observations in time are sufficiently separated for habitat dynamics to be observed (Habeeb et al. 2005).

METHODS

Data requirements

To estimate CLSs, at least three consecutive maps of the same area are required to build the attractor using the short-time-series analysis technique of Habeeb et al. (2005). We have shown elsewhere that the time intervals between successive maps can vary without affecting the CLS estimate, that they should be sufficiently long to allow at least some change in cover (arbitrarily at least ~10–20% of total initial cover) so that the dynamic can be detected, but not so long as to allow a complete turnover in the species or habitats sampled (Habeeb 2005). Complete turnover (i.e., loss of all of the original cover, which may or may not be replaced by new growth) is problematic since it is not possible to measure the magnitude of the dynamic once 100% of a map is changed. On a coral reef where massive coral colony sizes may exceed 3 m² (Meesters et al. 2001), intervals need to be on the order of years to decades, rather than months, to allow large-scale habitat change (Pandolfi 2002). The time scale of this study, which covered more than two decades, was considered ample to detect turnover of the habitat types on this reef, as is evident in Fig. 1.

For each map, the data need to be spatially contiguous, with no breaks in the landscape as, for example, might arise with cloud cover. Finally, to rebuild the attractor with the short-time-series method,

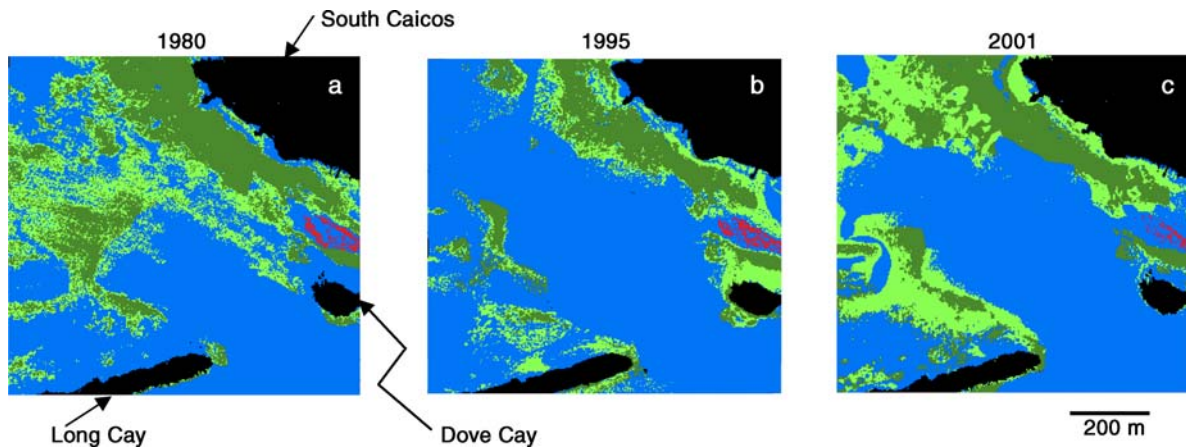


FIG. 1. Digitized maps of the benthic habitats at Cockburn Harbour (South Caicos) taken from (a) 1980 aerial photography, (b) 1995 CASI imagery, and (c) 2001 IKONOS imagery. The darker green regions indicate areas of dense seagrass, lighter green regions indicate areas of sparse seagrass, red regions indicate *Montastrea* patch reef, blue indicates deep ocean and unclassifiable reef habitats, and black regions indicate landmasses, which are named for reference in (a). Each map has a resolution of 4-m pixels.

the data must have high spatial resolution relative to the entire landscape mapped since meaningful detection of CLSs requires that the scale of map resolution is a smaller dimension than the CLS itself. Our data meet these requirements.

High-resolution maps from the Turks and Caicos, West Indies

The study site was a shallow reef ecosystem near Cockburn Harbour within the Turks and Caicos Islands, West Indies (Fig. 2) whose reefs have been mapped intensively (Mumby et al. 1998, Mumby and Edwards 2002). An aerial photograph from 1980 (2-m resolution), a Compact Airborne Spectrographic Imager (CASI) image from 1995 (1-m resolution), and an IKONOS satellite image from 2001 (4-m resolution), all of the same location and area, provided the short time sequence of spatial maps necessary for CLS estimation. Because of their different pixel sizes, the images were rescaled to a common (lowest) resolution of 4 m (i.e., 16 m² per pixel) by taking means. This provided a conservative estimate of resolution, which accounted for most of the error in the rectification of high-resolution airborne imagery (errors of ~3 m).

The benthic habitats captured in these images comprised reef-building corals, gorgonian communities, seagrass beds, and algal dominated substratum within a depth range of 3–25 m. Three maps, each with an area of ~1.4 km², were constructed (Fig. 1) based on the habitat classification system of Mumby and Harborne (1999). This area was considered large enough to capture the patterns of habitat variation through time because patches were considerably smaller than 1.4 km² (see Fig. 1). Standard image processing was achieved through the ERDAS image software. Images were geometrically corrected and co-registered, and supervised classification (which was directed by field surveys

of 60 sites within the harbor) was applied to spectral bands.

Three distinct habitats were examined in Cockburn Harbour. The first, aggregated colonies of the massive coral *Montastraea annularis* (sensu stricto; see Plate 1), bridge the zone between the main, hard-bottom forereef and the soft-sediment lagoon habitats in the harbor (which included the other two habitat types). The *Montastraea* zone straddles the main inlet to the harbor and attracts many fish because of its high structural complexity (the diameter of individual colonies often exceeds 1.5 m and is the result of decades to centuries of growth). The second and third habitat types, dense and sparse seagrass beds, are found within hundreds of meters of the *Montastraea* zone and are dominated by two seagrass species, *Thalassia testudinum* and *Syringodium filiforme* (see Mumby et al. 1997). The standing crop of the dense beds ranges from 51–230 g/m² with a mean species composition of 72% *Thalassia* and 28% *Syringodium*. The low-density beds typically have 80% *Thalassia*, 20% *Syringodium* and a lower standing crop of 1–50 g/m². These two seagrass habitat types have been shown to be distinct, harboring different assemblages of species (Mumby et al. 1997).

Estimating the CLSs

The original method of estimating CLSs based on the prediction r^2 metric (Pascual and Levin 1999) required very long time series of spatially resolved data that are unattainable for real ecological systems. Habeeb et al. (2005) modified this method so that CLSs could be estimated from very short time series of highly spatially resolved “maps” of species abundances. The new “short-time-series” method uses both temporal and spatial information and largely substitutes replication in space for replication in time. The drastic reduction in data requirements enables examining real ecosystems for the

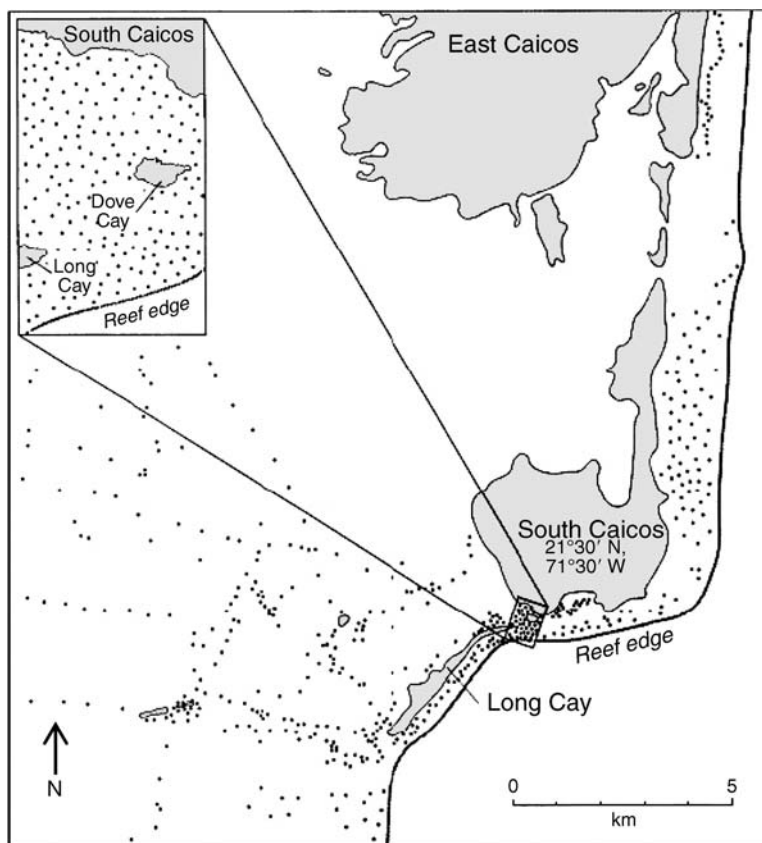


FIG. 2. Map of the Turks and Caicos Islands, West Indies. The inset shows the study area on the southern side of South Caicos Island. Dots show positions of sampling sites used to “ground-truth” remotely sensed images (see Mumby et al. 1998).

existence of CLSs. We applied the short-time-series technique to the sequence of three maps to reconstruct the attractor of this system and to generate curves of “variance” (as defined by the prediction r^2 metric) vs. scale of observation for each of the three habitat types. Prediction r^2 is a measure of the accuracy of the prediction of a system’s attractor from observations at a given scale (Pascual and Levin 1999). Primary CLSs are estimated as the first plateau in the prediction r^2 curve, and in this sense they represent a system-level scale threshold. Secondary CLSs are detected as subsequent peaks or plateaus in prediction r^2 .

RESULTS

Habitat level CLSs of a coral reef ecosystem

Prediction r^2 vs. scale curves were produced from analysis of each habitat type, and primary and secondary characteristic length scales (CLSs) were determined by visual inspection (Fig. 3). Analyses of each habitat type yielded similar and readily interpretable curves of the expected shape, with prediction r^2 increasing sharply to a plateau as the scale of observation increased. Primary CLSs estimated from all three habitats were similar at ~ 300 m. Secondary CLSs indicative of emergent dynamics, perhaps as a result of complex interactions

between habitat patches (Habeeb 2005, Habeeb et al. 2005), were evident when either type of seagrass habitat was used to reconstruct the attractor, with both habitats indicating a secondary length scale at ~ 600 m.

DISCUSSION

CLS estimation using habitat level data

The choice of sampling scales in ecology is critical for clear detection of ecosystem trends. Results can be clouded by noise if the sampling scale is too small and signals averaged out if the scale is too large (Pascual and Levin 1999). The characteristic length scale is a quantitative and objective estimate of the sampling scales which best reveal the nontrivial trends in an ecological dynamic. Here, we establish that CLSs can be estimated using data collected at the habitat level. This result demonstrates the versatility and potential applicability of this relatively new concept for use in ecosystem monitoring where remote sensing is used to map systems at the habitat level. Once landscape maps are acquired for a system, the scale at which to analyze those maps must be chosen. Thus, establishing a means to determine the scales of observation at which the deterministic dynamics of habitat change are most clearly in focus is a significant advance. The choice of

scale at which to analyze habitat maps can now be guided, at least in part, by estimating the CLS of the system. Furthermore, knowing the optimal size of sampling units to detect trends in habitat abundances, as determined using the techniques outlined here, may be particularly valuable in circumstances where limited resources prevent comprehensive sampling (Pressey and Logan 1998, Rouget 2003).

All three habitats provided interpretable curves of prediction r^2 vs. sampling scale (Fig. 3), and each curve yielded a similar estimate of the primary length scale (~ 300 m). The similarity in CLS estimates from independent analyses of the three habitats is noteworthy given the dissimilar absolute areal coverage of each habitat and dissimilar relative and absolute magnitudes of change in habitat cover over the 21-year observation period (Fig. 1). Thus, it appears that habitat change is indicative of an underlying system dynamic over the time scale assessed. The analysis indicates that sampling landscape maps of this reef at a scale of about 300×300 m (0.09 km^2 in area) will yield data reflecting the ecologically significant dynamics of the system at the habitat level. These results demonstrate clearly that natural scales can be estimated using spatial information, not only based on species abundances, but also based on habitat abundances, which will be useful for monitoring ecosystem dynamics at the habitat level.

Similarity of CLS estimates from different habitats

Given that the three habitat types studied here are comprised of taxonomically and functionally distinct species, manifest large differences in absolute cover, and show distinctly different changes in absolute and relative cover and spatial arrangement (Fig. 1), it is encouraging that all habitats nonetheless indicated a similar primary CLS at ~ 300 m. This result suggests that the three habitat types are components of a connected dynamic, thereby allowing unambiguous estimation of the system-level length scale. If the three habitats had indicated markedly dissimilar primary CLSs, this would indicate that their dynamics are largely independent of one another (Habeeb et al. 2005). Note that the close similarity of CLSs indicated by each habitat does not indicate the nature of the connectivity in dynamics, only that the connectivity exists. However, we suggest that at least part of this connected dynamic reflects that the habitats are subject to similar external forcings in the form of disturbance from storms. Five tropical storms or hurricanes were recorded in the study region during the 21 years of investigation (information *available online*).⁵ Hurricanes are major sources of disturbance to corals (Done 1992, Bythell et al. 2000) and may physically remove moderate-sized massive corals such as *Montastraea* (Massel and Done 1993). Likewise, recent work on comparable seagrass beds from else-

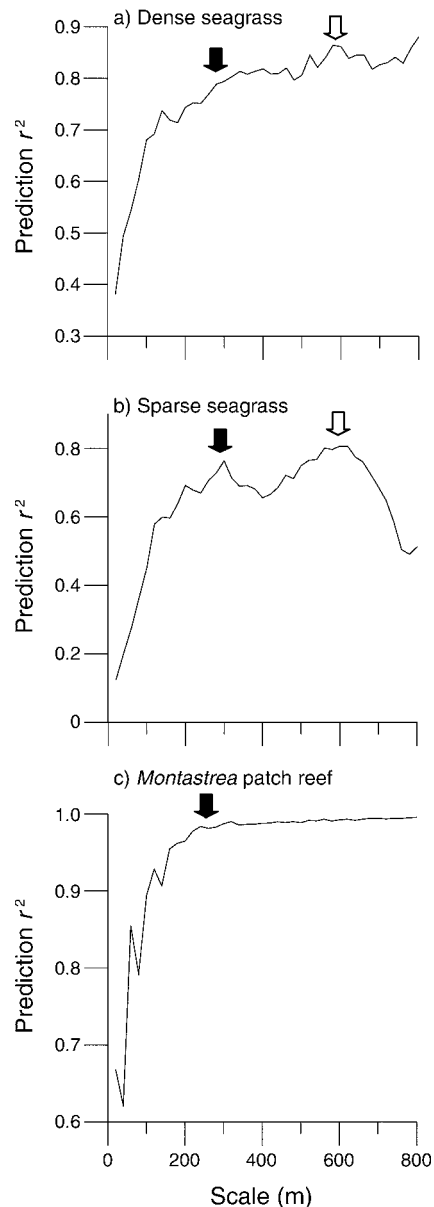


FIG. 3. Curves of prediction r^2 as a function of scale determined using the short-time-series method of attractor reconstruction, based on abundances of (a) dense seagrass, (b) sparse seagrass, and (c) *Montastrea* patch reef. Filled arrows indicate the approximate primary CLS, and open arrows indicate secondary CLSs.

where in the Caribbean illuminates the role of hurricanes in seagrass dynamics. For example, hurricanes may facilitate the spread of *Syringodium* by increasing seed dispersal (Kendall et al. 2004) and freeing space for growth (Fourqurean and Rutten 2004). The consistency of CLSs among habitats suggests that hurricanes may bring about coupled deterministic dynamics for strikingly different habitats.

The dynamics of different habitats will also be linked in circumstances where losses in one habitat are reflected

⁵ <http://hurricane.csc.noaa.gov/hurricanes/viewer.htm>

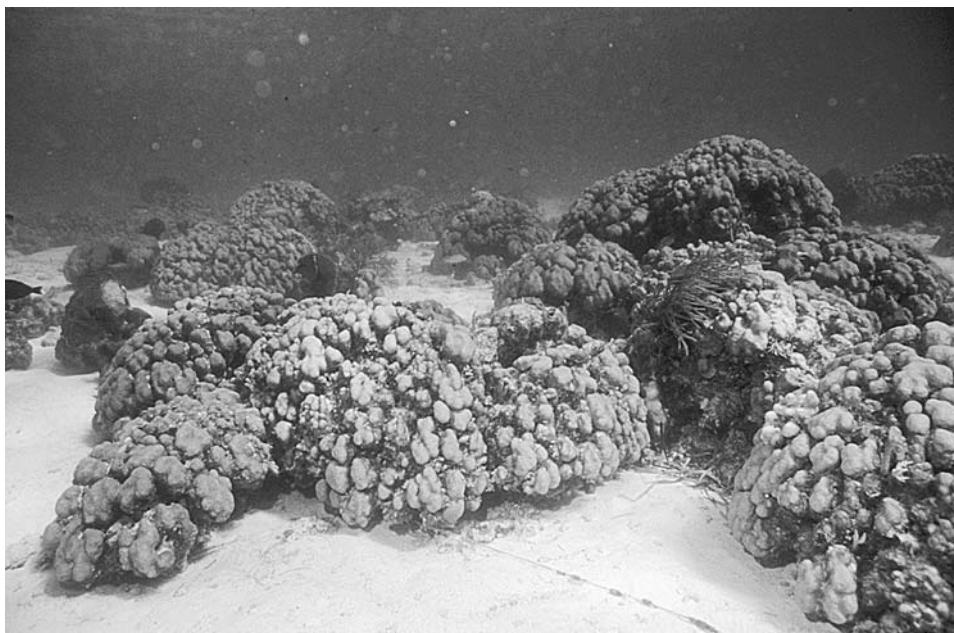


PLATE 1. Colonies of *Montastraea annularis* in Cockburn Harbour, Turks and Caicos Islands, West Indies. Photo credit: Edmund Green.

by gains in another. This circumstance would necessarily arise (as a “zero-sum game”) when a number of habitat types fully occupy a given area, but it is clear that this is not the case in the example presented in the present paper (see Fig. 1).

Secondary characteristic length scales

Prediction r^2 curves for both dense and sparse seagrass habitats indicated secondary CLSs at ~ 600 m, double the primary CLS (Fig. 3). Conversely, the curve derived from the space–time pattern of *Montastrea* reef patches showed only a primary CLS, indicating that detection of the secondary CLS is dependent on the habitat studied. This secondary scale likely reflects the large-scale loss and subsequent return of seagrass beds over the 21-year time period (Fig. 1), dynamics that were not evident for the more consistent *Montastrea* patch reef. Secondary length scales are likely to indicate the emergent dynamics of a system (Habeeb et al. 2005), usually the result of complex non-linear interactions between component entities, and may reflect spatial self-organizing, or the emergence of complex feedbacks or synergies. Accordingly, secondary CLSs tend to be more variable (Habeeb et al. 2005), so the consistency of estimates of the secondary CLSs among different habitats in this case is perhaps unusual.

Importance of estimating CLSs at a habitat level

Natural scales of coral reefs and other ecosystems worldwide will be determined more commonly as archives of well resolved satellite images revealing habitat structure and dynamics become more readily

available (e.g., for coral reef satellite images [*available online*]).⁶ Large-scale implementation of the method in this way may enable the use of CLSs, not only to define observational scales, but also as baseline metrics in their own right, which could be used to detect shifts in the dynamics of ecosystems. If CLSs of a system are calculated regularly, then a change in the length scale from one time to the next is likely to indicate a shift in the attractor (Habeeb et al. 2005), which may warrant further investigation into the cause of such a fundamental shift.

In addition, estimating CLSs on the basis of the space–time dynamics of a variety of habitat types within a system could be used to identify habitats that are dynamically, and perhaps functionally, linked. This kind of information may be important in informing management decisions. Within a defined system, habitats indicating similar CLSs are likely to be dynamically interdependent in some way, and perhaps influenced by similar processes. In contrast, habitats with distinctly different CLSs are unlikely to be linked dynamically, either by “internal” patterns of interaction or by external forcings.

Comparing habitat-level CLSs between regions may also be beneficial. Similar habitat types in different regions that indicate dissimilar CLSs would suggest fundamental differences in the processes most strongly influencing them. This may arise, for example, where anthropogenic effects are prevalent in one region but not in another. Using the CLS as an index per se for these

⁶ (<http://seawifs.gsfc.nasa.gov/cgi/landsat.pl>)

and other comparisons may provide valuable clues about the underlying dynamical behaviors of the ecological systems being monitored.

Conclusions

We have demonstrated that natural length scales can be estimated using data taken at the habitat level rather than at the species level. Distinct but spatially connected habitats provided similar length scales, reflecting the ecosystem nature of the estimate and the dynamical linkage of the habitats. This development provides new possibilities for a broader use of CLS estimates in ecology, particularly in that ecosystem monitoring is often based on assessment of suites of species or habitat types rather than on individual species, and that long-term sequences of remote sensing imagery are becoming increasingly available. Estimating the CLS of a landscape on the basis of habitat dynamics, whether terrestrial or marine, will both enable sampling at appropriate scales for detecting dynamical ecosystem trends and provide a metric to describe and assess space–time variation in ecosystem dynamics.

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