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Comments on and implications of a steady-state in coastal marine ecosystems

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Coastal ecosystems can be thought of as being established by a number of physico-geochemical drivers, e.g. geochemistry and bathymetry of the basins, climate, tidal and freshwater flows, natural and anthropogenic inputs of nutrients and toxins, all of which exert an influence on the resulting communities of organisms. Depending on the interactions among the major drivers, ecosystems may occur on both large and small scales and be basin-wide or within basins. For individual and separate ecosystems to exist with some permanence in time, e.g. reach a steady-state, they also have to be 'defended'. Defences are mechanisms that counter changes to maintain the status quo. We argue, and present evidence to support the notion, that the defence mechanisms are inextricably tied to primary production and the biogeochemical cycling of organic matter and provide buffers that mitigate potentially adverse impacts by trace toxins. Colloid pumping, production of complexing ligands and sulfide formation are some of the mechanisms that control trace substances. Current methods for assessing ecosystems do not address the issue of steady-state, nor do they take account of defence activities, e.g. buffering. Therefore, they cannot assess the 'robustness' of ecosystems or their ability to resist change, for good or bad. Also, defence mechanisms may, for a time, mask future potentially serious impacts, suggesting that monitoring efforts with limited budgets should consider the measurement of the inputs into ecosystems as well as the immediate or short-term result of the inputs.

Keywords: coastal ecosystems; steady-state; interdependence; 'drivers'; defences; impacts; monitoring

1. Introduction

Recently, there has been a resurgence of interest directed at the development of criteria for assessing the ecological state of estuarine and coastal environments, primarily to assess eutrophication [1–3]. With the same purpose in mind, this effort, based on our experience working in the Venice (Italy) Lagoon and in San Diego Bay (CA, USA) attempts to structure our understanding of those factors that may affect the ecosystems of shallow lagoons and other coastal waters, and points to the importance of autochthonous organic matter in the maintenance of these ecosystems.

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1.1. *Physical and geochemical forcing*

From a modelling perspective, any ground-up, structured, representation of an ecosystem needs to begin with the physical characteristics (bathymetry) of the basin: its dimensions, shape and structures, e.g., islands, mudflats, marshes, channels and canals. The basin and its features can be represented by a mathematical grid that constitutes the container [4] within which the ecosystem is established. Logically, physical forcing by drivers follows, and this includes: (1) tidal flow; (2) net freshwater inputs (river and stream flows plus precipitation minus evaporation); and (3) climate, e.g. solar radiance, atmospheric pressure and characteristic winds. These may be considered the independent physical variables. Other, commonly measured variables are really a result of these three (plus bathymetry): currents are primarily a function of tidal and wind forcing, hydrodynamic residence times are functions of currents, waves are a function of wind, tidal forcing, bathymetry and bottom roughness. Temperature and evaporation result from the absorption of solar radiation; gas exchanges with the atmosphere are a function of winds and radiation; turbulence depends on tidal patterns, winds, bottom roughness, etc.

A fourth independent component consists of the seed organisms that provide life to the ecosystem and lead to established communities. A fifth independent component consists of 'chemical drivers', often referred to as 'pressures' [5,6]. It includes the flows of nutrients, trace substances, vitamins and organic matter that enter the basin via freshwater sources, the tides and the atmosphere, to promote and support algal growth, develop planktonic and benthic communities and so forth. A byproduct of this growth is the formation of organic matter in the water column, both particulate and dissolved, which plays an important role in the maintenance of the community, both as a food source and as a buffering mechanism against toxins.

We define toxic substances as another class of 'chemical drivers' but in a negative sense, e.g. substances that could limit or even eliminate primary productivity, if present in sufficient concentrations to overwhelm the natural system of defences. These would include heavy metals, chlorofluorocarbons, polychlorinated biphenyls (PCBs), aromatic hydrocarbons and dioxins. In the above context, we define as 'passengers' substances that participate in the biogeochemical cycle of production, respiration and sedimentation without materially affecting its course. Passengers would include common pollutants such as Cd, Pb, Cu and Zn, which, at trace concentrations, 'ride' on the organic biogeochemical cycle without having significant toxic effects. Here, it must be stated that 'significant' in this article has an ecological modelling perspective that considers only primary production and 'without having significant toxic effects' means unable to materially change carbon fluxes and balances. Clearly, even small changes in trace metal or pesticide concentrations could potentially affect planktonic and benthic species diversity [7] and body size [8] without changing biomass, but this study does not deal with that. Nor does this work deal with the potentially infinite complexities of interspecies interactions [9,10].

Finally, the benthos must also come to terms with the average (and persisting) physico-chemical conditions of the overlying water column. Over prolonged periods, the benthic community will diversify and grow in a way that optimises the available resources which, in the main, are provided from above. If conditions persist unchanged, at some point the geochemical composition of the sediments and the benthic community will be at a steady-state with each other and with the overlying water column [10]. Indeed, sedimentary processes may become the dominant factors that control the 'chemistry' of shallow coastal lagoons [11]. Figure 1 shows how drivers may affect local conditions. Figure 2 shows one result of these drivers.

In summary, to be classified as an 'ecosystem' and maintain its integrity, any biological system must be near 'steady-state'¹ for a substantial length of time, and therefore its integrity must be supported by a number of 'defences' or buffers that mitigate the effects of substances entering the system. In estuarine waters, key defences are linked to the production and recycling of organic matter.

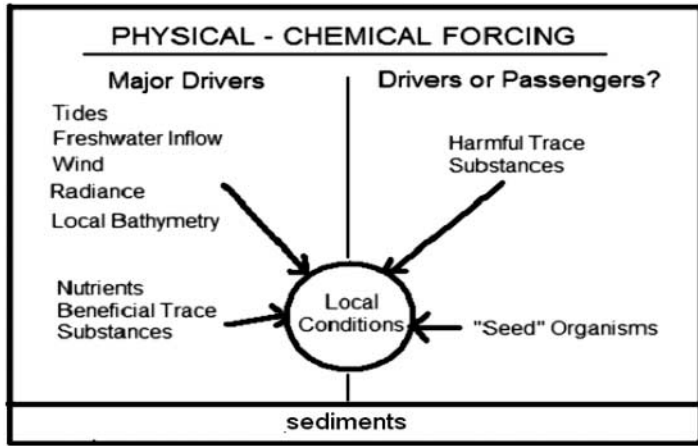


Figure 1. Physical and chemical 'drivers' determine local conditions in the water column and in the sediments.



Figure 2. Image of the Venice Lagoon (Google Earth). Inset: an expanded view of the lagoon floor between the Islands of Murano, San Michele and Isola Le Vignole, as well as of historic Venice itself. Even though separate portions of the image have been captured and processed separately, it is still possible to differentiate zones within each section. Inset shows that the differences in the hues of the lagoon floor also exist at much smaller scales. The yellow tacks indicate three locations of persistently different salinities that are discussed later in this study.

1.2. Ecological defences

1.2.1. Colloid pumping

One of these defences is known as colloid pumping and is well described by Santschi and colleagues [12–15]. Colloid pumping refers to the agglomeration of dissolved organic matter (DOM) into colloidal particles, their cementation into larger particles and ultimate settling to the bottom. Although a portion of the sediment so formed is remineralised and fed back into the pump, net transport is almost always towards the bottom. The source of the organic matter is predominantly local photosynthesis, but a minor component may be from freshwater sources. Figure 3 shows this process.

In an estuary, sedimentation competes with residual (tidal) currents that carry a portion of the suspended material out of the estuary. This process depends on a number of factors that contribute to the turbulence of the water column. Indeed, shear stresses induce simultaneous coagulation and fragmentation of particles. Given sufficient time, the floc size reaches a distribution that reflects the long-term average of the balance between coagulation and fragmentation. Ultimately, at steady-state, the local forcings will lead to an average, typical, suspended particle size [16] and perhaps, an average concentration of dissolved and colloidal organic matter.

The process of colloid pumping provides a defence mechanism for organisms because trace toxic foreign substances are adsorbed onto colloidal organic matter and then are transported either to the sediments or out of the estuary, minimising their concentration in solution. By contrast, trace substances necessary for growth are also adsorbed on particles. On the whole, however, the ecosystem probably benefits because the concentration of free or unbound substances, toxic or not, is controlled (buffered) by the particle-bound fraction, ensuring that they are available at proper levels [17].

The process of colloid pumping is non-specific, applies to trace metals as well as trace organics, and continues until the concentration of toxic pollutants in solution begins to interfere with photosynthesis, the source of the dissolved organic matter produced *in situ*.

1.2.2. The complexation capacity

The property of seawater that binds with microconstituents has been termed the complexation capacity (CC), and includes covalent bonding among dissolved ions and molecules as well as

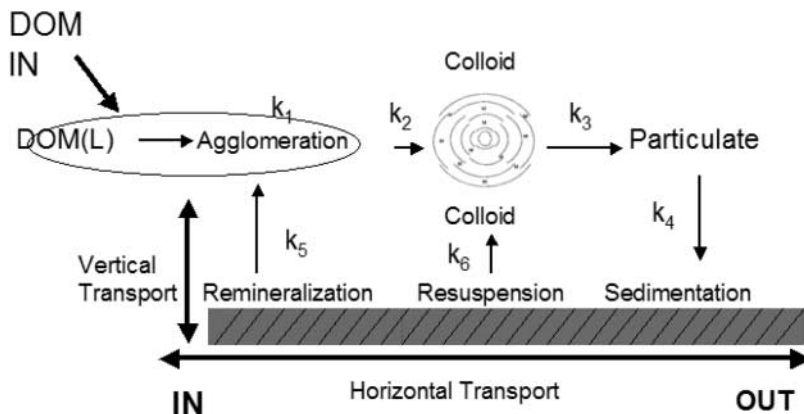


Figure 3. Agglomeration of dissolved organic matter into colloids, colloids into particles and ultimate fate of particles. k 's are rate constants and horizontal transport refers primarily to tidal currents. DOM(L) refers to organic ligands in true solution.

adsorption of microconstituents on colloids and particles (in unfiltered seawater). Although the CC may be heterogenous, it is nevertheless primarily attributed to ‘dissolved’ (dissolved and colloidal) organic matter in seawater. Organic complexation of trace metals has been considered the main controller of bioavailability and toxicity of trace metals to phytoplankton [18]. In general, complexation of a metal cation by organic ligands can diminish its toxicity by decreasing the free ion form of the metal [19,20].

Because free (hydrated) Cu^{2+} is a powerful algacide and Cu is the major component of antifouling paints, most studies of the effectiveness of the CC in reducing toxicity have been performed with this metal. In general, the CuCC exceeds and appears to be related to the concentration of Cu [18]. In Venice Lagoon [19], San Diego Bay [21], and Galveston Bay [22], the CuCC is at least 4–5 times the available Cu. Despite its affinity for Cu, the CC is probably a general property of the water that is available to all microsubstances and is a function of the concentration of the available organic matter [19]. Because this organic matter is derived from primary production, the CC can be considered an inherent defence against possible toxins in the water column. The CC is also not an independent variable as it is also inextricably tied to colloid pumping and therefore also related to the level of productivity, turbulence, and particle formation.

1.2.3. Sulfide formation

For heavy metals, and perhaps for other substances, sub-bottom formation of hydrogen sulfide must also be considered a defence mechanism, because sulfides immobilise heavy metals (Hg, Cd, Pb, Fe, Mn, Zn) and essentially render them biologically inert. This concept is usually expressed as the difference between the concentration of the simultaneously extracted metals (SEM) and the concentration of acid-volatile sulfide (AVS) present in the sediment [23]. In the case of Fe and Mn, however, sulfides allow for the reduced forms of these metals (Fe^{2+} , Mn^{2+}) to leave the insoluble oxide phase and re-enter the water column where they can be reassimilated by organisms if not immediately re-oxidised. Phosphate adsorbed on the solid or colloidal iron and manganese oxides is also controlled by this process [1]. Once again, the availability of sulfides is not independent but is linked to the rate of primary production, tidal flushing, and vertical mixing.

2. The steady-state

2.1. Steady-state at large spatial scales

Based on 2001–2003 MELA 1 [24] monthly monitoring data consisting of 20 or more water quality variables, Solidoro et al. [25] were able to statistically partition the Venice Lagoon into three principal zones, essentially aligned along the long axis of the lagoon: (1) a ‘marine’ zone, heavily influenced by tidal flushing and with a salinity of ~ 34 PSU; (2) a ‘source’ zone, adjacent to the mainland sources of freshwater, with an average salinity of ~ 22 PSU; and (3) an intermediate zone, between the first two with an average salinity of 27 PSU (Figure 4a). The calculated hydrodynamic residence times in the lagoon coincides with the distribution of salinity and are shown in Figure 4b. They range from 1 to 3 days (light blue) near the entrances to 20 days (brown) close to the mainland.

A recent analysis of more than 8 years of data from 2000 to 2008 (no data for 2006) of 11 stations distributed throughout the lagoon shows that despite the vigorous twice daily tidal flushing their individual characteristics have persisted over time, and confirms the original divisions made by Solidoro and colleagues [25]. Figure 5a shows that plots of the 8-year average concentrations the dissolved nutrients elements (represented in Figure 5a by total dissolved phosphate and total dissolved nitrogen) against salinity are almost perfectly linear, indicating that, on an annual basis, horizontal mixing between freshwater sources and waters from the Gulf of Venice is the

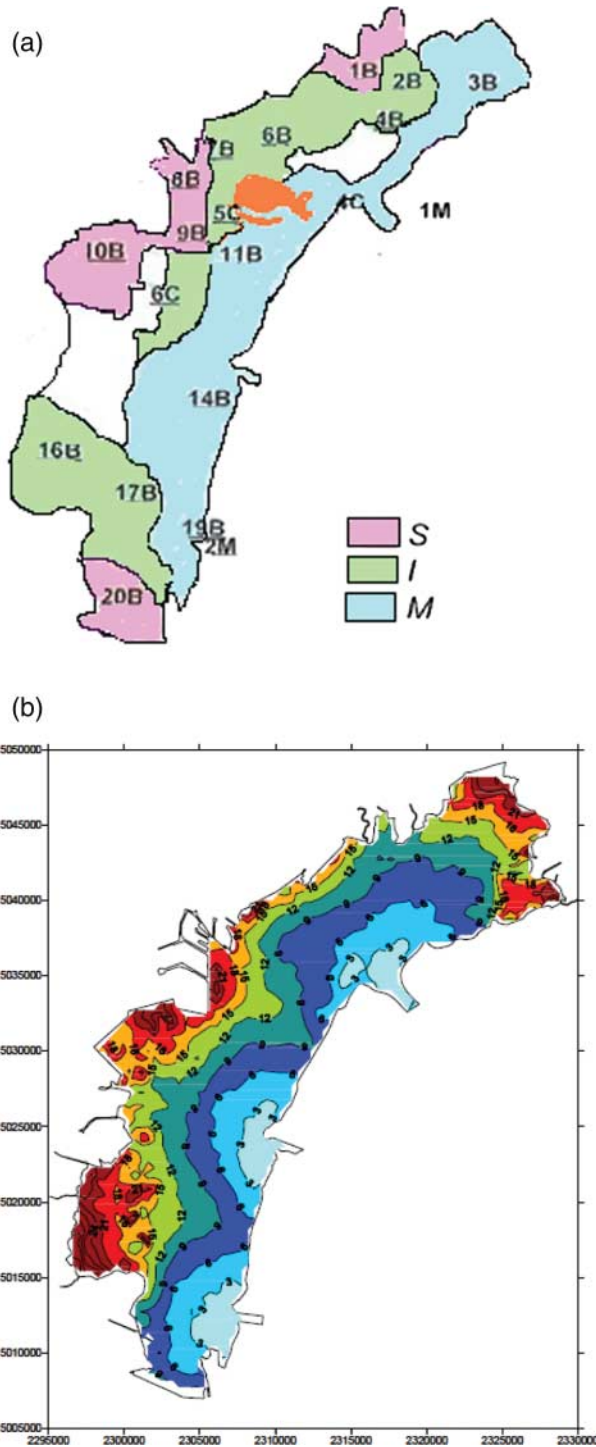


Figure 4. (a) Partitioning of the lagoon based on cluster analysis of hydrogeochemical data from 20 MELa stations sampled from 2001 to 2003 [24] (S = Source, I = Intermediate, M = Marine). (b) Calculated hydrodynamic residence times in the Venice Lagoon were obtained using a finite element model. Each colour band spans three days.

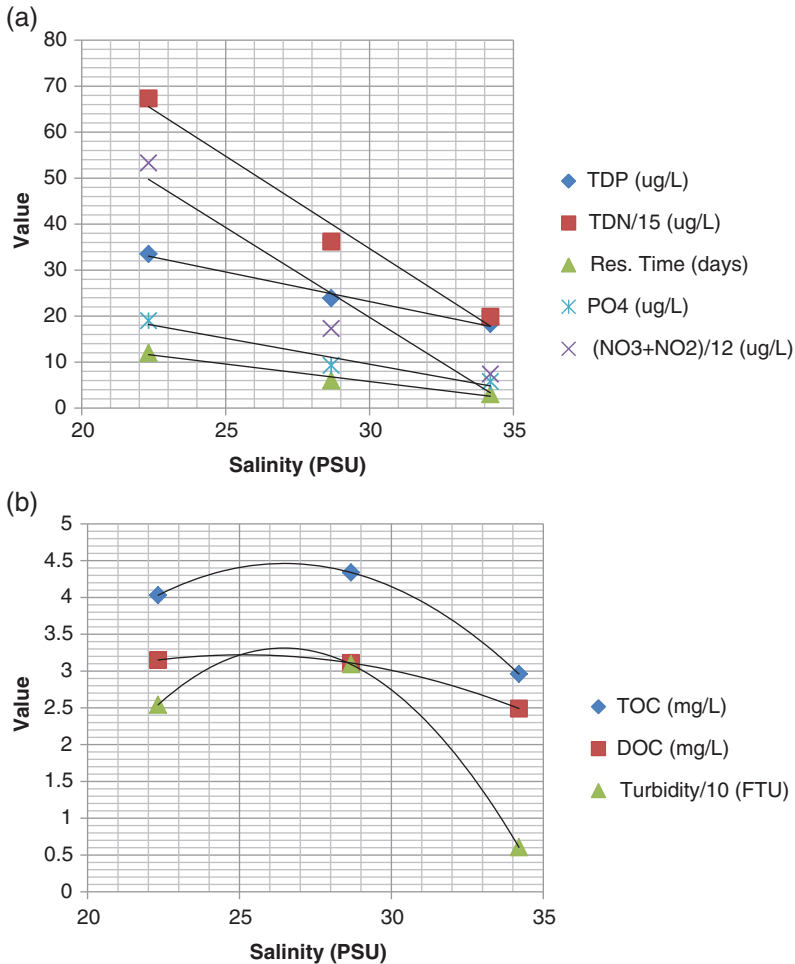


Figure 5. (a) Eight-year average concentrations of nutrients and residence times at Stations 1B, 6B and 14B plotted against 8-year average salinities. (b) Eight-year average total organic carbon (TOC), dissolved organic carbon (DOC), and turbidity in formazin turbidity units (FTU) at Stations 1B, 6B, and 14B plotted against 8-year average salinities.

primary process that controls their concentrations in the lagoon. Indeed, the lagoon is principally characterised by a strong NW–SE gradient, where nutrient-rich, low-salinity water from the north mixes with nutrient-poor, high-salinity water from the Adriatic Sea [26].

However, this does not mean that local effects are not evident at various locations within the lagoon, but rather that the rapid flushing and mixing that occurs tends to mask this information. Indeed, it can be seen in Figure 5a that nutrients at Station 6B lie below the mixing line, giving rise to high concentrations of particulates and dissolved organic matter (Figure 5b). Thus, although two-point mixing dominates the entire lagoon, it is still possible to develop independent environments within it.

Recent work [27] studied the distribution of hard bottom benthic communities in the lagoon. Three distinct communities were identified using a fuzzy clustering algorithm: a marine community, a confined community that coincided with the area adjoining the land, and an intermediate community with characteristics between the two others. Similar results were obtained by Tagliapietra et al. [28] using conventional cluster analysis. Earlier, a study named ICSEL [29] indicated that there was a substantial difference in the phytoplankton and micro- and mesozooplankton

populations at the extremes of the existing salinity gradient. The association of specific and different communities of organisms with their respectively different physico-chemical environments confirmed that for the past eight years the Venice Lagoon consisted of at least three major ecosystems.

2.2. Steady-states at smaller scales

Within the major features, differing ecological regimes based on local differences in physical forcing, bathymetry, distance from fresh water sources, etc., as well as sources of seeding organisms, will develop. Within a basin, different mini-environments become evident from consistent, long-term differences in temperature, salinity, residence time, nutrient content, chlorophyll *a* concentration, dissolved and particulate matter. Differing mini-environments must ultimately (at steady-state) lead to differences in the biota in both the water column and in the sediments and to distinct, sub-ecosystems within the larger, basin-wide ecosystem.

A screen capture of a Google Earth image of the Venice Lagoon is shown in Figure 2. The boundaries of the lagoon, with the historical city of Venice in the centre, are plainly visible. Because the average depth of the lagoon is only ~ 1.5 m, what mostly shows in the image is the colour of the lagoon floor. The differences in hue are due to differences in benthic coverings that result from local differences in circulation, residence times and differing inputs of freshwater and nutrients. The north, central, and southern portions, separated by the entrance canals, are quite distinguishable, as are smaller environments (inset). Again, these smaller systems within the lagoon must possess a degree of stability that allows their differences to persist. As already mentioned, this stability is a result of a number of processes or defences that have evolved over time. At steady-state, defences support stability, and in turn, stability supports defences, on all temporal and spatial scales.

Figure 6 shows a plot of the calculated residual currents that exist in the area of the Venice Lagoon (Figure 2). Residual currents represent the net difference between currents at ebb and flood tide. The residual circulation is not only primarily back and forth but the lagoon also contains many bathymetry-forced, large- and small-scale eddies, presumably all at steady-state. This supports

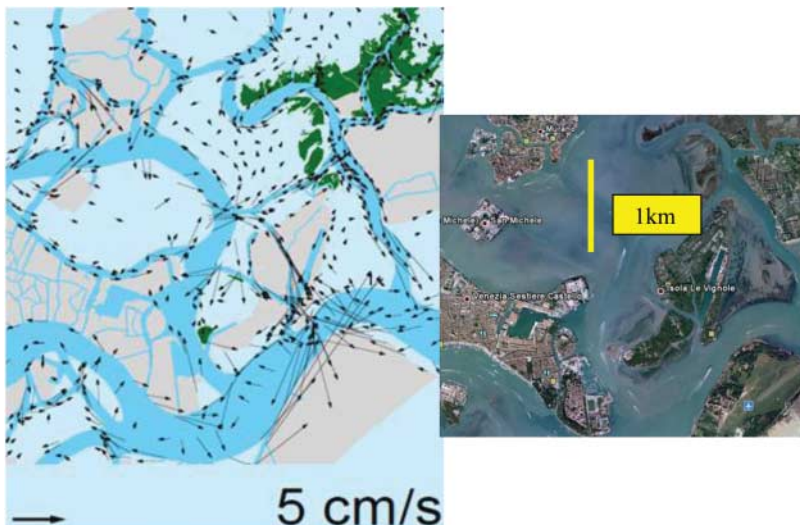


Figure 6. (Left) Structure of the residual circulation in the Venice Lagoon near the historical city of Venice calculated with a hydrodynamic model. (Right) Satellite view of same area (Figure 2).



Figure 7. Sediments from area SS0 were used to build banks V1 and V2 in areas SS1 and SS2.

the hypothesis that separate steady-state environments may occur at all spatial and temporal scales even in a very dynamic coastal environment [30].

2.3. *The SIOSED study and monitored natural recovery*

The SIOSED programme [31], carried out jointly by the Scripps Institution of Oceanography (La Jolla, CA, USA) and Tethys, S.p.A. (Venice, Italy) was essentially based on one specific field experiment. This consisted of ‘building sub-tidal banks using sediment containing the least concentrated range of contaminants (as reported by other programmes), and in monitoring the fate of those contaminants after dredging and transplanting the sediment’. The original location of the dredged sediment (SS0) and the locations of the new banks V1 and V2 placed on top of existing sediments SS1 and SS2, respectively, is shown in Figure 7. A significant observation made in that study was that ‘new’ banks were almost denuded of organisms, and colonised more in accordance with the sediment of their area of deposition (SS1 and S2) than with their area of origin (SS0). The initial effect of dredging and deposition lead to an initial dramatic reduction of organisms and biomass. This was attributed to the presence of ammonia and sulfides in the newly dredged sediments. After about a year, the constructed banks V1 and V2 had recovered, but differently, reflecting the disparities in their immediate physical environments. The complete development of colonisation appears to require several years [32].

The results of the SIOSED experiment confirm the principle behind an approved US EPA sediment recovery method known as monitored natural recovery (MNR).² Although MNR has mainly been applied to contaminated terrestrial sediments, the principles are the same: sediment from an area in which the drivers would cause it to reach a particular steady-state is exposed to drivers that would cause it to reach a different steady-state.

2.4. Toxicity

Evidence that the steady-state condition is defended by controlling toxicity is found in San Diego Bay, home port to many ships of the US Navy, which spend about 9 months each year tied to their respective piers. Copper from their antifouling paints continually leaches into the bay, and water column concentrations at certain locations in the bay often exceed the EPA-mandated limit of $3.1 \mu\text{g} \cdot \text{L}^{-1}$ (50 nM) [33]. Despite the steady influx of copper, water concentrations of this element over the last 20 years have not changed and the bay appears to be at steady-state [34]. Toxicity in the water column has not been detected. This has been attributed to the excess Cu CC of the water [20,35–37]. Complexation with ‘natural’ organic matter reduces the amount of free copper (the best indicator of Cu toxicity) to values of $\sim 10^{-12}$ to 10^{-13} M (pCu 12–13). pCu values below 11 are deemed potentially toxic [38].

2.5. Comparison of water column variables between San Diego Bay and the Venice Lagoon

The Venice Lagoon and San Diego Bay differ considerably in climate, size (but not depth) and freshwater input. Throughout the year, the Venice Lagoon receives moderate inputs of nutrient-laden freshwater from several rivers and canals, whereas there is almost no freshwater input into San Diego Bay between approximately April to November, and very little during the other months. Both basins may be considered to be at steady-state. The Venice Lagoon receives inputs of heavy metals and organic pollutants from the industrial area that surround it, whereas there is no known parallel input into San Diego Bay. The latter, however, is laden with Cu. Despite the physical differences, the hydrodynamic residence times from entrance(s) to the innermost locations of both basins are quite similar, e.g. 1 to 30–40 days. Table 1 shows average water column concentrations of common variables that are indices of water quality in the respective basins. Remarkable is that the while the macroconstituents (nutrients, alkalinity, chlorophyll *a*) in each basin differ as expected, with the Venice Lagoon having a much greater load, the concentrations of the microconstituents

Table 1. Typical concentrations of ecosystem variables in San Diego Bay and in the Venice Lagoon

Parameters	San Diego Bay ^a	Venice Lagoon ^b
Salinity (psu)	34.2	31.2
Oxygen (% saturation)	99	97.8
pH (SW scale)	7.9	8.07
TA ($\mu\text{eq} \cdot \text{kg}^{-1}$)	2400	3070
DOC ($\text{mg} \cdot \text{kg}^{-1}$)	1.3	2.85
TSS ($\text{mg} \cdot \text{kg}^{-1}$)	3.6	22.1
Chlorophyll <i>a</i> ($\mu\text{g} \cdot \text{kg}^{-1}$)	1.4	2.48
Phaeopigments ($\mu\text{g} \cdot \text{kg}^{-1}$)	0.9	7.68
NO ₃ (μM)	0.2	17.4
NO ₂ (μM)	0.05	0.53
NH ₃ (μM)	0.06	16.9
PO ₄ (μM)	0.6	0.31
CuCC ($\mu\text{g} \cdot \text{L}^{-1}$)	16	32 ^d
Cu ($\mu\text{g} \cdot \text{L}^{-1}$)	1.8 ^c	1.9
Zn ($\mu\text{g} \cdot \text{L}^{-1}$)	8 ^c	7.5
Pb ($\mu\text{g} \cdot \text{L}^{-1}$)	0.2 ^c	0.4
Cd ($\mu\text{g} \cdot \text{L}^{-1}$)	0.02 ^e	0.05

Note: TA, titration alkalinity; DOC, dissolved organic carbon; TSS, total suspended solids. ^aBay-wide average, 27 May 2001, $n = 27$. ^bLagoon-wide average, MELa 1 Data, September 2001 to August 2002, $n = 540$ [24]. ^c[43,44]. ^d[19]. ^e[Zirino, unpublished].

(Cu, Zn, Pb, Cd) are similar to each other and comparable to trace metal concentrations reported for San Francisco Bay [34,39], Narragansett Bay [40], and Galveston Bay [22]. From this, we may infer that the concentrations of macroconstituents are mostly regulated by their rate of input and degree of mixing, whereas the concentrations of the trace heavy metals are buffered by internal regulatory processes. Even though we do not have a comparative measure of the rate of input of the heavy metals in each basin, it is highly unlikely that they are uniformly equal everywhere. Again, this supports the existence of a defence mechanism that regulates the availability of potentially toxic microconstituents. It is not a new thought. In a seminal paper, Krauskopf [41] considered the concentration of 13 trace metals in seawater, and came to the conclusion that adsorption on particles and organic matter (with subsequent settling) controlled the water column concentrations of most of them. What is new here, is that we view the concentration-controlling processes holistically, as complex functions of all of the ecological drivers, and applicable to most trace substances.

3. Application to monitoring

In this work, we have taken the hierarchical view that the major drivers of coastal ecosystems must be at steady-state before the ecosystem itself can be at steady-state, and before smaller scale ecosystems can be at steady-state. Any significant change in one or more macrovariables constitutes a major perturbation to the overall ecosystem, and to the smaller ecosystems within it. However, perturbations on large spatial and short temporal scales are rare and, within reason, steady-states may be assumed. Once assumed, they must also be defined and tested across the applicable spatial and temporal scales. This can only be performed by frequent, periodic, monitoring.

In the European Union it is legislated that similar water bodies be compared and judgements be made as to their comparative ecological condition [5]. Rigorous comparisons of water bodies can only be done if they are at steady-state and if their steady-states are similarly defined. (A transitory state has no robustness and may have changed by the time the assessment is completed). Also, monitoring protocols should be standardised to encompass the features of the water bodies that one wishes to compare. Finally, the influence or irrelevance of ‘passengers’ on an ecosystem can only be quantitatively determined if the defences can also be evaluated. This may, in fact, portend new measurements.

Buffering defences cause the monitoring of macro- and microconstituents in the water column to yield only indirect or partial information about its health. For the purpose of foretelling ecosystem problems, it may be more fruitful to determine future status from changes in the direct inputs rather than the short-term *results* of inputs. It may also be more economical, given that many contaminants are generally introduced via freshwaters that, in general, are much more easy to analyse than seawater. Ecosystem managers should focus on controlling inputs above all else.

4. Conclusions

In summary, the limited field data support a model of a coastal ecosystem dominated by a few physical and biochemical chemical drivers in which organisms adapt and fill every trophic niche. Despite the highly dynamic setting provided by tidal flushing, on average, these drivers will lead to stable ecosystems, and smaller, but stable, mini-ecosystems. The drivers and the resulting defences are completely interdependent on all spatial and temporal scales. Figure 8 shows how an ecosystem might change over time, achieving steady-state between times of transition (perturbations). The time required to reach steady-state is a function of the scale of the perturbation and the type and number of organisms considered.

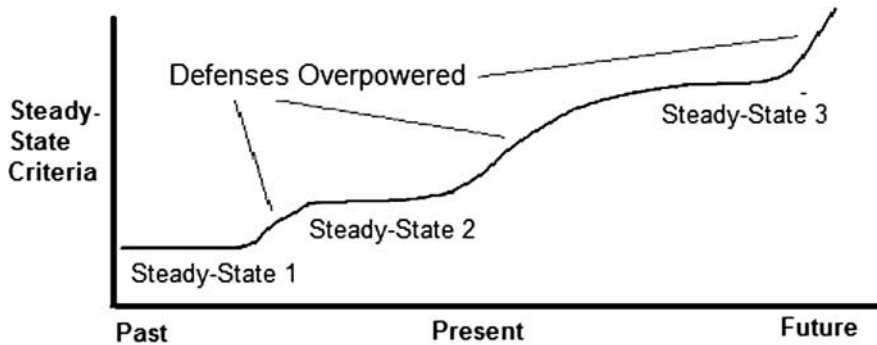


Figure 8. Evolution of temporal changes in a hypothetical ecosystem.

Because the defences of the ecosystem are tied to the supply of organic nutrients, productivity and toxicity are not independent. Severe toxicity will cause the defences to crumble and ultimately arrest productivity. Thus, it is important to be able to measure or assess quantitatively the available defences. Perhaps measurements of CC or the measurement of the colloid-pumping capacity are the first steps in this process.

Monitoring programmes should be designed to determine whether ecosystems are at steady-state (after defining the steady-state conditions) and comparative judgements of the ecological state of similar environments should also be done at steady-state.

Finally, current methods for assessing ecosystems do not take into account the steady-state, or the processes that maintain it. Therefore, they cannot assess the ‘robustness’ of ecosystems or their ability to resist change, for good or bad. The assessment of ecosystems could be improved by studying their inherent stability and by developing analytical methods for this purpose. Ecosystem computer models such as EPA’s AQUATOX [42] that include these defence processes may provide a low cost means of estimating the robustness of defences and assessing the impacts of contaminants.

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Notes

1. In chemistry, a steady-state is a condition in which all state variables are, *on average*, constant in spite of ongoing processes that strive to change them. Here we refer to an ecosystem as being at steady-state in the physico-chemical sense, e.g., small changes are permitted, but the system returns to the original condition. Furthermore, we differentiate steady-state from equilibrium, in that no source of energy is required to maintain equilibrium, while a continual input of energy (e.g., tidal action, in our case) is required to maintain the system at steady-state.
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