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### Response of diatom and dinoflagellate lifeforms to reduced phosphorus loading

Gowen, R. J.; Collos, Y.; Tett, P.; Scherer, C.; Bec, B.; Abadie, E.; Allen, M.; O'Brien, T.

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1                   **The response of diatom and dinoflagellate lifeforms to**  
2                   **reduced phosphorus loading: a case study in the Thau Lagoon**

3  
4   Gowen R J<sup>1\*</sup>, Y Collos<sup>2</sup>, Tett P<sup>3</sup>, Scherer C<sup>1</sup>, Bec B<sup>2</sup>, Abadie E<sup>4</sup>, Allen M<sup>5</sup>, O'Brien T<sup>6</sup>

5  
6   <sup>1</sup>Fisheries and Aquatic Ecosystems Branch, SAFSD, Agri-Food and Biosciences Institute,  
7   Belfast BT9 5PX UK

8   <sup>2</sup>Université Montpellier 2, CNRS, Ifremer, UMR 5119 Ecologie des Systèmes Marins  
9   Côtiers, CC093, 34095 Montpellier Cedex 5, France

10   <sup>3</sup>Scottish Association for Marine Science, Scottish Marine Institute, Oban, Argyll, PA37  
11   1QA, UK

12   <sup>4</sup>Ifremer, Laboratoire Environnement Ressources, BP 171, 34203 Sète, France

13   <sup>5</sup>Biometrics Information & Systems Branch, FCAD, Agri-Food and Biosciences Institute,  
14   Belfast, BT9 5PX, UK

15   <sup>6</sup>National Marine Fisheries Service, NOAA, Silver Spring, Maryland USA

16  
17  
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19   distance

20  
21   \*Corresponding Author.

22   *E-mail address:* [richard.gowen@afbini.gov.uk](mailto:richard.gowen@afbini.gov.uk) (R.J. Gowen)

23  
24  
25   **Abstract**

26  
27   The basin of Thau in southern France is a shallow, weakly flushed lagoon which is an  
28   important location for oyster cultivation. Phytoplankton analyses were carried out in 1975-  
29   1976 and then (almost) continuously since 1987. We report an investigation of 'the balance  
30   of organisms' in Thau phytoplankton in relation to reductions in phosphorus loading, using  
31   two new tools based on phytoplankton lifeforms: the Plankton Index for Phytoplankton (PIp);  
32   Euclidean distance in state space. Our results show the utility of the tools for analysing  
33   changes in the 'balance of organisms' at the level of functional groups (in our study diatoms  
34   and dinoflagellates) but also illustrate the difficulties in demonstrating the reversal of human  
35   impacts resulting from eutrophication.

36  
37   The comparison between 1987-89 and 1976 showed the expected 'de-eutrophication', with a  
38   decrease in dinoflagellate abundance. Since 1989, year to year variation in annual mean  
39   concentrations of dissolved inorganic phosphate (DIP) may have contributed to inter-annual  
40   variability in the balance of the two lifeforms, but the data suggest that the system has  
41   remained in a dynamically stable regime: (i) there was no long-term trend in Euclidean  
42   distance from the reference; (ii) there was no increase in inter-annual variability about the  
43   time-series mean Euclidean distance suggesting there has been no decrease in resilience  
44   which might signal the likelihood of a change in regime.

1 Integrated management of human activities will be required to manage (and reduce) total P in  
2 the system. Monitoring phytoplankton and nutrients concentrations to determine how primary  
3 production and the balance of species respond to further changes in the nutrient status of the  
4 lagoon should be an integral part of any management programme.  
5  
6

## 7 **1. Introduction**

8

9 Marine eutrophication is considered a recent problem (Nixon, 1995) but one that can  
10 potentially impact coastal water bodies world-wide and is of increasing severity (McIntyre,  
11 1995). There is evidence that anthropogenic nutrient enrichment of some Northern European  
12 coastal regions has increased phytoplankton biomass and production (Radach et al., 1990;  
13 Schaub and Gieskes, 1991; De Jonge et al., 1996; Gowen et al., 2000; Andersen et al., 2011;  
14 Ærtebjerg et al., 2001; Conley et al., 2002; Rousseau et al. eds, 2006). Cloern (2001) argued  
15 that coastal eutrophication involved more than the stimulation of primary production because  
16 the input of nutrients to coastal water bodies can disrupt the balance between the production  
17 and turnover of organic matter and alter the seasonality of ecosystem functions. Also of  
18 concern are changes in the floristic composition of the phytoplankton (Gillbricht, 1988;  
19 Lancelot et al., 2006) that can result in: “visible algal blooms, algal scum” (Vollenweider,  
20 1992); “the presence of noxious phytoplankton and bottom water anoxia” (Justic et al., 1995);  
21 the occurrence (including an increase in frequency, size and duration) of harmful algal  
22 blooms as has been the case in the Seto Inland Sea of Japan and Tolo Harbour Hong Kong  
23 (see Gowen et al., 2012A and references cited therein).  
24

25 In many countries, legislation has been introduced to mitigate anthropogenically driven  
26 coastal eutrophication. In addition to national legislation, the 28 member states of the  
27 European Union are subject to EU directives. In 2004, the European Court of Justice ruled  
28 (Case C-280/02: <http://curia.europa.eu>) that the ‘Thau lake’, a shallow lagoon in southern

1 France, should be 'identified as an area sensitive to eutrophication within the meaning of  
2 Directive 91/271' (the Urban Waste Water Treatment Directive, CEC, 1991). This directive  
3 (see also Ferreira et al., 2011) defines eutrophication as a process culminating in an  
4 undesirable disturbance to the balance of organisms and to the quality of the water concerned.  
5 Stimulation of the growth of one or more phytoplankton species is considered a disturbance  
6 and that of a nuisance or harmful species undesirable. However, the populations of species  
7 that make up the phytoplankton are not constant in time or space (Gowen et al., 2012B) and  
8 against this background of natural variability, quantifying a disturbance to the balance of  
9 organisms is not a trivial task.

10

11 The Thau Lagoon is a small (75 km<sup>2</sup>) marine lagoon located on the French Mediterranean  
12 coast (Figure 1). The lagoon is shallow (mean depth 4m) and is connected to the sea by 3  
13 narrow channels. Approximately 10% of French oyster (*Crassostrea gigas*) production takes  
14 place in the lagoon. Picot et al (1990) reported the production to be 20,000 tonnes per year. A  
15 number of studies suggest that the lagoon is a predominantly nitrogen (N) limited system  
16 (Collos et al., 1997; Souchu et al., 1998, 2001; Bec et al., 2005). There is an input of N via  
17 freshwater inflow during the winter which supports phytoplankton growth and sometimes  
18 leads to DIP limitation (Collos et al., 2014), but during the spring and summer the input of N  
19 via freshwater inflow is low. The nutrient dynamics of the lagoon are complicated by anoxic  
20 events which promote the sediment efflux of nutrients which support enhanced  
21 phytoplankton production. During one such event during the summer of 1994, Souchu et al.  
22 (1998) measured maximum bottom water concentrations of 24.0 µM ammonium (NH<sub>4</sub>), 5.0  
23 µM (DIP) and 57.0 µM silicate (Si). Phytoplankton biomass measured as chlorophyll  
24 concentration reached 10 and 15 mg m<sup>-3</sup> in surface (1m) and bottom (8m) water respectively.

1 Since the 1960s there has been a programme to reduce anthropogenic waste input to the  
2 lagoon. A gradual increase in the number of houses connected to waste water treatment  
3 culminated in approximately 95 % of houses in the catchment having been connected by  
4 1990 (La Jeunesse and Elliott, 2004). The installation of a waste water treatment plant for the  
5 city of Sète in 1972 which was designed to divert waste water from the lagoon, the  
6 introduction of activated sludge treatment between 1975 and 1987 and the establishment of a  
7 French national limit on phosphorus (P) in detergent in 1990, have collectively contributed to  
8 the reduction in P loading to the lagoon (Souchu et al., 1998, La Jeunesse and Elliott, 2004).  
9 Water-column concentrations of DIP have decreased by 90% between 1971 and 1994 (La  
10 Jeunesse and Elliott, 2004). The reductions in domestic N and P loading were expected to  
11 have brought about a reduction in bacterial biomass and anoxic events (which caused  
12 mortality of oysters) in the Thau Lagoon. Thirty years later, that particular goal was reached  
13 (Souchu et al., 1998) but one unexpected consequence was the emergence of  
14 picocyanobacteria and the toxic dinoflagellate *Alexandrium catenella* (Collos et al., 2009).  
15 In this paper we report an investigation of this 'balance of organisms' using two new tools.  
16 One tool, the Plankton Index for Phytoplankton (PIp) is derived from the Phytoplankton  
17 Community Index of Tett et al. (2008). The second involves the calculation of Euclidean  
18 distance in state space (Tett et al., 2013). There are few records of phytoplankton  
19 composition before nutrient enrichment of the lagoon and so we did not initially hypothesize  
20 what the 'natural balance' would be like. Instead, the study focussed on change over the  
21 period of data availability.

22

## 23 **2. Methods**

### 24 2.1 Data sets

1 The data sets used in the study are summarised in Table 1. Diatom and dinoflagellate  
2 abundance data were taken from phytoplankton counts from Hénard (1978) for the years  
3 1975-1976 and from the French REPHY monitoring programme:  
4 ([http://envlit.ifremer.fr/surveillance/phytoplankton\\_phycotoxines](http://envlit.ifremer.fr/surveillance/phytoplankton_phycotoxines)) from 1987 and onwards.  
5 Annual mean water temperature and DIP concentrations are from Souchu et al. (1998),  
6 Collos et al. (2009) and from the REPHY monitoring programme. Annual mean  
7 concentrations of DIP were derived from monthly values. The silicate data are  
8 from: <http://envlit.ifremer.fr/documents/bulletins/rno> and the oyster data from Deslous-Paoli  
9 et al. (1998).

10

11 Regular phytoplankton analyses were carried out in 1975-1976 and after a ten year gap  
12 almost continuously since 1987. Both the Plankton Index for Phytoplankton and the  
13 Euclidean distance tools require a reference condition which should ideally include several  
14 years, to account for the short-term inter-annual variation, so we chose the first three years  
15 (1987-89) of the continuously-sampled period. This allowed us to make: (i) a backwards  
16 comparison with the 1970s data; (ii) a forward comparison with more recent data (1990 to  
17 2009) to identify any trend in the more recent data.

18

## 19 2.2 Lifeform and state-space tools

20 The concept of phytoplankton lifeforms was developed by Margalef (1978) (see also Pingree  
21 et al., 1978; Bowman et al., 1981; Jones and Gowen, 1990), each lifeform being considered a  
22 different set of adaptations to survival in a turbulent environment. This is a perspective that  
23 starts from species, but recent ecological theory (Folke et al., 2004; Hooper et al., 2005) is  
24 tending to the view that it is functional diversity rather than species diversity that underpins  
25 the operation and resilience of ecosystems. Lifeforms are, in principle, units of ecosystem

1 functional diversity and a lifeform can be defined as: a group of species (not necessarily  
2 taxonomically related) that carry out the same important functional role in the marine  
3 ecosystem. Monitoring changes in lifeform abundances thus provides a means to monitor  
4 changes in the organization of plankton communities which in our opinion should be taken  
5 into account when assessing the response of the planktonic component of the pelagic  
6 ecosystem to anthropogenic pressure. The term 'organization' derives from [Costanza \(1992\)](#)  
7 and [Mageau et al. \(1995\)](#), who use it to label the trophic and biogeochemical connections  
8 amongst ecosystem components, in distinction from 'vigour', the flow of energy and  
9 materials through ecosystems that maintains their organization. In the case of terrestrial and  
10 benthic communities, spatial arrangements should, we think, be seen as part of organization;  
11 in the case of pelagic communities, we consider that the seasonal succession of lifeforms  
12 makes an analogous contribution and so needs to be taken into account by methods for  
13 tracking change in ecosystem state.

14

15 Based on General Systems Theory ([von Bertalanffy, 1968](#)), [Tett et al. \(2008\)](#) proposed to  
16 track changes in the state of the phytoplankton community by means of plots in a state-space  
17 and calculating a Plankton Community Index (referred to here as a Plankton Index, PI). The  
18 conceptual framework ([Tett et al., 2013](#)) is that ecosystems can be viewed as systems with an  
19 instantaneous state defined by values of a set of system state variables which are attributes of  
20 the system that change with time in response to each other and external conditions. Our  
21 method assumes that the abundances of lifeforms of pelagic micro-algae are suitable  
22 variables to provide coordinates that define system state in multidimensional 'lifeform state  
23 space', and in principle the mathematical treatments we use can be generalised to multiple  
24 dimensions. In practice it is difficult to visualise graphs in more than 3 dimensions, and so we

1 suggest the use of 2-D plots leading to values of Plankton Indices that can be combined by  
2 simple averaging.

3

4 In the present work we use the abundances of two lifeforms, diatoms and dinoflagellates, to  
5 define axes in a state space of 2 dimensions, corresponding to a Cartesian co-ordinate system  
6 in which each point in a plane is specified uniquely by a pair of numerical coordinates. The  
7 main genera and species (and size ranges) that made up the two lifeforms are given in Table  
8 2. Matlab™ scripts with accessory functions were written to generate the state space plots  
9 and calculate values of (in this case) the Plankton Index for phytoplankton (PIp). An  
10 ecosystem state can be defined as a single point in state-space, with co-ordinates provided by  
11 the values of the set of state variables - i.e. by lifeform abundances. A trajectory connects two  
12 or more points. Such trajectories often show several components of variability: (i) cyclic; (ii)  
13 medium-term; and (iii) long term. In the case of temperate latitude plankton the first can be  
14 interpreted as seasonal variation and thus as part of community organization. Both (i) and (ii)  
15 can be seen in terms of systems theory as movement around an attractor or within a basin of  
16 attraction (Holling, 1973) corresponding to a particular regime (or group of states and  
17 trajectories) of the ecosystem. Long term variability (iii) may show a persistent trend of  
18 movement away from a starting point in state space.

19

20 Given the seasonal nature of plankton production and the succession of species, and assuming  
21 approximately constant external pressures, the data collected from a particular location over a  
22 period of years forms a cloud of points in state-space: a regime. Such regimes can be defined  
23 by drawing an envelope around the group of points, using a convex hull method (Sunday,  
24 2004; Weisstein, 2006). Because of theoretical arguments (see Tett, 2014) that the envelope



1 should be 'doughnut' shaped with a central hole, bounding curves can be fitted outside and  
2 inside the cloud of points.

3

4 Both the Plankton Index and the Euclidean distance (see below) tools require a reference  
5 condition against which change can be quantified. This should ideally include several years  
6 of data to account for short-term inter-annual variation. Here the term 'reference' is used  
7 simply to denote the data set against which comparisons will be made and does not imply  
8 pristine conditions. Tett et al. (2008) found that the size and shape of the envelope was  
9 sensitive to sampling frequency and the total numbers of samples. Large envelopes generated  
10 by including extreme outer or inner points are less sensitive to change in the distribution of  
11 points in state space and therefore to detecting a change in condition. Conversely, if the  
12 envelope is made smaller by excluding too many points, even minor changes will be  
13 statistically significant. We decided to include a proportion ( $p = 0.9$ ) of the points: with 5%  
14 of points that were most distant from the cloud's centre, and 5% of points that were closest to  
15 the centre excluded.

16

17 The index is based on a comparison between the reference envelope and a new set of data by  
18 plotting the latter onto the reference envelope and is calculated as the ratio of new points  
19 inside the envelope (or to be precise, between the inner and outer envelopes) to the total  
20 number of new points. The maximum value of the index which can be calculated is 1 which  
21 indicates no change. The minimum value, 0 indicates a complete change (i.e. all new points  
22 fall outside of the reference envelope). In fact, since the reference envelope included only  
23 proportion  $p$  of the reference data, a PI $_p$  value of  $p$  also indicated no change. Statistical  
24 significance was assessed by an exact binomial calculation of the probability of getting a  
25 value of the PI $_p$  given  $n$  (new points) and  $p$ . The software and mode details of the method are

1 available from: [www.sams.ac.uk/paul-tett](http://www.sams.ac.uk/paul-tett).

2

3 In the Thau Lagoon, regular phytoplankton analyses were carried out in 1975-1976 and after  
4 a ten year gap almost continuously since 1987. We therefore selected the first three years  
5 (1987-89) of the continuously-sampled period as the reference which provided 39 pairs of  
6 data. This allowed us to make: (i) a backwards comparison with the eutrophic conditions of  
7 the 1970s; and (ii) a forward comparison with more recent data (1990 to 2009), to identify  
8 any trend in the more recent data. For the backwards comparison 22 new points were  
9 compared with the reference envelope. Forward comparisons, between the reference period  
10 and data collected between 1990 and 2009, was made by re-plotting the reference envelope  
11 and adding n new points for each year of data, to calculate a value of the index for each year  
12 and generate a time-series.

13

## 14 2.2 The Euclidean distance method

15

16 The state-space approach was also used for an Euclidean distance method, which provided a  
17 means of quantifying system variability as well as estimating a trend away from a starting  
18 point in state space. The Euclidian distance is a positive scalar, the square root of the sum of  
19 squares of movement along each axis of the state space. Logarithmic transformation of the  
20 original co-ordinates avoids the calculated distance being dominated by any one axis. The  
21 conceptual framework for this method was presented by [Tett et al. \(2013\)](#) and is based on  
22 [Scheffer et al. \(2009\)](#) and [Scheffer \(2010\)](#) who proposed that increased variability was a sign  
23 of decreasing system resilience, and would thus give an early warning of regime shift. Tett et  
24 al. (2013) suggested that an ecosystem close to a regime shift could be viewed as being  
25 pulled in several directions by ‘attractors’ for the old and new regimes, hence the increase in

1 variability as a tipping point was approached; they suggested using medium-term variability  
2 as a proxy for (inverse) resilience.

3

4 We applied this method to the 1988-2009 data from the Thau Lagoon. The annual median  
5 (base 10 logarithmic) abundance of each lifeform was plotted in 2D state space, and a time-  
6 series was calculated of the Euclidean distance of each annual median from the 1987-1989  
7 reference point in state space. Like Tett et al. (2013), we evaluated medium-term variability  
8 as the scatter of annual values of the distance about a low-order polynomial fitted to the  
9 Euclidian distance time-series.

10

11

12

13

### 14 2.3 Time-series and cross correlation analysis

15

16 Each time series was screened for autocorrelation and where necessary an appropriate model  
17 applied to induce stationarity before cross-correlating to detect significant lags. If a model  
18 was applied to a time series prior to cross-correlation, the model's residuals were used in the  
19 cross-correlation analysis. The Mann-Kendal (M-K) test for monotonic trends (Hirsch and  
20 Slack, 1984) and regression analysis were applied to the raw data. For the latter, year and  
21 year<sup>2</sup> was fitted as the explanatory variable and the Thau Lagoon time series as the response,  
22 to detect linear and non-linear trends, respectively. The regression residuals were assessed for  
23 non-normality and stationarity. The Run's Test for Randomness was applied to each time  
24 series to assess if the time-series was randomly fluctuating about the mean of the time-series.

25

1 For the forward comparison between the reference data with more recent data, PIP (the output  
2 time series), was cross-correlated with the pressure variables (the input time series), to detect  
3 lagged responses. Cross correlation was based on year to year variation and not on long-term  
4 trends. It was assumed that the relationship was one-sided and feedback mechanisms were  
5 not investigated.

6  
7  
8

### 9 **3. Results**

10 The time-series of annual mean water temperature and oyster biomass were non-stationary.  
11 Stationarity was induced by applying an auto-regression AR(1) model to the temperature data  
12 and an AR(2) model to the Oyster biomass data before further analysis. The time-series on  
13 annual median DIP concentration was stationary. There were too many gaps in the silicate  
14 time-series for analysis although the data suggest that there has not been a long-term change  
15 in the concentration in the lagoon (Figure 2D). For the other three variables, there were  
16 significant trends in the time-series: non-linear for annual mean water temperature and oyster  
17 biomass and linear for the annual mean concentration of DIP. Annual mean water  
18 temperature increased from 14.8 °C (1974-1976 mean) to a 2008-2010 mean of 15.6 °C. The  
19 annual mean concentration of DIP and concentrations from which annual means were derived  
20 are shown in Figure 2B. The annual mean decreased from a 1975-1976 value of 2.96 µM  
21 (range 0.66-7.92 µM, n = 24) to a mean 1987-1989 concentration of 1.51 µM (range 0.20-  
22 2.80 µM, n = 27) and a 2002-2003 mean concentration of 0.47 µM (range 0.08-0.86 µM, n =  
23 21) Over the time-series, oyster biomass increased from a mean (1970-1972) stock of 2300t  
24 to a maximum of 19,000t in 1987. Thereafter biomass was 12,500t (mean 1999-2001). No  
25 significant (year to year) cross correlations between the PIP and annual mean water

1 temperature or oyster biomass were identified but the correlation between the PIP and annual  
2 mean DIP was significant ( $P < 0.05$ ) with a positively lag of zero.

3

4 For the backwards comparison between the reference period and eutrophic conditions of the  
5 1970s, the 2D diatom and dinoflagellate state space plot was constructed for the reference  
6 years 1987-1989 (Figure 3A). In Figure 3B, the 1970s data have been plotted onto the  
7 reference plot and shows that dinoflagellate abundance was much higher in the 1970s. The  
8 two data sets were significantly different (binomial probability  $P \ll 0.001$ ). For the forward  
9 comparison, between the reference conditions and data collected between 1990 and 2011, the  
10 index appeared to show a downward trend (Figure 4). However, time-series analysis showed  
11 that this was not significant and annual values fluctuated randomly (Run's Test:  $P > 0.05$ )  
12 about the time-series mean value of 0.62.

13

14 Plotting annual median values of each lifeform in diatom-dinoflagellate state space (Figure 5)  
15 shows that there was considerable inter-annual variability. For example, the co-ordinates for  
16 1993 approached those for 1975/1976 and the years 1997 and 2000 had high diatom  
17 abundance relative to the median reference condition. Analysis of the time-series of  
18 Euclidean distance (Figure 6A) shows that there was no long-term trend and annual values  
19 fluctuated randomly (Run's Test:  $P > 0.05$ ) about the time-series mean of 0.58. Furthermore,  
20 there was no long-term trend in the annual deviation from the time-series mean (Figure 6B).

21

## 22 **4. Discussion**

23 Previous studies of the Thau Lagoon (Vaquer et al., 1996; Collos et al., 2009) have reported  
24 changes in the abundances of particular species or genera, such as *Alexandrium catenella* and  
25 *Skeletonema costatum*, and tried to interpret these in relation to natural and anthropogenic

1 environmental change. It is, however, difficult to reach firm conclusions given the  
2 complexity of change at this level of analysis. Our approach, in the present paper, has been at  
3 the level of functional groups, and our results show the utility of the lifeform and state-space  
4 tools for analysing change in the 'balance of organisms' at this level. The Plankton Index  
5 comparison between 1987-89 and 1976 (Figure 3) shows more dinoflagellates in 1976  
6 compared with the 1987-89 reference, and seems to confirm the expected 'de-eutrophication'  
7 in the 1980s. Furthermore, the significant positive cross (year to year) correlation between  
8 PIp and annual mean DIP concentration between 1988 and 2007, suggests that the balance of  
9 organisms in the phytoplankton did respond to changes in water column DIP. However, the  
10 results also demonstrate the difficulties in clearly demonstrating the reversal of human impact  
11 resulting from coastal eutrophication. Crucially the lack of phytoplankton data between 1977  
12 and 1987 makes investigation of the likely cause of the observed changes difficult.

13

14 It could be argued that the absence of a significant long-term trend in PIp after 1989 simply  
15 indicates that by that year, water-column DIP concentrations (Figure 2B) were already below  
16 a critical level. In other words, the lagoon had already shifted from the 1970s 'eutrophicated'  
17 regime with high DIP, to the 'moderately eutrophicated' regime that was diagnosed by Collos  
18 et al. (2009) for the period 1998-2003. Thus, although the year to year variation in the annual  
19 mean concentration of P may have contributed to the inter-annual variability in the balance of  
20 the two lifeforms as shown in the plot of medians in state-space (Figure 5), the results of our  
21 analysis suggest that, the system has remained (since 1989) in a dynamically stable regime.  
22 First, there was no long-term trend in Euclidean distance from the reference condition (Figure  
23 6A). Second, there was no increase in inter-annual variability about the time-series mean  
24 Euclidean distance (Figure 6B). Based on Scheffer et al. (2009), Tett et al. (2013) suggested  
25 that such variability may serve as a proxy for inverse ecosystem resilience Thus, the absence

1 of long-term trends in this variability suggests there has been no change in resilience such as  
2 that which might signal a change in ecosystem regime.

3

4 There was much inter-annual variability in the abundance of the two lifeforms. This may in  
5 part have been due to the year to year variation in concentrations of DIP but the similarity in  
6 dinoflagellate abundance in 1993 and 1976 and diatom abundance in 1997 and 2000 (Figure  
7 5) suggests that factors other than concentrations of DIP may be involved. It is evident that  
8 differences between the high and low DIP regimes include more than a reduction in  
9 phosphorus loading to the lagoon. Pressure variables for which we have data include  
10 increasing temperatures (Figure 2A) which may favour the growth of picocyanobacteria  
11 (Collos et al., 2009), higher oyster biomass (Figure 2C) which can exert a differential grazing  
12 pressure on different size classes of phytoplankton (Vaquer et al., 1996) and dissolved silica  
13 (Figure 2D) which appears not to have changed much over the time-series. Unknowns  
14 include nitrogen loading (probably decreasing; see Tournoud et al., 2006), flushing rates, and  
15 the phytoplankton flora in the Mediterranean outside the lagoon.

16

17 Although the comparison between 1975-76 and 1987-89 indicates that there was a shift in the  
18 balance of the two lifeforms, this does not appear to have influenced the main human use of  
19 the lagoon, namely oyster production. In contrast, one possible consequence of the reduction  
20 in water column concentrations of DIP (in combination with the increase in water  
21 temperature) for ecosystem services is the sudden appearance of picocyanobacteria (mostly  
22 species of *Synechococcus*) and the saxitoxin producing mixotrophic dinoflagellate  
23 *Alexandrium catenella* during the early 1990s. *Alexandrium* counts have been included in the  
24 abundances of the dinoflagellate lifeform, and there seems reliable evidence (from  
25 microscopic analyses) that *A. catenella* was absent or rare before this time.

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According to Collos et al. (2009) *Synechococcus* is thought to have emerged in Thau lagoon following oligotrophication (especially the reduction in P) and increasing water temperatures. During the hot summers of 2003 and 2006, when record *Synechococcus* cell numbers were observed, cell abundances of dominant diatom species such as *Chaetoceros* spp., *Skeletonema* spp., *Leptocylindrus danicus* and *L. minimus* were reduced by a factor of 2 to ten relative to those during the cooler summers of 2004 or 2005. In contrast, the diatom *Ceratoneis closterium* was absent in those summers. Concerning dinoflagellates, *Alexandrium catenella* was probably stimulated by *Synechococcus* as a food source (Collos et al., 2009). Other dinoflagellates such as *Gyrodinium spirale* and *Protoperidinium bipes* were absent during the hot summers. But over the time-series, the presence of *Synechococcus* does not seem to have displaced other phytoplankters in the lagoon (Figure 7).

Collos et al. (2009) hypothesized that species of picocyanobacteria were better able to exploit the low DIP and warmer water temperature conditions than other phytoplankters and may have provided an additional N source for the mixotrophic dinoflagellate. This and other examples of what might be considered as ‘unforeseen’ consequences of nutrient management, (e.g. harmful algal blooms in the Seto Inland Sea of Japan of *Alexandrium tamarense* and *Gymnodinium catenatum*, both able to utilize dissolved organic phosphorus, Yamamoto et al., 2002) exemplify the difficulty faced when attempting to manage nutrient loadings with the expectation of achieving a particular target such as minimising the risk of harmful algal blooms or returning the balance of organisms to a notional pristine state in which diatoms dominate. Interestingly, the emergence of *Synechococcus* spp. and *Alexandrium catenella*, both of which have caused major problems in the Thau lagoon in terms of economics and



1 human health (Lilly et al., 2002; Masseret et al., 2013), does not seem to have had an impact  
2 on phytoplankton biodiversity.

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4 Although our analysis suggests that with respect to diatoms and dinoflagellates, the system  
5 has remained in a dynamically stable regime since 1989, continuation of the current  
6 anthropogenic waste management policy could result in a shift to a third regime which has  
7 implications for the future productivity of the lagoon and shellfish production. Souchu et al.  
8 (1998) suggested that the 'drastic reductions in nutrient inputs could lead to a decline in  
9 primary production in the Thau Lagoon'. According to La Jeunesse and Elliott (2004) there  
10 was a substantial P reservoir (>3000 tonnes) stored in the top 5 cm of sediment in the early  
11 1990s with ~250 tonnes mobilized each year, although a future reduction in the frequency  
12 and intensity of anoxic events (Souchu et al., 1998) is likely to influence the internal cycling  
13 of P and other nutrients in the lagoon. Losses of P from the system include ~12 t yr<sup>-1</sup> in  
14 harvested shellfish and an unknown amount by flushing of the lagoon by Mediterranean  
15 seawater. Nevertheless, the budget presented by La Jeunesse and Elliott (2004) suggests that  
16 annual (mainly anthropogenic) loads continue to exceed annual losses and further reductions  
17 in anthropogenic loading (and perhaps increased flushing) may be required to turn the budget  
18 negative and so begin reductions in the total P in the system. Finally, although there has been  
19 an expensive investment in reducing anthropogenic waste input to the lagoon, and much  
20 study, the current scientific evidence is insufficient to evaluate the prospects for a return of  
21 the 'balance of organisms' to something like an unperturbed state. Clearly, it is highly  
22 desirable that monitoring of phytoplankton lifeforms and of the concentrations of nutrients in  
23 the lagoon continues in order to determine how phytoplankton production and the balance of  
24 species respond to further changes in the nutrient status of the Thau Lagoon.

25

1 **5. Acknowledgements**

2 The work presented in this paper was supported in part by SCOR (SCOR WG 137: Global  
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1 Table 1. A summary of the data sets used in the analysis. (The annual phosphate data were  
 2 derived from a minimum of 6 monthly values spread over the year).

Variable	Time series	Notes
Diatom abundance (cells L <sup>-1</sup> )	1975-1976 and 1987-2009	1977-1985 data missing
Dinoflagellate abundance (cells L <sup>-1</sup> )	1975-1976 and 1987-2009	1977-1985 data missing
Annual mean water temperature (°C)	1972 – 2010	(1973 and 1984 missing)
Annual mean phosphate (µM)	1972 - 2007	Annual values missing (only 10 values between 1987 and 2007)
Annual Oyster stock (tonnes)	1960 and 1970 - 2001	1993-1997 data missing: mean 1990-1992 used 2002-2007 data missing: mean 1999-2001 used

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1 Table 2.

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3 Table 2. The important (abundant) genera and species of phytoplankton contributing to the  
4 lifeforms used in this paper. The size classes are: large = >20µm equivalent spherical  
5 diameter (taking account of chains of **typical length?**); medium = 5-20 µm ESD (taking  
6 account of **chain formation**); small = 2.5 µm ESD. The reference source for taxonomic names  
7 is the World Register of Marine Species (WoRMS <http://marinespecies.org/>). <sup>1</sup>previously  
8 *Cylindrotheca closterium*; <sup>2</sup>previously known as *Prorocentrum minimum*.  
9

Lifeform	Species	Size range
Diatoms	<i>Asterionellopsis glacialis</i>	
	<i>Chaetoceros</i> spp.	
	<i>Ceratoneis closterium</i> <sup>1</sup>	
	<i>Dactyliosolen fragilissimus</i>	
	<i>Ditylum</i> spp.	
	<i>Guinardia striata</i>	
	<i>Leptocylindrus danicus</i>	
	<i>Leptocylindrus minimus</i>	
	<i>Nitzschia</i> spp.	
	<i>Pseudo-nitzschia</i> spp.	
	<i>Rhizosolenia</i> spp.	
	<i>Rhizosolenia pungens/setigera</i> complex	
	<i>Skeletonema</i> spp.	
	<i>Thalassionema nitzschioides</i>	
	<i>Thalassiosira</i> spp.	
	<i>Thalassiosira</i> spp.	
Dinoflagellates	<i>Alexandrium catenella/tamarense</i> species complex	
	<i>Dinophysis acuminata</i>	
	<i>Dinophysis sacculus</i>	
	<i>Gyrodinium spirale</i>	
	<i>Heterocapsa triquetra</i>	
	<i>Peridinium quinquecorne</i>	
	<i>Prorocentrum cordatum</i> <sup>2</sup>	
	<i>Protoperidinium bipes</i>	

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1 Figure legends

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3 Figure 1. A map of the Thau Lagoon in southern France.

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5 Figure 2. Time-series of Thau Lagoon data. A) annual mean water temperature (°C) 1972-  
6 2009; B) Concentrations ( $\mu\text{M}$ ) of dissolved inorganic phosphate (DIP) 1972-2007 (open  
7 circles individual sample concentrations, filled circles and dashed line annual mean  
8 concentration; C) standing stock (tonnes) of oysters (*Crassostrea gigas*) 1996-2001; D)  
9 concentrations ( $\mu\text{M}$ ) of silicate 1975-2003.

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11 Figure 3. Diatom and dinoflagellate state space envelopes. A) For the reference period 1987-  
12 1989; B) The 1975-1976 data plotted into the reference envelope.

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14 Figure 4. The time-series of the Plankton Index for phytoplankton (PIp).

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16 Figure 5. A 2D state space plot of the annual median values of  $\text{Log}_{10}$  diatom and  
17 dinoflagellate abundance.

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19 Figure 6. Time-series of Euclidean distance. A) The Euclidean distance of each year from the  
20 reference (1987-1989) point; B) the annual deviation from the time-series mean Euclidean  
21 distance.

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23 Figure 7. State space plot of median monthly abundances of three lifeforms in Thau lagoon  
24 during Jun, July and August of each year. This plot adds picocyanobacterial abundance,  
25 determined by flow cytometer, to that of diatom and dinoflagellate abundances determined by  
26 microscopic analysis. Adequate flow cytometer data were available from 1992-1994 and then  
27 from 1999 onwards. The 'shadows' on the walls of the 3-D plot show change in each pair of  
28 2-D spaces: for example, the left-hand back wall plots change in logarithmic median diatom  
29 abundance against change in logarithmic median cyanobacterial abundance. Drawn using  
30 Matlab TM 'plot3' function with additional code for the shadows (available on request).

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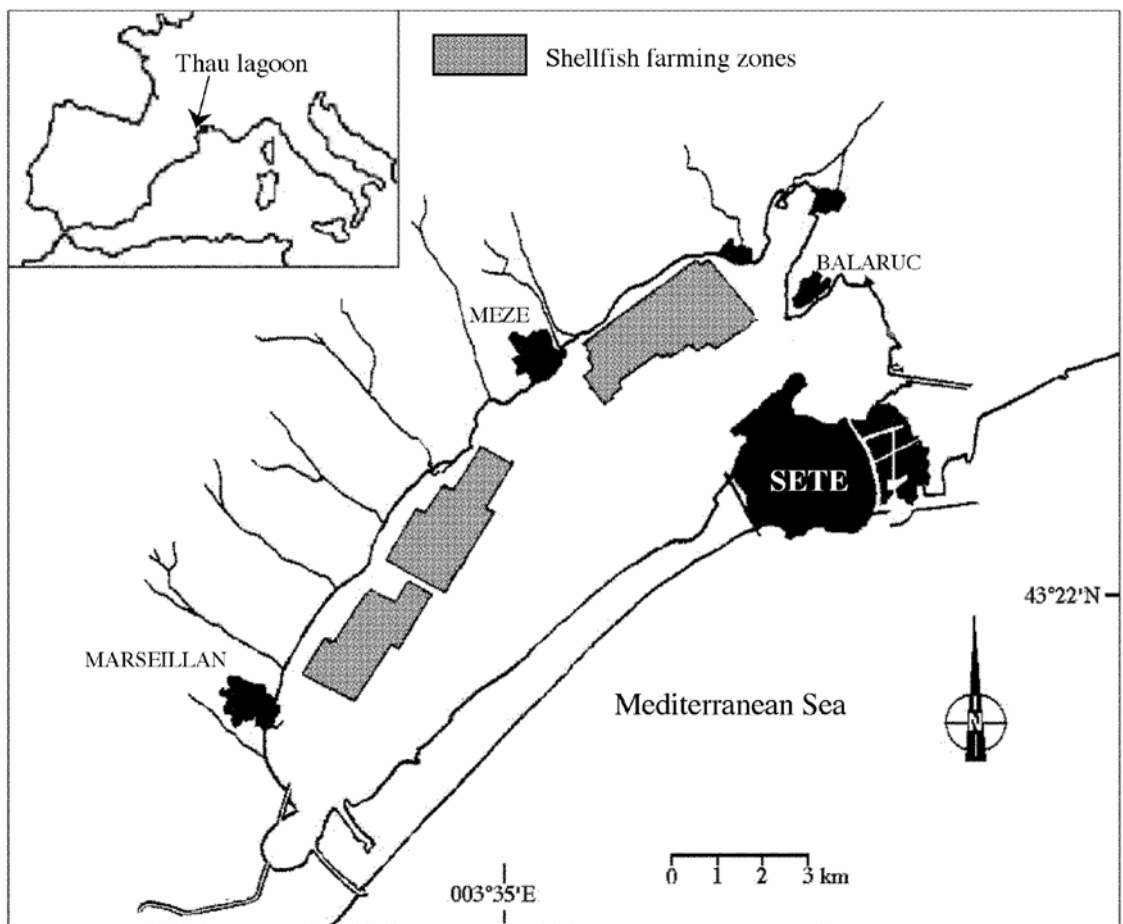
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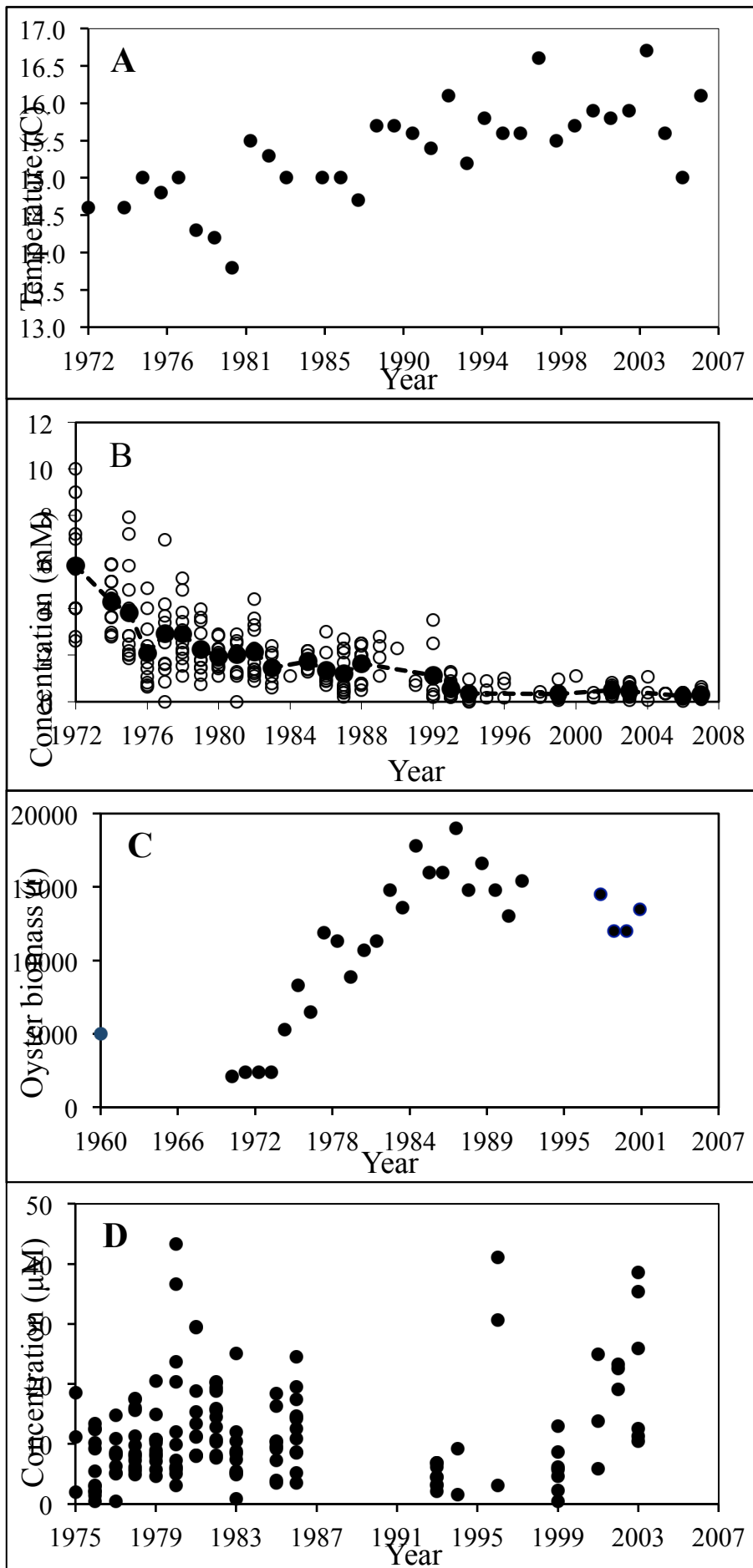
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Fig. 2



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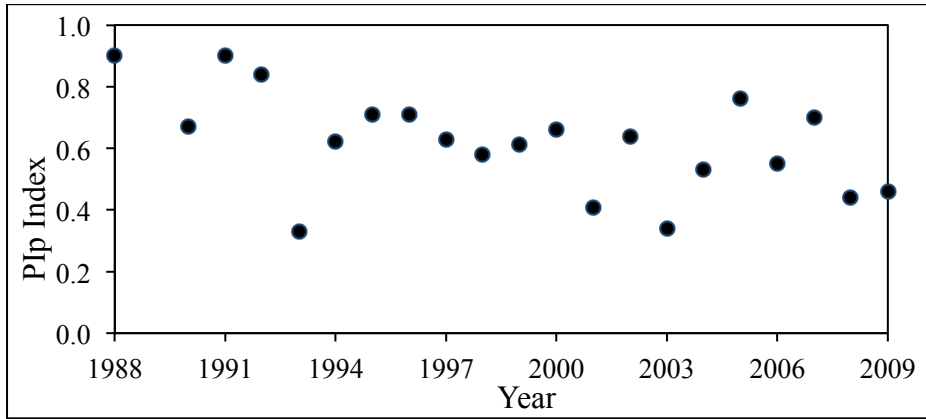
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Fig 4



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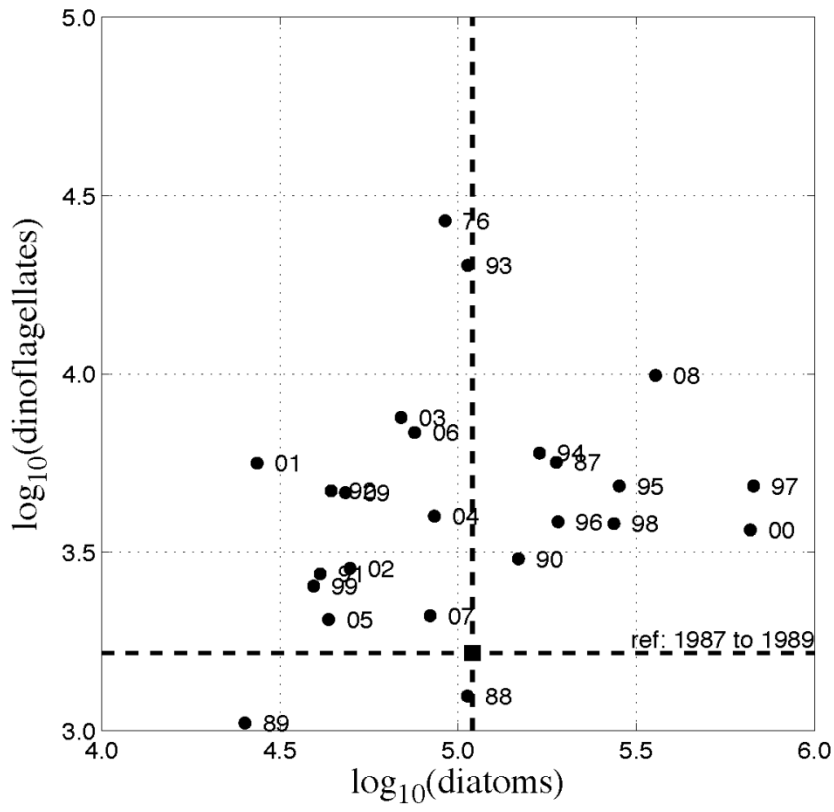
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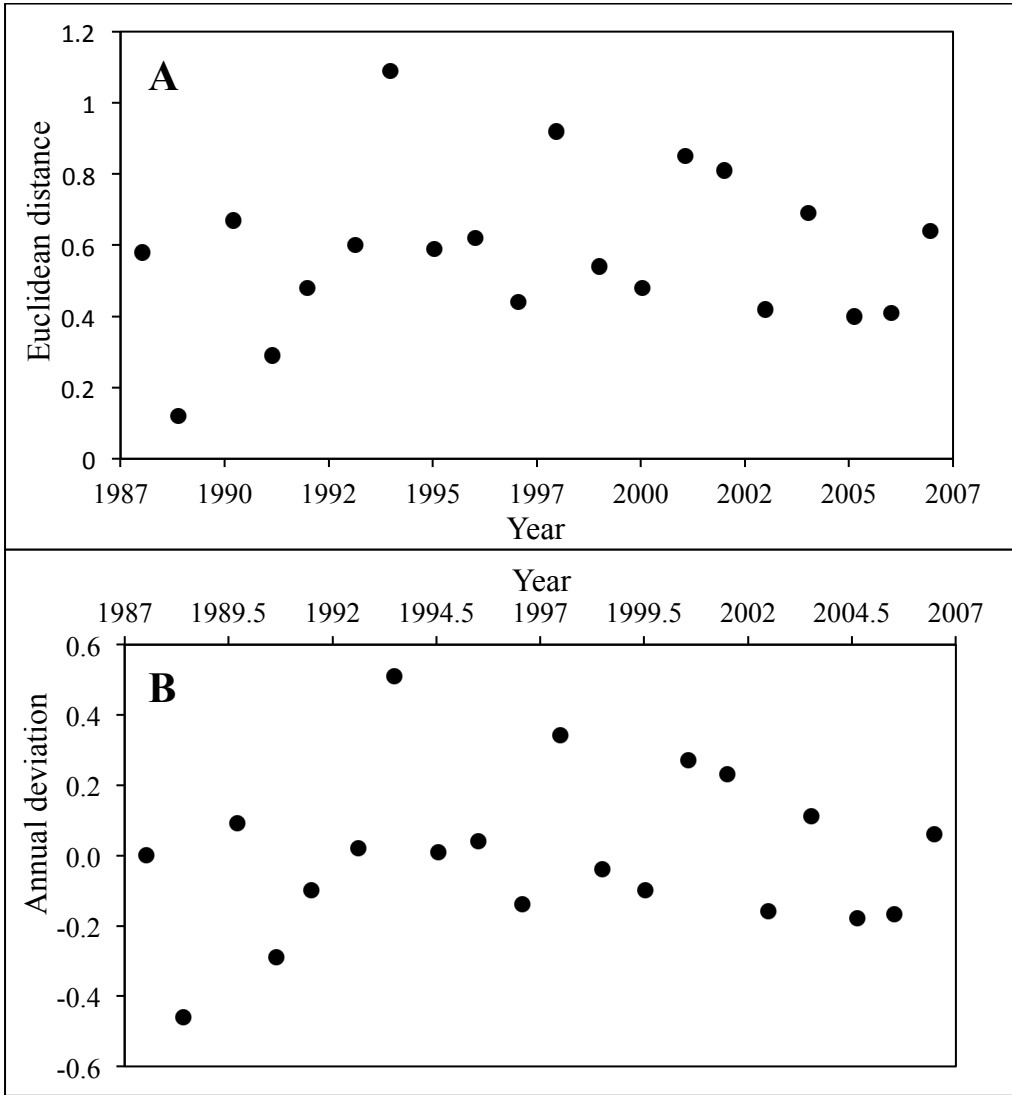
Fig 5





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Fig 6



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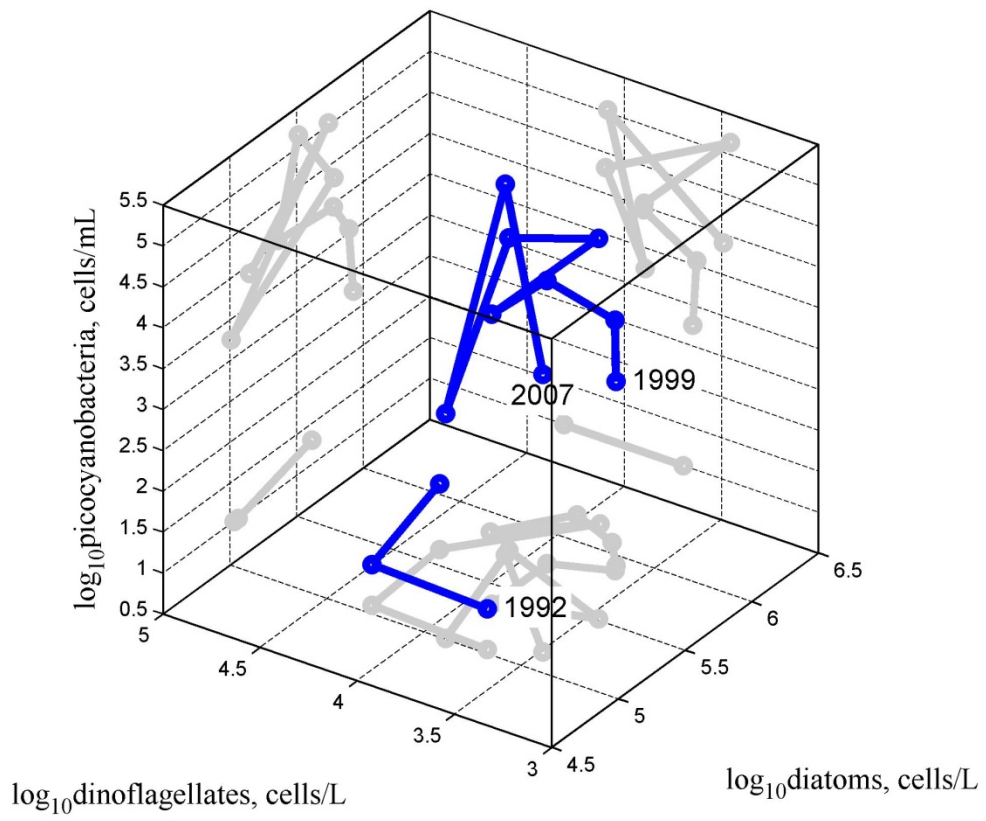
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Figure 7.



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