HORIZONS

The legacy of the last cruise of the Carnegie: a lesson in the value of dusty old taxonomic monographs

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Large online databases contain a wealth of information from modern oceanographic campaigns. While efforts have been made to “rescue” data from the older literature, the assumption should not be made that all the good data that exist are online, waiting to be downloaded and analysed. Here, I show an example of what can be gleaned from the old literature. Three monographs from the last cruise of the Carnegie catalogued the species of the phytoplankton genus Ceratium, the tintinnid ciliates of the microzooplankton, and the copepod species of the zooplankton. The samples employed were from plankton net tows or a “Pettersson plankton pump” from 160 stations in the North and Central Atlantic, the Central, Southern and Northern Pacific. From each monograph, the species records were keyed into spreadsheets to allow station by station comparisons. Plotting species richness along the cruise track showed roughly parallel changes among the three groups with peaks and troughs corresponding with low and high latitudes. For Ceratium, tintinnid ciliates, and copepods, very similar latitudinal diversity gradients were evident after binning the species richness of each group into 5° bands of latitude. The data extracted from the reports of the last cruise of the Carnegie revealed close correspondence of diversity in planktonic organisms among the protists and metazoan taxa of distinct trophic levels. The group with the most widespread species was the copepods.

KEYWORDS: biodiversity; data rescue; taxonomy; latitudinal diversity gradient; species distribution

Taxonomic monographs often contain little ancillary or quantitative data. In contrast, data-rich reports from oceanographic campaigns and the large online databases often contain data of low taxonomic resolution or based on uncertain expertise. Thus, a recent study of large-scale patterns of diversity in marine...
copepods was forced to pool by genus for many species (Rombouts et al., 2009). There appears to be little reason to hope for improvement in oceanographic data yet to be gathered as marked declines in the numbers of taxonomists, and an uncertain future for taxonomy overall is generally admitted (e.g. Wheeler, 2004; McManus and Katz, 2009). Paradoxically, interest in biodiversity and recognition of its importance has increased dramatically in recent years (e.g. Sachs et al., 2009). One partial solution to this conundrum, an increasing need for data no longer being produced, is perhaps better to exploit the taxonomy of the past. For physical and chemical data, “data rescue” and “data mining” have been extensively employed, for example, in the World Oceanographic Data center (WOD). Few equivalents exist for detailed biological data. The WOD contains zooplankton data for the most part as biomass (NOAA, 2011). Exceptions exist, such as “COPEPOD” the Coastal & Oceanic Plankton Ecology, Production & Observation Database (O’Brien, 2010). However, plankton “composition” is often the third priority, following abundance and biomass. Furthermore, different groups of organisms appear to have been rarely treated with the same degree of detail in any single data set.

Here I show the results of a simple individual effort to compare trends among distinct planktonic groups by transcribing species records in monographs from an oceanographic campaign that has been largely forgotten. The monographs catalogued species occurrences in the stations sampled during Cruise VII in 1928 and 1929, which turned out to be the last cruise of the Carnegie. The “non-magnetic” yacht Carnegie built in 1909 was one of the first vessels designed and built for oceanographic work (Treadwell et al., 1988). Owned and operated by the Carnegie Institute of Terrestrial Magnetism, the wooden ship was made with a minimum amount of iron, as its primary mission was to measure variability in magnetism. Cruise VII was planned as a global survey to focus on the acquisition of physical and chemical data of the world’s oceans but included a strong, apparently ICES-inspired plankton component (Fleming, 1928; Pettersson, 1928; Seiwell, 1929). Three groups received special attention when the samples were analysed: copepods, the dinoflagellate genus Ceratium of the phytoplankton and the tintinnids of the microzooplankton.

The Carnegie acquired physical and chemical data and collected samples along a cruise track comprising 160 stations. The voyage began with a trans-Atlantic “shake-down” passage from Virginia to Plymouth (UK) in the spring of 1928. The Carnegie made a call in Kiel (Germany) to consult, and eventually recruit, H. Sverdrup as a consultant for physical oceanography. The ship then headed south through the North Atlantic, sampled across the Sargasso Sea into the Caribbean Sea, and passed through the Panama Canal into the central Pacific in October 1928. The high latitudes of the South Pacific were sampled in the winter of 1928 and the Northern Pacific in the summer of 1929. The Carnegie returned to the South Pacific in autumn of 1929 and was destroyed by an explosion and the ensuing fire while refuelling in Samoa (Fig. 1). The captain, James Ault, who was also the chief scientist, was killed. Fortunately, no samples or data were lost as these were shipped back to Washington DC at each port call. However, results of Cruise VII, the last of the Carnegie, were slow to appear, no doubt in large part due to the loss of the chief scientist. A series of monographic reports was published between 1942 and 1946 (Table I).

The physical data were widely disseminated and exploited (e.g. Moberg, 1930). Articles appeared in the popular press on the vertical structure of the ocean

Fig. 1. The Carnegie under full sail and in flames following an explosion while re-fuelling in Samoa. Reproduced with permission from the Carnegie Institute for Science.
The biological results were also widely distributed, at least in part, as the *Ceratium* results were partially published in Ecological Monographs (Graham, 1941). However, the Carnegie reports are rarely cited. Based on the Web of Science data, in the 66 years since the last report was published, the copepod monograph has been cited 42 times and the tintinnid monograph but 22 times. The overwhelming majority of citations appear in taxonomic works. The reports taken together represent a unique database as three groups, representing distinct trophic levels, were described from the same sampling by experts in the respective taxa.

Below I will describe the methods and material used on the Carnegie as well as those in extracting data from the Carnegie monographs on species occurrences in *Ceratium*, tintinnid ciliates and copepods. The trends in species abundances of these three distinct groups of planktonic organisms collected on the last cruise of the Carnegie will be explored. My intention here is to illustrate the rich record of historical biological data in cruise reports and to encourage others to explore and exploit such historical data.

Plankton sampling was part of the standard station protocol. Two methods were used, net tows and a “plankton pump”. The plankton nets were of two sizes, 1 and 0.5-m diameter, and were made with different types of Dufour silk bolting cloth (Seiwell, 1929). Nets of 1-m diameter and 4.5 m in length were made with three different combinations of silk for the upper, middle and lower sections. The combinations used for upper, middle and lower sections (respectively) were, (i) 0000-10-15, (ii) 0000-5-10 and (iii) 0000-0-2. The smaller nets of 0.5-m diameter were 2.75-m long. They were made with two different combinations of silk for the upper and lower portions (respectively): either silk no. 5 and 10 or 10 and 15. Besides the nets, a “plankton pump” was deployed. The “plankton pump” was a submersible device for *in situ* pumping of seawater into a cylinder of silk bolting cloth and on the Carnegie no. 20 silk was employed (Pettersson, 1928). In principle, the volume of water filtered using the plankton pump could be estimated allowing quantitative sampling. The aperture sizes of the Dufour silk cloth employed are given in a table by Sverdrup et al. (Sverdrup, 1942, p. 378; 0000 = 1364, 0 = 569, 2 = 282, 10 = 158, 15 = 94, 20 = 76 μm). Thus, the most coarse sampling made was with a net with the smallest aperture of 366 μm and the finest with the “plankton pump” with an aperture of 76 μm.

Sampling began early in the day and for plankton was completed before 12:00. Plankton net tows were made at the surface, 50 and 100 m using 1-m diameter nets in calm weather and 0.5-m diameter nets in rough weather. The 50 and 100 m nets were attached to a single cable while a separate cable was used for the surface net. The nets were lowered and left at depth while the boat drifted for 30–60 min. The nets were not equipped with opening and closing lines as these proved often-times unmanageable. The nets then were open when deployed and retrieved. The “plankton pump” was used to sample at 0, 50 and 100 m. I found no indications of what volumes of water were thought to have been sampled with the “plankton pump”. All sampling was then of the surface layer during daytime.

The theoretical consistency of sampling at three standard depths was marred as it appears that exactly which plankton net was sampled was not noted (I can find no mention) and the plankton pump frequently malfunctioned (Paul, 1932). None of the Carnegie reports presents a complete list of the samples gathered by the Carnegie and of the taxonomic monographs, only the copepod study by Wilson explicitly lists the samples examined. Nonetheless, the same set of samples was examined by Charles Wilson producing an account of the copepods, by Herbert Graham and Natalia Bronikovsky, producing an account of *Ceratium* species, and by Author Campbell, producing an account of the tintinnids.

The copepod monograph (Wilson, 1942) presented the species encountered at each station by depth strata

<table>
<thead>
<tr>
<th>Subject</th>
<th>Author(s)</th>
<th>Year</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chemical results</td>
<td>Graham and Moberg</td>
<td>1942</td>
</tr>
<tr>
<td>Biology-I copepods</td>
<td>Wilson</td>
<td>1942</td>
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<tr>
<td>Biology-I tintinnids</td>
<td>Campbell</td>
<td>1942</td>
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<tr>
<td>Biology-II peridiniales</td>
<td>Graham</td>
<td>1942</td>
</tr>
<tr>
<td>Biology-IV “biological results”</td>
<td>Graham and others</td>
<td>1943</td>
</tr>
<tr>
<td>Biology-V Ceratium</td>
<td>Graham and Bronikovsky</td>
<td>1944</td>
</tr>
<tr>
<td>Oceanography-I-A physical oceanography</td>
<td>Sverdrup and others</td>
<td>1944</td>
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<tr>
<td>Oceanography-II bottom samples</td>
<td>Revelle and Piggot</td>
<td>1944</td>
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<tr>
<td>Oceanography-III ocean-atmosphere electric</td>
<td>Torreson and others</td>
<td>1946</td>
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<tr>
<td>Oceanography-IV summary</td>
<td>Ault and others</td>
<td>1946</td>
</tr>
<tr>
<td>Meteorology-II meteorological results</td>
<td>Jacobs and Clarke</td>
<td>1943</td>
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<td>Meteorology-II upper-wind observations</td>
<td>Thomson</td>
<td>1943</td>
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All the publications are available through the Biodiversity Heritage Library: http://www.biodiversitylibrary.org/creator/5323
sampled. Abundances were given in qualitative terms. No mention was made of “plankton pump” samples; the samples examined appear to have been only the net samples. A total of 280 species were found. Data were entered as presence, pooling all depths, into a spreadsheet with 280 species names as rows and the 160 stations as columns. Data entry was restricted to station reports (some samples taken between stations were examined) and free-living taxa, resulting in station by station records for 259 of the 280 species reported. Copepod species names were verified for synonyms and names as currently accepted using the World Wide Web site of Walter and Boxshall (Walter and Boxshall, 2008).

The Ceratium monograph (Graham and Bronikovsky, 1944) described the occurrences of 54 species of Ceratium, with abundance reported qualitatively in the samples examined (net or pump and depth). Data were entered as presence for each station occurrence, pooling all depths and sample types, in a spreadsheet with 53 species names as rows (one species listed is currently recognized as a synonym) and the 160 stations as columns. Data entry was restricted to station reports (some samples taken between stations were examined) resulting in station by station records each of 53 Ceratium species. Ceratium species names were verified for synonyms and names as currently accepted using the AlgaeBase website of Guiry and Guiry (Guiry and Guiry, 2011).

The tintinnid monograph by Campbell lists the species found through examining both net and plankton pump samples (Campbell, 1942). He states that “648 phials”, 272 from net samples and 376 plankton pump samples, were examined and that no net sample material remained for stations 86–94. The remark significantly suggests that Carnegie samples were progressively consumed by individual investigators, likely having examined different portions of the samples. Campbell listed a total of 307 species found giving the occurrence as in either net and or pump samples, usually without reference to depth. Of the 307 species, 288 are currently recognized. Data were entered as presence for each station occurrence, in a spreadsheet with the 288 species names as rows and the 160 stations as columns. Data entry was restricted to station reports (some samples taken between stations were examined) resulting in station by station records for each of 288 tintinnid species.

Despite having pooled all the station data for a given species, ignoring sample depth and type, over 10,000 species records were entered. This simple presence/absence data extracted from the reports was used to qualitatively compare the species abundance trends of copepods, Ceratium and tintinnids. Changes in species richness from one station to the next along the cruise track of the Carnegie were plotted for each group. As the results suggested similar trends of high species richness in low-latitude stations and low species richness in high-latitude stations, latitudinal diversity gradients were examined. Stations were sorted by latitude and the average species richness in 5° bands of latitude was calculated and plotted for each group. The number of stations at which each species was recorded was also tallied to compare patterns of species occurrences among groups.

The data extracted from the three monographs are available as supplementary data in the form of a single spreadsheet file and has been submitted to the COPEPOD site (O’Brien, 2010). Changes in species richness from station to station along the cruise track of the Carnegie showed some striking similarities among the three groups (Fig. 2). Changes from station to station were roughly parallel. Copepods, Ceratium and tintinnids all showed relatively high species richness in low-latitude stations (e.g. Sargasso Sea stations 23, 24, 25) and the lowest species richness in the high-latitudes both north (e.g. North Atlantic station 10, North Pacific station 125) and south (e.g. South Pacific station 60). The species richness trends suggested a latitudinal diversity pattern for all three groups.

The average species richness reported for each station in bands of 5° of latitude for the copepods, Ceratium and tintinnids is shown in Fig. 3. Although Pacific Ocean stations dominate the data, the classic global latitudinal diversity gradient is clear for each of three groups. The close correspondence in species richness among the three groups is reflected in scatterplots using the same data, average number of species in stations grouped by latitude (Fig. 4). The average number of tintinnid species is correlated with both average Ceratium species richness as well as copepod species richness. The data are insufficient for rigorous comparison of southern versus northern patterns or comparing the Pacific and Atlantic (note that the Southern Atlantic had yet to be sampled when the ship was destroyed).

Among planktonic organisms, as in terrestrial organisms, latitudinal diversity gradients appear to be common. The gradient has been described previously for foraminifera (Rutherford et al., 1999), tintinnids (Dolan and Gallegos, 2001) and copepods (Rombouts et al., 2009). Remarkably, such a gradient may not be common among the marine phytoplankton; distinct patterns have been found for diatoms and coccolithophorids in the Atlantic Ocean (Cermeno et al., 2008). The mechanisms behind the latitudinal diversity gradient have been debated extensively and literally dozens of theories proposed. Indeed, the latitudinal diversity gradient has been termed “The Holy Grail of Ecology” (Adams, 2009). What the Carnegie data add to the
Fig. 2. The cruise map of the last cruise of the Carnegie (reproduced with permission of the Carnegie Institute for Science) and species richness of Ceratium, tintinnids and copepods along the cruise track of the Carnegie.
debate is the observation of a common pattern in a protistan genus of the phytoplankton, a protistan group of the microzooplankton, and the metazoan copepods of the zooplankton, all of which were sampled together.

Thus, the gradient is common to different groups of protists, occasionally claimed to not show a biogeography (e.g. Finlay et al., 2006), and to organisms of distinct trophic levels. In passing it may be noted that assemblages of *Ceratium*, tintinnids and large copepods have been shown to share similar species abundance patterns over a time-scale of weeks in the NW Mediterranean Sea (Raybaud et al., 2009).

For all three groups, most of the species catalogued appeared to be rare, found in a very few stations while...
a comparative handful of species were common. However, plotting occupancy or occurrence for the species of each group revealed some interesting differences (Fig. 5). The group with the “most ubiquitous” species (found in nearly every station) was the copepods. *Oithona similis* was found in 154 stations followed closely by *Paracalanus parvus* and *Pseudocalanus minutus*. The small copepod species were more widely distributed than the most common species of *Ceratium*: *C. tripos*, *C. massilense* and *C. macroceras* (all relatively large forms). The most common tintinnid species, *Epiplocylis undella* and *Eutintinnus lasus-undae* and *E. fraknoii* (all of moderate size) were recorded from only ~25% of the stations. The relatively low ubiquity score of the most common widespread tintinnids could be because less material was available for examination by Campbell looking for tintinnids rather than a real pattern. This underlines one of the drawbacks of using historical records, the fragmentary nature of the data.

The species of both copepods and tintinnids showed ubiquity distributions that followed a log-normal or log-series pattern. In contrast, the *Ceratium* species distribution appeared nearly linear. A log series distribution of species occurrence has been described as characterizing benthic foraminifera in which most species are rare (Buzas and Culver, 1999). However, the significance, and indeed reality, of apparent differences in occupancy frequency distributions are unclear (e.g. McGeech and Gaston, 2002). What is noteworthy in the Carnegie data is evidence that “everything is everywhere” describes better the metazoan copepods than the microbial protists.

When the Census of Marine Life was inaugurated in 2000 (Longhurst, 2000) in a letter to *Oceanography* commented, among other things, “Has everyone forgotten what is in the literature?” The value of historical records as evidence that “everything is everywhere” describes better the metazoan copepods than the microbial protists.

SUPPLEMENTARY DATA

Supplementary data can be found online at http://plankt.oxfordjournals.org.

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