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Letters

Insights from study of the last intact neritic marine ecosystem

David Ainley

H.T. Harvey and Associates, 3150 Almaden Expressway, Suite 145, San Jose, CA 95118, USA

I am pleased to see the recent article 'The ups and downs of trophic control in continental shelf ecosystems' by Frank *et al.* [1] because it summarizes a growing literature indicating that, after all, open-water marine ecosystems can be forced by top-down factors. I would like to offer perspective garnered from working in the last yet-to-be-altered neritic marine ecosystem on Earth, the Ross Sea, which is also the largest continental shelf ecosystem of the Antarctic (the size of southern Europe). Frank *et al.* [1] described for the fish fauna of exploited North Atlantic shelf ecosystems an interesting pattern, whereby, depending on ocean temperature and biodiversity, food webs could be forced by either top-down (cold, low diversity) or bottom-up (warm, high diversity) factors. According to these 'rules', the Ross Sea neritic ecosystem – or at least the fish fauna – should be structured by predation. One portion of the Ross Sea seems to follow these rules but another does not, seemingly owing to the irregular distribution of still-existing upper-most trophic levels, that is, the cetaceans, flightless seabirds, seals and large predatory fish long since extirpated from the North Atlantic.

As recently reviewed [2], the central Ross Sea, driven by processes producing a large polynya (persistent open-water area within the pack ice), experiences a bloom of the colonial haptophyte *Phaeocystis antarctica*, which, in part, is responsible for the Ross Sea becoming the most productive stretch of water of comparable size south of the Polar Front [3]. Owing to its intensity, fuelled by sunlight and abundant macronutrients but constrained by availability of micronutrients, the bloom lasts for only a few months. The main grazers seem to be pteropods, and the fish fauna of the next higher trophic level is sparse, at least judged by the avoidance of this area by higher-level predators [4]. Much of the production is either re-mineralized or sinks to the benthos. Though species poor, this truly is a system driven by resource availability.

By contrast, the food web of the marginal ice zone (MIZ) ringing the polynya, especially to the west, begins with single-celled diatoms and harbors a much higher diversity and abundance of grazers, piscine predators and upper-level predators [2–4]. These diatoms, which experience the same nutrient and insolation resources as the haptophytes, can dominate where melting pack ice stabilizes the water column [5], unlike the wind-mixed central portion of the shelf. The MIZ, too, is highly productive [3], but interestingly an appreciable portion of phytoplankton is ungrazed [6]. This is in accord with seemingly and unexpected low densities of grazers (especially euphausiids [7]) and with the main piscine predator of zooplankton, the silverfish *Pleuragramma antarcticum* (the so-called anchovy of the Antarctic), becoming cannibalistic in the late summer [8]. What are unexpected given the apparent paucity of large grazers are huge populations of baleen whales (minke *Balaenoptera bonaerensis*), fish-eating killer whales (*Orcinus orca*), seals and penguins [9]. Indeed, so tight is the predator–prey relationship that the seasonal arrival of the whales forces penguins to change diet from krill to silverfish and dramatically increase their foraging effort. One has to conclude that the thousands of marine mammals and millions of penguins, along with the still abundant predatory Antarctic toothfish (*Dissostichus mawsoni*), are depleting the grazers with repercussions for phytoplankton biomass (i.e. a trophic cascade). The food web in this portion of the Ross Sea, despite higher biodiversity, seems to be forced by top-down processes.

Such a side-by-side scenario of top-down and bottom-up forcing emphasizes the message of Pauly and Maclean [10], which has been most recently discussed by Schrope [11], that, because most marine biologists must work in broken ecosystems [1], we must be careful in drawing conclusions about how open-water marine systems once worked based on modern investigations. It is a pity that industrial fishers for toothfish (Chilean sea bass) and minke whales from New Zealand and Japan, respectively, have discovered the yet-to-be-depleted biotic riches of the Ross Sea. It could have been a wonderful laboratory in which to discover the workings of unaltered marine ecosystems [12]. The question then arises, if the whales, seals, flightless seabirds and large predatory fish are removed, as in the North Atlantic, will the Ross Sea behave as described by Aebischer *et al.* [13], or will top-down forcing still be important?

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Corresponding author: Ainley, D. (dainley@penguinscience.com).

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What role should null-hypothesis significance tests have in statistical education and hypothesis falsification?

James M. Gibbons[1], Neil M.J. Crout[2] and John R. Healey[1]

[1] School of the Environment and Natural Resources, College of Natural Sciences, University of Wales, Bangor, LL57 2UW, UK
[2] Division of Agricultural and Environmental Sciences, School of Biosciences, University of Nottingham, NG7 2RD, UK

We welcome the recent opinion of Stephens *et al.* [1] about inference in ecology, and agree that statistical methods are widely misused and misinterpreted. The technical issues raised by the authors about null-hypothesis significance tests (NHSTs) [1] have been debated elsewhere [2–4] and we have demonstrated the value of alternative approaches when selecting parsimonious models [5], which is not possible with NHSTs. However, we have reservations about the suggestions, in particular: (i) how ecologists should educate themselves about statistical methods, and (ii) the role of statistical methods in the falsification of scientific hypotheses. We argue that preferred statistical methods should clearly present information in data relevant to research hypotheses.

(i) Ecologists must take responsibility for the statistical methods they use, either by educating themselves or by involving statistical experts in data collection and analysis. Stephens *et al.* [1] imply that NHSTs are a good means of statistical education and that ecologists should educate themselves about methods largely from the ecological literature (as evidenced by the references they cite). We disagree, and suggest that much of the misunderstanding and misuse arises from the unintuitive and restrictive nature of NHSTs. The limitations of NHSTs have long been recognized but few alternatives were historically available (for example, see Ref. [6]). Developments in statistical theory (e.g. information theoretic criteria) and increases in computing power (enabling widespread application of Bayesian methods) now provide alternatives that are far less restrictive and more intuitive. For example, it is a common misunderstanding that the P value produced by a NHST is the probability of the null hypothesis given the data, whereas the reverse is actually true. Surely the former is a more intuitively natural and useful quantity and it can be estimated using Bayesian methods. Selecting appropriate methods for inference is a problem that is universal to all sciences, yet much of the ecological debate about statistical methods (for example, Ref. [1]) takes place in isolation from other fields and, most importantly, from the statistical literature (for example, see Ref. [7]).

(ii) Stephens *et al.* [1] suggest that NHSTs will remain fundamental to the falsification of scientific hypotheses. We agree that such falsification is fundamental but disagree with the implicit assertion that falsification is the role of the statistical method. Scientists falsify with evidence inferred using statistical methods. The role of the statistical method is to provide an appropriate support for inference rather than a route to automatic falsification. We think that the methods that most clearly illuminate the support should be preferred.

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Corresponding author: Gibbons, J.M. (j.gibbons@bangor.ac.uk).