The Biophysicist

Designing and Delivering an Interdisciplinary Undergraduate Degree in Quantitative Biology

Timothy E. Saunders[1,*], **Robert A. Cross**[1], **Andrew J. Bowman**[1]

[1]Division of Biomedical Science, Warwick Medical School, University of Warwick, Coventry, UK

ABSTRACT With the arrival of new technologies, the biological sciences have become significantly more quantitative over the past 30 years. These new approaches have drawn in researchers from a broad range of disciplines; for example, trained physicists are now commonplace among biology department faculty. Yet, education in the biological sciences often does not reflect this large shift. Here, we outline a new program developed and taught at the University of Warwick to tackle the challenge of bringing quantitative, interdisciplinary education to the biosciences. We provide an overview of the course and the rationale for its structure. We then discuss lessons learned to aid others planning to implement interdisciplinary undergraduate courses based on teaching from research.

KEY WORDS natural sciences; quantitative biology; course development; teaching from research

I. INTRODUCTION

The past 30 years has seen a revolution in research in the biosciences. The advent of powerful cell biological approaches—such as green fluorescent protein for live imaging, microscopy advances including super-resolution microscopy, and genome sequencing and editing tools that allow unprecedented control of biological systems at the molecular level—means that we now have access to quantitative information about the cell machinery. The cumulative effect of these (and other) advances is that quantitative skills—including mathematics, statistics, optics, and coding—are becoming a greater necessity for modern medical and bioscience research (1). For example, the rise of "big data"—both genomic and imaging—requires researchers to have the tools to integrate the vast amount of data that is collected into results that are digestible. In tandem with these advances, there is increasing interest from different disciplines in biological processes. It is now common to find faculty in biology and medicine departments with physics, chemistry, statistics, and engineering backgrounds. Increasingly, interdisciplinary approaches and collaboration are becoming essential in many cell biology laboratories (2, 3). However, a major problem remains in training biologists to engage constructively with new approaches and interact meaningfully with collaborators (4–8). The impact of this challenging problem is seen, for example, in the citation pattern of papers (9).

It is important to recognize that such quantitative approaches are not done for their own sake but have driven major advances in our

"*" corresponding author

Received: 29 November 2022
Accepted: 30 May 2024
Published: 25 July 2024

understanding of biology. In developmental biology, utilizing information theory concepts has revealed that the early *Drosophila* embryo is able to "optimally decode" positional information provided by morphogen gradients (10). Super-resolution microscopy (11) has revealed how molecular motors generate mechanical force (12), and we can now probe the structural organization of the nucleus (13). These biophysical and theoretical approaches are essential in modern cell biology contexts.

The changes at the research coal face—with increasing acceptance of a plethora of different disciplines in solving problems relevant to biology—requires adaption of courses taught to undergraduate students to prepare them for future academic and industrial research (14). Many biology courses still focus on transferring content, rather than developing skills in biophysical quantitative methods. Research into biology-specific education is also still a nascent area (15). These issues are not new and have been extensively discussed, including in two major reports from the USA National Academy of Sciences: "Bio 2010 Transforming Undergraduate Education for Future Research Scientists" and "A New Biology for the 21st Century," published in 2003 and 2009, respectively (16, 17). Key conclusions regarding life science education include (1) that life science students must develop strong foundations in the physical sciences—particularly at a level higher than those typically achieved in most undergraduate courses; (2) interdisciplinary learning must be encouraged, and courses between disciplines must be integrated more effectively; (3) active teaching methods need to be more comprehensively used; (4) more examples of current research need to be brought into undergraduate syllabi; (5) mathematics needs to be integrated more comprehensively within undergraduate courses to equip biologists with the tools they need, and such additions may also entice students more inclined toward the physical sciences to consider biology. This work both built on and motivated attempts to modernize biology teaching (18–24). Despite a number of innovations in undergraduate teaching of quantitative methods for biologists (25–31), computer and numerical literacy is still generally weak among biologists compared to the physical and computational sciences (24, 32–34), partially due to resistance within universities to educational reform (35). This appears to be true in countries with broad undergraduate education (e.g., the US with more subject choice and major/minor programs) as well as those with more narrowly defined degree programs (as is the norm in the UK).

The patchy uptake of quantitative sciences into undergraduate biology curricula has resulted in students entering the workforce, biotech, and graduate programs with a wide range of capabilities in computational and analytical techniques. A corollary to these issues is that biology students often struggle to engage with students and researchers from other disciplines because of communication difficulties—biologists and physicists can describe the same process in very different terms. For example, biologists often frame results within an evolutionary perspective, asking not only how the process works (proximate mechanism) but also why it works that way (distal cause); such an approach is alien to most researchers from the physical sciences. Despite interdisciplinary science requiring clear communication, cross-discipline training is still not common (36, 37). Master's/PhD-level courses have been developed (38; see https://physics-of-life.tu-dresden.de/en/career-education/msc and https://www.cellphysics-master.com/), but these arguably come too late in the pipeline.

There is a clear need to reform undergraduate biology courses to emphasize quantitation and more accurately serve the demands of both academia and industry (39). To address this, we have developed a new, interdisciplinary program at the University of Warwick: Integrated Natural Sciences. The course is focused around answering biologically relevant questions (how does life work?) but using tools from biophysics, computer science, chemistry, mathematics, and the biosciences. In effect, we integrate different disciplines within a 4-year program to tackle problems in biology. This compromise (rather than trying to teach all STEM disciplines in a truly "natural science" way) reflects the vast size of each individual discipline; by applying a focus point (e.g., biology) but with clear and regular integration of other disciplines, we provide a broad scientific education without resorting to low-level modules. As an example, we incorporate biophysics throughout the program: Year 1 includes Brownian motion and light microscopy; Years 2 and 3 involve in-depth modules on dynamic systems, feedback, and modeling; and Year 4 has a module focused on the physical biology of the cell.

The course is highly hands on, with classroom teaching led by research-active principal investigators, with both wet and dry lab work closely interlocked. The course was originally inspired by outstanding programs in Integrated Science at Princeton (https://lsi.princeton.edu/integratedscience) and Harvard (https://projects.iq.harvard.edu/ls50/home) universities, both of which are focused on first-year students. To adapt these approaches for the UK environment, we have created a coherent 4-year undergraduate program, leading to a master's-level degree. In this article, we outline the course structure and lessons learned so far from its implementation at a research-oriented university. We discuss methods for ensuring interdisciplinary teaching (meaning lecturers integrate approaches from different sciences within their lectures) and how we integrate active learning concepts throughout the course. Such information should be helpful to other academics looking at implementing new undergraduate programs that better reflect the reality of modern biology and the rapidly evolving world of its quantitation.

II. COURSE STRUCTURE

Integrated Natural Sciences (INS) at Warwick is taught over 4 years and is run primarily by Warwick Medical School. Here, we breakdown each year (Fig 1) and highlight key learning objectives.

A. Year 1

The first year is the most distinctive and innovative element of the course. It is organized into 2-week blocks, where challenges in biology are tackled, starting from the molecular scale and finishing at organismal levels. In this way, we teach from research, driving each 2-week block with a set of questions about the world (e.g., how do cells divide?). Our first-year course comprises 13 blocks, with the instructor and the scientific questions changing every 2 weeks.

At the beginning of the year, students undergo an intense 2-week Python training to introduce the coding language that underpins the course. Further, training is provided in Overleaf, because assignments are required in LaTeX. Although challenging for students, setting in place these coding fundamentals enables us to address more interesting topics later in the year. Students are given extensive support (a ratio of approximately 1 teaching support staff to 8 students) and encouraged to collaborate so that those who have never coded can learn from those who have. The cohort is small, and a cohort mentality of mutual self-help begins to develop. This carries forward into the rest of the course. Students come to the course from different backgrounds (all incoming students have advanced level math, but some have only studied one science to advanced level); students thereby build experience in working both individually and collaboratively.

The wet labs begin at the scale of molecules (e.g., DNA). Although the aim of this article is to give an overview of the course, we provide an example 2-week block in Box 1. As the year progresses, the students move on to blocks focusing on organelles and cells. The year finishes at the scale of organisms; for example, how do tissues form specific shapes and sizes? Each block is led by an active researcher whose teaching is motivated and informed by their own lab work. In the latter part of the year, there is a focus on the model organisms (zebrafish and *Drosophila*). Overall, the first year is a bold initiative that encompasses a broad canvas of modern biology, built on a core ambition

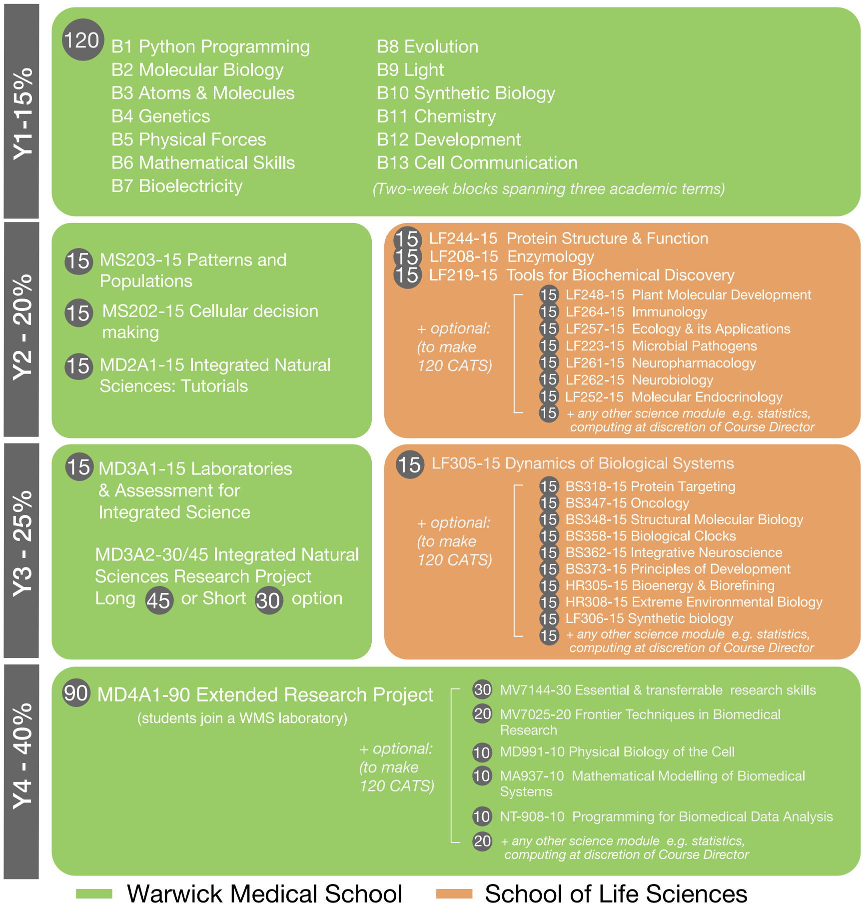


Fig 1. INS course structure. In the left hand column, percentages correspond to the weighted contribution to the final grade. CATS, Credit Accumulation Transfer Scheme.

at Warwick to drive teaching with the expertise and enthusiasm of researchers.

Across the year, the blocks are interdisciplinary, representing biophysics (particle diffusion, light and microscopy, bioelectricity, forces in development), chemistry (synthetic biology, chemistry of life), math, and computing. To ensure that the blocks are synergistically working to enhance interdisciplinarity, we have a dedicated Year 1 lead. This academic (who also teaches in Year 1), regularly meets with block leads and ensures that material in later blocks is building on earlier foundations. A key role is to ensure that interdisciplinarity is not teaching different topics as separate entities but instead to maintain focus on a common theme ("how life works").

As demonstrated in Box 1, the blocks interweave wet labs with the students regularly using coding. For example, they develop software to perform single-molecule tracking and subsequently explore diffusion inside biological systems. We provide simplified fluorescent microscopes (eduWOSMs, Fig 2) to enable students to collect their own data. Importantly, these microscopes are modular, enabling students to take them apart to see how a microscope is constructed. The reinforcement of coding skills through the blocks has two important purposes: (1) it embeds the students coding skills for later years, and (2) it builds the habit of applying quantitative thinking in modern biology.

Students are assessed in Year 1 by way of performance in the labs (20%), a lab report in the style of a scientific paper (50%), and a year-end short answer written exam (30%) in the familiar "problem set" form, similar to those given during classroom teaching. Initially, reports are scaffolded to ease the transition into scientific writing, with students focussing on figure making and presenting results. The scaffolding is then gradually removed, leaving the students to compile full reports by block six. The marks for Year 1

Box 1. Example 2-week block structure from Year 1

This block follows on from the Python programming and introduces biology as a data science. Seminars are pitched so that students without A-level biology can get up to speed, while providing a new angle on life as a coding problem for those who have previously studied biology. Seminars start at the "central dogma." We then discuss ways to manipulate DNA by genetic engineering. This is followed by the basic molecular principles of transcription and translation, linking genotype to phenotype. We end the conceptual teaching with an introduction to BLAST and multiple sequence alignments.

Daily problem sets reinforce concepts set out in the seminars. These involve coding (e.g., algorithms to translate DNA into protein and pick out open reading frames) or performing multiple sequence alignments to identify the active site of a protease enzyme. Students also get to flex their creative muscles in a science communication task where they each present a topic covered in the block in laymen's terms in the form of a digital flip-book animation (Video S1).

In the accompanying lab sessions (Box Figure), students learn how to engineer DNA by introducing point mutations into a plasmid encoding GFP. These mutations alter the emission and excitation spectra of GFP, producing blue- or red-shifted variants. This builds on the concept of genotype (DNA mutation) being linked to phenotype (fluorescent spectrum) and further drives home the idea of biology as information science. The lab session is spaced over 6 d, with a 1-d break between sessions 2 and 3 and a weekend break between sessions 4 and 5. An itinerary of lab activities that fits this arrangement is shown below but could be easily adapted to other schedules:

- Lab 1: Assemble and run a PCR reaction using site-direct mutagenesis. Pour an agarose gel.
- Lab 2: Assess PCR amplification using agarose gel electrophoresis. Transform DNA into bacteria.
- Bridging day: Course technician picks colonies for plasmid preps and patches colonies onto protein expression plates.
- Lab 3: Purify plasmid DNA and prepare for external Sanger sequencing.
- Lab 4: Make protein extracts from patched colonies and measure excitation and emission spectra by using a 96-well plate reader.
- Weekend break
- Lab 5: Separate protein extracts by SDS-PAGE and image under UV light to visualize fluorescent proteins, and stain for total protein by using Coomassie.
- Lab 6: Dry practical—analysis of returned Sanger sequencing runs to identify introduced mutations.

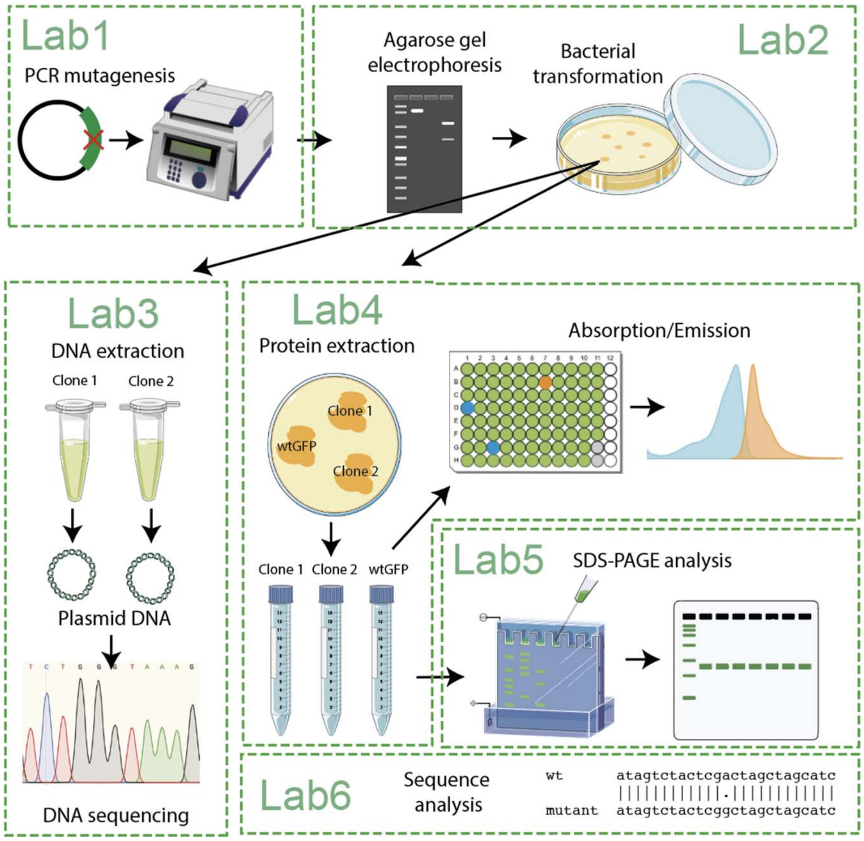
count only 15% toward the students' total for their degree (Fig 1). We have introduced the lab performance mark after student feedback. The time commitment for our Year 1 students was much greater than for most Year 1 programs at our university. This also provided the lecturers with an avenue to more holistically grade student attainment throughout the year. While apparently subjective, the marking of this is straightforward, given the time spent in labs between student and lecturer (marking rubric in the Supplementary Material).

Comparing our students with those taught through more traditional biology first years, we notice the following qualitative observations: (1) the students are much more confident in laboratory settings; (2) students are able to tackle questions more independently, rather than assuming they'll be taught answers; and (3) the students have a developed sense of teamwork, because much of the work is carried out collaboratively. These skills are all essential for modern biology research. Of course, one must take these observations with caution: the class size is very small ($<$25 per year), compared with more classical biology programs, which often have $>$200 students per year. Are our results simply a consequence of the class size and staff ratio? Further investigation across a larger student number is required to rigorously test this.

B. Year 2

Here, the course becomes roughly split in 2. In the first half, the students undertake dedicated modules from INS. These are largely numerical/theoretical in nature.

In the first module, Cellular Decision Making, students develop their mathematical tools to understand how feedback and feedforward motifs can enable cells to "make decisions," such as switching or having a pulse generator (40). The class is taught in a flipped style, with each class based around solving questions at



Box Figure. Schematic of laboratory sessions. Each session is based around a 3-hour teaching window.

whiteboards in groups. They can also tackle harder voluntary questions numerically by using Python as part of homework problems. As one example, the students tackle how a gene regulatory network patterns the neural tube (41). Students are required to deconstruct the gene regulatory network to identify specific motifs underlying particular behavior. They learn how to apply concepts from mathematics and engineering (feedback) to understand how a complex biological system operates. This module also introduces the concept of noise in biology and how this affects systems (e.g., through negative feedback to buffer variability) (42, 43). We use morphogen gradients and their readout as an example of where robustness in the presence of noise is important (44).

The second module, Patterns and Populations, uses computational, mathematical, and biophysics approaches to tackle problems in sequence analysis and population biology. The students learn how to analyze sequencing data (45, 46) and identify common errors. Finally, the students study populations (e.g., the Lokta-Volterra model). This includes a field trip (https://www.field-studies-council.org/locations/dalefort/) to collect data and carry out statistical analysis on "real" data. This final part of Year 2 is deliberately left unstructured; through the student experience across the first 2 years, we expect the students to develop the independence to analyze and present their data without significant oversight.

The students also undertake a tutorial-style module, exploring the scientific process: for example, publishing and refereeing. This gives them a better overview of what the scientific process is really like. They gain experience in preparing and delivering presentations, developing broader skills. After feedback from our first cohort, this module now includes more traditional exam preparation later in the year to support our students in taking exams in their second year.

The second half of Year 2 is focused on building the students core knowledge. This is done in collaboration with the School of Life Sciences at

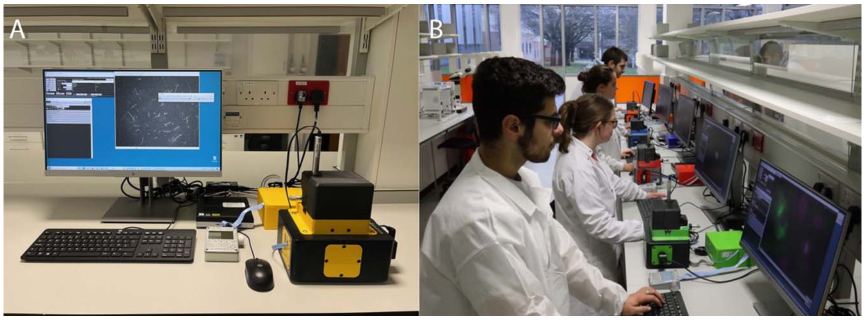


Fig 2. Quantitative biology in the classroom. (A) Dedicated microscope (termed eduWOSM) is provided at a ratio of 1 to every 4 students (yellow-and-black unit on right). This enables students to collect their own quantitative data in the lab. (B) Students using the eduWOSM in the teaching lab (reproduced with permission from the students).

the University of Warwick. The students attend courses on biochemistry to ensure that they have a strong base. They then choose from a menu of options, including neurobiology, immunology, ecology, plant molecular development, and endocrinology. Year 2 reinforces the use of biophysics and computational approaches in understanding biology. Importantly, students are also encouraged to take a module from outside the biological/medical sciences. Students have successfully undertaken modules from mathematics, computer science, physics, and the business school. This further encourages a broader education than is typically achieved within the UK setting.

C. Year 3

In this year, we focus largely on developing the students' laboratory skills. Half of the year's grade is dedicated to research projects in individual labs and an associated skills module, which are carried out throughout the year. This gives the students sufficient time to develop a meaningful piece of scientific work that goes beyond the level of typical third-year labs. The labs are chosen to be ones that encourage interdisciplinarity, and many are biophysical in nature. In conjunction with labs, the lab skills module focuses on quantitative methods. This includes gaining experience on different microscopes and important statistical approaches.

The second half of the year is left open to students to choose courses, mainly from the School of Life Sciences. These include oncology, developmental biology, and extreme biology. Students are also able to take a course from outside the biomedical/biological sciences (e.g., statistics and machine learning courses).

D. Year 4

The climax of the course is the final master's-level year. The students join a host lab and spend 3/4 of their time pursuing a self-designed research project. Students are helped to design powerful and effective research questions and given sufficient time and support to make significant progress. Students are hosted within active research labs. Master's-level instructional courses are also available, such as Physical Biology of the Cell and more advanced laboratory methods, which deepen students' intellectual understanding of quantitative biology.

Overall, the course provides a novel, holistic approach to mold a new generation of quantitative biologists. Years 1 and 4 are heavily lab based and build essential laboratory skills. Years 2 and 3 focus on developing core knowledge, taught through various techniques, while still keeping active learning elements as a significant percentage of the year.

III. LESSONS LEARNED

A. Small cohorts

Consistent with experiences at other institutions, we have found that small class sizes are a necessity. We limit the course to 24 students (based on the size of our Year 1 lab space). This number enables 1 professor with a teaching support to effectively engage with the students. Frequently, PhD students and postdocs from the instructor's labs lend a hand, and we find that postgraduate and postdoctoral researchers are often keen to help and to thereby gain teaching experience. A staff ratio of roughly 1:8 in the first year is a requirement given the extent of the staff-student interactions.

B. Motivation

The course is challenging to students. Many come from a school environment where open-ended problems and unanswered questions are not common. Students who engage with the material perform very well. Therefore, our advice is to be selective in recruitment for students displaying a keen interest in applying techniques from biophysics and other disciplines to biology.

C. Research engagement

An initial concern in building the course was getting the buy-in of research-oriented professors. Thankfully, this was not in the end an issue; indeed, most staff proactively expressed interest in being part of the course. As has been said: "This is the course I wish I had done as an undergraduate." Framing the course as a novel approach to modern biology teaching has ensured strong staff participation.

D. Be relaxed

The course is intense, with extended staff-student interactions. Therefore, it is important to provide an environment regularly where students and staff can mix more informally. We hold a weekly coffee morning, where students can discuss with each other and with the course team. We also use this as a chance to highlight any emerging issues with course delivery, and we try if we can to fix these on the fly. We run an "e-lab," an optional session providing help with coding problems.

E. Feedback is central

Implementing such a course will be challenging, both for the students and the staff. It will also take on unique flavors depending on the institution—we definitely do not think our model is a one-size-fits-all one. Therefore, getting regular feedback is critical. We do this through informal channels (e.g., a "course breakfast") and by using the university's mechanisms for polling student views. One of these is a student-chaired Staff-Student Liaison Committee, where any concerns can be raised and solutions found. This has been helpful, for example, in better understanding the students' coding needs. We have a mentoring scheme whereby more experienced students in the course volunteer to advise newer recruits.

F. Assessment

Assessing an interdisciplinary program can be challenging because of the differing student skill sets (35). We combine continuous assessment (lab reports written in a paper style, 50%, and lab performance, 20%) with exams (30%). A similar balance of assessment is used in the second-year course. In the final 2 years, the laboratory work represents a substantial proportion of the grade (at least 50%), reflecting our learning objective to encourage lab-based learning. Finding a suitable balance of coursework and examination is probably highly course specific, and flexibility is needed. Relatedly, we made sure that our external examiner was an interdisciplinary scientist who could bring independent expertise to assessing the course progress.

We have also provided regular updates to our staff about the course developments. We have welcomed staff input and made changes to the course in response. This has probably aided with staff buy-in to the course, even though the teaching is more involved and involving than traditional lectures.

IV. CAREER DEVELOPMENT

The first cohort will graduate in July 2024. Because they are the first group to go through the whole course, we sent them a questionnaire focused on their career choices and how the course material had influenced this. The cohort is small (9 students), limiting the strength of conclusions that can be drawn, but we had a 100% response rate. The questionnaire is provided as Supplementary Material and was done with approval from Warwick Biomedical and Scientific Research Ethics Committee.

Seven of 9 of our students either have or are applying for PhD positions starting in October 2024. Of these students, all but one said that the course focus on lab time had directly influenced their decision to undertake a PhD (the other student stated they knew they wanted to do a PhD before beginning the course). Of these students, there was an even split between those planning a future career in academia (2) and industry (2), with three either undecided or not specified. One student is focusing on research assistant roles. Finally, one student is going to train as a secondary school science teacher, with a focus on physics. We believe it is a testament to our course that despite the biology focus, we have provided a basis for such a decision. Indeed, this student highlights how the course has given them confidence to teach across biology, physics, and chemistry.

A striking element of the questionnaire—though perhaps not surprising in retrospect given the high percentage applying for PhDs—was the positivity about the large number of labs (8 out of 9 students, with 1 neutral). This was not limited to the first year, with the independent research project in Year 2 and the lab projects in Years 3 and 4 gaining multiple positive mentions. As our cohort has increased in size (now 20–24 students in the lower years), we have seen a broader spread in attitude toward the labs. In particular, some students have struggled with the high time demands of the experimental work. It will be important to follow up over the next few years to see how students respond to the intense style of teaching, with large amounts of hands-on experience.

We asked the students about the part of the course that affected their career choices. Although the labs were not a surprising response, it was noteworthy that 4/9 students highlighted that the mathematics-oriented modules in Years 2 and 3 played a role in determining their choice of PhD study. One student highlighted that this had led them toward a bioinformatics PhD, which they would not have considered at the start of the program. It will be interesting to track whether this is a repeated trend in future years.

V. CONCLUSIONS

The first year is an innovative pedagogical approach to introduce undergraduate students to modern biology. The block structure ensures that the time commitment of individual instructors is tightly focused. For 2 weeks, a single instructor concentrates on delivering their block, supported by the Year 1 lead, a dedicated course technician, and any lab members willing to help out. We have seen strong proactivity from the research staff in developing their teaching, and the students have responded very positively to the highly engaged teaching environment.

The 2-week block structure also ensures that if things go wrong (which is inevitable to at least some degree within such a course), the damage is limited to a single 2-week block. For example, in our pioneering year we were severely affected by COVID restrictions (2020–2021). A number of key experiments were not given full practice run-throughs before delivery, and some labs had to be hastily redesigned to comply with restrictions. Thankfully, most blocks worked as hoped, and the course largely progressed unhindered. The block structure also ensures students are exposed to a range of teaching styles. The content and order of delivery of the blocks can also be changed to suit local needs. We strongly suggest using a blocklike structure for such a course—at least in the first year—because it gives the flexibility and responsiveness necessary for such a hands-on and intensive course.

Of course, biology is not alone in undergoing research and pedagogical transformations over the past 30 years. Chemistry degrees have had large changes in both content and methods of teaching (47). A focus on targeted learning outcomes, aligned to student needs, is essential for effective learning (48). As more biology courses alter their content to introduce more quantitative approaches, it will be interesting to explore how effective these are in terms of engaging and driving student learning (49). Biology students traditionally are considered to have less-developed mathematical skills than other STEM students; it is possible that this could influence the effectiveness of introducing quantitative techniques into the undergraduate syllabus. In our course, we have not faced this issue, but we preselect for students who have a good mathematical background.

In summary, our experience since 2020 has shown that it is possible to deliver a modern quantitative biology undergraduate program that is integrated between biology, physics, and other physical sciences. It is important to have a sufficient staff-to-student ratio and material support from the university. For example, cross-departmental support can be essential in delivering such a broad range of learning (50). We also believe that such a program is not limited to biology-oriented departments. Such an “integrated” natural science program could well be embedded within chemistry, physics, or engineering departments; that is, the underlying theme is subject specific, but the course brings knowledge and skills from other disciplines to enhance the student learning. The key is to have motivated and dedicated staff interested in engaging across disciplines.

A caveat to the above conclusions is that the nascent field of quantitative biology does not yet have widely accepted definitions of learning objectives and “concept inventories” that are essential for measuring success in teaching. This in part reflects the differing views on what quantitative biology is: for example, a physicist often views the field very differently from a biologist or an engineer. We hope that one outcome of this work is to motivate further discussion across teachers of quantitative biology to realize defined metrics for evaluation. We note that there are provisional attempts at such work, and it will be interesting to see how this develops (51, 52). A further restraint is that our work is within the UK higher education environment. It is possible to have effective curricula across different approaches (53, 54), but applications to different contexts would probably require reworking of parts of the course. Finally, we note that there is potential for such a course—with its high intensity and considerable contact time—to discourage students from some backgrounds. Across our first 50 students, we have gender balance and diversity in our student body. We provide both personal tutors and student mentors to support students, which can be important in supporting a diversity of students (55). We will carefully track such information through the next few years to identify potential problems restricting student accessibility.

AUTHOR CONTRIBUTIONS

All authors contributed to the development of the course, with RAC initiating the course in 2020. TES wrote the first draft of the manuscript. All authors wrote the final manuscript. All authors designed the questionnaire. TES analyzed the questionnaire responses.

ACKNOWLEDGMENTS

We are very grateful to our pioneering student cohorts for their enthusiasm and willingness to try something new and to our instructors and lecturers who have dedicated so much time to ensuring the course quality. We thank Mohan Balasubramanian, Andrew McAinsh, Bill Wickstead, Kirbie Smith, and Dorota Boehm for their help in initiating and supporting the course. The authors declare no competing interests.

REFERENCES

1. Hastings, A., P. Arzberger, B. Bolker, S. Collins, A. R. Ives, and N. A. Johnson. 2005. Quantitative bioscience for the 21st century. *BioScience* 55:511–517.
2. Cech, T. R., and G. M. Rubin. 2004. Nurturing interdisciplinary research. *Nature Structural & Molecular Biology* 11:1166–1169.
3. Kosik, K. S. 2020. A biologist talks to a physicist. *Nature* 577:281–283.
4. Knight, J. 2002. Physics meets biology: bridging the culture gap. *Nature* 419:244–247.
5. Fletcher, H. 2002. Culture gap: in biology, what works, continues. *Nature* 419:878.
6. Laughlin, R. B. 2014. A perspective: Robert B Laughlin. *Phys Biol* 11:053003.
7. Onuchic, J. N. 2014. Physics transforming the life sciences. *Phys Biol* 11:053006.
8. Shukla, K. 2014. Research at the interface of physics and biology: bridging the two fields. *Phys Biol* 11:053007.
9. Fawcett, T. W., and A. D. Higginson. 2012. Heavy use of equations impedes communication among biologists. *Proc Natl Acad Sci USA* 109:11735.
10. Petkova, M. D., G. Tkacik, W. Bialek, E. F. Wieschaus, and T. Gregor. 2019. Optimal Decoding of cellular identities in a genetic network. *Cell* 176:844–855.
11. Prakash, K., B. Diederich, R. Heintzmann, and L. Schermelleh. 2022. Super-resolution microscopy: a brief history and new avenues. *Philos Trans A Math Phys Eng Sci* 380:20210110.
12. Deguchi, T., M. K. Iwanski, E.-M. Schentarra, C. Heidebrecht, L. Schmidt, J. Heck, *et al*. 2023. Direct observation of motor protein stepping in living cells using MINFLUX. *Science* 379:1010–1015.
13. Lieberman-Aiden, E., N. L. van Berkum, L. Williams, M. Imakaev, T. Ragoczy, A. Telling, *et al*. 2009. Comprehensive mapping of long-range interactions reveals folding principles of the human genome. *Science* 326:289–293.
14. Bialek, W., and D. Botstein. Introductory science and mathematics education for 21st-century biologists. *Science* 303:788–790.

15. Hsu, J. L., A. Chen, E. Cruz-Hinojoza, D. Dinh-Dang, E. A. Roth-Johnson, and B. K. Sato. 2021. Characterizing biology education research: perspectives from practitioners and scholars in the field. *J Microbiol Biol Educ* 22:e00147-21.
16. National Research Council, *et al*. 2003. BIO2010: Transforming undergraduate education for future research biologists.
17. National Research Council, *et al*. 2009. A new biology for the 21st century. National Academies Press, Washington, DC.
18. Labov, J. B., A. H. Reid, K. R. Yamamoto. 2010. Integrated biology and undergraduate science education: a new biology education for the twenty-first century? *CBE Life Sci Educ* 9:10–16.
19. Gross, L. J. 2004. Points of view: the interface of mathematics and biology: interdisciplinarity and the undergraduate biology curriculum: finding a balance. *Cell Biol Educ* 3:85–87.
20. Karsai, I, and J. Knisley. 2009. The role of institutes in interdisciplinary research and education. *J Coll Sci Teach* 38:32–37.
21. Matthews, K. E, P. Adams, and M. Goos. 2010. Using the principles of BIO2010 to develop an introductory, interdisciplinary course for biology students. *CBE Life Sci Educ* 9:290–297.
22. Tra, Y. V., and I. M. Evans. 2010. Enhancing interdisciplinary mathematics and biology education: a microarray data analysis course bridging these disciplines. *CBE Life Sci Educ* 9:217–226.
23. Thompson, K. V., J. Chmielewski, M. S. Gaines, C. A. Hrycyna, and W. R. LaCourse. 2013. Competency-based reforms of the undergraduate biology curriculum: integrating the physical and biological sciences. *CBE Life Sci Educ* 12:162–169.
24. Aikens, M. L., and E. L. Dolan. 2014. Teaching quantitative biology: goals, assessments, and resources. *Mol Biol Cell* 25:3478–3481.
25. Aegerter-Wilmsen, T., and T. Bisseling. 2005. Biology by numbers–introducing quantitation into life science education. *PLoS Biol* 3:e1.
26. Smolinski, T. G. 2010. Computer literacy for life sciences: helping the digital-era biology undergraduates face today's research. *CBE Life Sci Educ*; 9:357–363.
27. Speth, E. B., J. L. Momsen, G. A. Moyerbrailean, D. Ebert-May, T. M. Long, and S. Wyse. 2010. 1, 2, 3, 4: infusing quantitative literacy into introductory biology. *CBE Life Sci Educ* 9:323–332.
28. Depelteau, A. M., K. H. Joplin, A. Govett, H. A. Miller, 3rd, and E. Seier. 2010. SYMBIOSIS: development, implementation, and assessment of a model curriculum across biology and mathematics at the introductory level. *CBE Life Sci Educ* 9:342–347.
29. Colon-Berlingeri, M., and P. A. Burrowes. 2011. Teaching biology through statistics: application of statistical methods in genetics and zoology courses. *CBE Life Sci Educ* 10:259–267.
30. Rylands, L., V. Simbag, K. E. Matthews, C. Coady, and S. Belward. 2013. Scientists and mathematicians collaborating to build quantitative skills in undergraduate science. *Int J Math Educ Sci Technol* 44:834–845.
31. Hoffman, K., S. Leupen, K. Dowell, K. Kephart, and J. Leips. 2016. Development and assessment of modules to integrate quantitative skills in introductory biology courses. *CBE Life Sci Educ* 15:ar14.
32. Pevzner, P., and R. Shamir. 2009. Computing has changed biology—biology education must catch up. *Science* 325:541–542.
33. Pursell, D. P. 2009. Enhancing interdisciplinary, mathematics, and physical science in an undergraduate life science program through physical chemistry. *CBE Life Sci Educ* 8:15–28.
34. Rubinstein, A., and B. Chor. 2014. Computational thinking in life science education. *PLoS Comput Biol* 10:e1003897.
35. Anderson, W. A., U. Banerjee, C. L. Drennan, S. C. Elgin, I. Epstein, J. Handelsman, *et al*. 2011. Changing the culture of science education at research universities. *Science* 331:152–153.
36. Salazar, C, J. Schutze, O. Ebenhoh. 2006. Bioinformatics meets systems biology. *Genome Biol* 7:303.
37. Knisley, J., and E. Behravesh. 2010. Developing student collaborations across disciplines, distances, and institutions. *CBE Life Sci Edu*c 9:364–369.
38. Saunders, T. E., C. Y. He, P. Koehl, L. L. S. Ong, P. T. C. So. 2018. Eleven quick tips for running an interdisciplinary short course for new graduate students. *PLoS Comput Biol* 14:e1006039.
39. Duncan, S. I., P. Bishop, and S. Lenhart. 2010. Preparing the "new" biologist of the future: student research at the interface of mathematics and biology. *CBE Life Sci Educ* 9:311–315.
40. Milo, R., S. Shen-Orr, S. Itzkovitz, N. Kashtan, D. Chklovskii, and U. Alon. 2002. Network motifs: simple building blocks of complex networks. *Science* 298:824–827.
41. Balaskas, N., A. Ribeiro, J. Panovska, E. Dessaud, N. Sasai, K. M. Page, *et al*. 2012. Gene regulatory logic for reading the Sonic Hedgehog signaling gradient in the vertebrate neural tube. *Cell* 148:273–284.
42. Rosenfeld, N., J. W. Young, U. Alon, P. S. Swain, and M. B. Elowitz. 2005. Gene regulation at the single-cell level. *Science* 307:1962–1965.
43. Honegger, K., and B. de Bivort. 2018. Stochasticity, individuality and behavior. *Curr Biol* 28:R8–R12.
44. Saka, Y., and J. C. Smith. 2007. A mechanism for the sharp transition of morphogen gradient interpretation in Xenopus. *BMC Dev Biol* 7:47.
45. Bergen, V., R. A. Soldatov, P. V. Kharchenko, F. J. Theis. 2021. RNA velocity—current challenges and future perspectives. *Mol Syst Biol* 17:e10282.
46. Vrljicak, P., E. S. Lucas, M. Tryfonos, J. Muter, S. Ott, and J. J. Brosens. 2023. Dynamic chromatin remodeling in cycling human endometrium at single-cell level. *Cell Rep* 42:113525.
47. Cooper, M. M., and R. L. Stowe 2018. Chemistry education research-from personal empiricism to evidence, theory, and informed practice. *Chem Rev* 118:6053–6087.
48. Cary, T. L., C. J. Wienhold, and J. Branchaw. 2019. A Biology Core Concept Instrument (BCCI) to teach and assess student conceptual understanding. *CBE Life Sci Educ* 18:ar46.
49. Taylor, R. T., P. R. Bishop, S. Lenhart, L. J. Gross, and K. Sturner. 2020. Development of the BioCalculus Assessment (BCA). *CBE Life Sci Educ* 19: ar6.
50. Cai, Y., and A. Lönnqvist. 2021. Overcoming the barriers to establishing interdisciplinary degree programmes: the perspective of managing organisational innovation. *High Educ Policy* 35:946–968.
51. Latham, D. R., J. Alper, and H. Sanabria. 2023. Biophysics concept inventory survey: an assessment in biophysical undergraduate education. *Biophys J* 122:554a.
52. Clemmons, A. W., J. Timbrook, J. C. Herron, and A. J. Crowe. 2020. BioSkills Guide: Development and national validation of a tool for interpreting the Vision and Change core competencies. *CBE Life Sci Educ* 19:ar53.
53. Hand, B., L. D. Yore, S. Jagger, V. Prain. 2010. Connecting research in science literacy and classroom practice: a review of science teaching journals in Australia, the UK and the United States, 1998–2008. *Stud Sci Educ* 46:45–68.
54. Bovill, C. 2013. An investigation of co-created curricula within higher education in the UK, Ireland and the USA. *Innov Educ Teach Int* 51:15–25.
55. Marshall, A. G., Z. Vue, C. B. Palavicino-Maggio, K. Neikirk, H. K. Beasley, E. Garza-Lopez, *et al*. 2022. The role of mentoring in promoting diversity equity and inclusion in STEM Education and Research. *Pathog Dis* 80:ftac019.