

Thinking Models:

The Slippery Anthropology of Cephalopod Science

Claire Fedoruk

Department of Anthropology & Social Studies of Medicine

McGill University, Montreal

August 2019

A thesis submitted to McGill University in partial fulfillment of the requirements of the degree
of Master of Arts.

© Claire Fedoruk 2019

ABSTRACT

Cephalopods occupy a place of tension in biological discourse: simultaneously configured as radically “alien,” singularly innovative, unfathomable, and indeterminate, they also must be subjugated to scientific ideals in order to be justified as tractable model organisms. At the Marine Biological Laboratory (MBL) in Woods Hole, Massachusetts, neurobiologist Josh Rosenthal is spearheading an institute-wide initiative to establish a subclass of “intelligent” cephalopods (octopuses, squids, and cuttlefish) that have the ability to edit their own genes as novel marine model organisms. The present thesis explores the consequences of this attempt to produce cephalopods as neuroscientific models of intelligence: how, in practice, does one enact a “thinking model” and what are the conceptual stakes of such an endeavor? In addressing these questions, the cephalopod becomes visible as a site of considerable conceptual turbulence: for conventional scientific conceptions of model organisms as tools that come epistemically *after* a research question, for the notion of “intelligence” as a centralized and uniquely human capacity, and for forms of anthropology that take for granted “the” human as a uniquely thinking entity against a backdrop of unthinking nature. Indeterminacies arising from attempts to biologically map the cephalopod have generated questions that escape existing frameworks for model organisms and anthropocentric notions of intelligence.

RÉSUMÉ

Les céphalopodes occupent une place de tension dans le discours biologique: simultanément configurés comme radicalement «étrangers», singulièrement novateurs, insondables et indéterminés, ils doivent également être soumis aux idéaux scientifiques pour être justifiés en tant qu’organismes modèles traitables. Le neurobiologiste Josh Rosenthal du Laboratoire de biologie marine (Marine Biological Laboratory; MBL) de Woods Hole, dans le Massachusetts, dirige une initiative de l’institut visant à créer une sous-classe de céphalopodes «intelligents» (poulpes, calamars et seiches) capables de modifier leurs propres gènes comme nouveaux organismes modèles marins. La présente thèse explore les conséquences de cette tentative de produire des céphalopodes en tant que modèles neuroscientifiques de l’intelligence: comment, en pratique, actualiser un «modèle capable de pensée» et quels sont les enjeux conceptuels d’une telle entreprise? En abordant ces questions, le céphalopode devient un site de turbulence conceptuelle considérable: pour les conceptions scientifiques classiques des organismes modèles comme outils épistémiques *après* une question de recherche, pour la notion d’«intelligence» en tant que capacité centralisée et uniquement humaine, et pour les formes d’anthropologie qui tiennent pour acquis «l’humain» en tant qu’entité pensante unique sur un fond de nature irréfléchie. Les indéterminations résultantes des tentatives de cartographie biologique des céphalopodes ont généré des questions qui échappent aux cadres existants pour les organismes modèles et aux notions anthropocentriques d’intelligence.

TABLE OF CONTENTS

Acknowledgements	i
Introduction	1
Chapter I	5
The right animal for the job	6
A biology lab by the sea	12
A thinking model	16
Aliens on Earth	22
Chapter II	28
Enactments	29
Chapter III	39
Cephalopod culture	40
Conclusion	47
References	49

ACKNOWLEDGEMENTS

This thesis would not exist without a veritable multitude of people:

My interlocutors at the Marine Biological Laboratory, who were remarkably generous and open with their time, patiently explaining their research in terms that even I could understand. Additionally, I want to thank Jon Valencia and the group of graduate students taking the two-week Gene Regulatory Networks course at the MBL, who welcomed me into their evening activities and helped a newly-minted ethnographer feel more at ease in the field. My time at the MBL was peppered with unforgettable memories of squid fishing, matsutake hunting, quiet afternoons at the library, and witnessing the bioluminescent flashes of sea organisms along the beach at night. Thank you for infusing this project with your passion for biology and for the “supremely weird”!

My supervisor, Tobias Rees, whose deft guidance and support have been indispensable throughout this process, and whose anthropological sensibilities have always challenged me to work outside my established modes of thinking.

The members of my writing group, Kathleen Godfrey, Jason Hirsch, and Emmanuel Précourt Senécal, who provided much-needed intellectual and social nourishment. Other members of the anthropology department: Dortë Bemme, Adam Fleischmann, Jonathan Wald, Federico De Musso, Lluís Ferrer, Josh Friesen, Naim Clément, Samar Zora, and all those who toil in Peterson Hall.

All of the friends who have patiently supported me throughout this process, despite my infrequent but mostly incomprehensible ramblings about cephalopods. Thank you so much Jennifer Yadoo, Julia Nordlund, Naz Saadat, Karl Schmidt, Rine Vieth, Asad Walji, Saman Tabasinejad, David Protetch, Lillian Ross-Millard, Celeste Billung-Meyer, Starr Wang, Katie Elder, and Kimberly Turner. And thank you to Liam Cobbe for filling up the bucket at times when I needed it most. A special “bonus” thanks to Julia Nordlund for helping with the translation of my abstract, and for sticking around for all of these years!

Above all, I am grateful to my parents. Your distinctive mixture of unconditional support, vicarious anxiety, encouragement and advice, confusion, and a few much-warranted pushes have motivated me to finish this thesis like nothing else. I love you – thank you for everything.

INTRODUCTION

One evening at a local pub that the researchers tend to frequent, I find myself sitting with a visiting Professor in the MBL's two-week course on gene regulatory networks and a few graduate and post-doctoral students. During a lull in their animated conversation about the relative explanatory importance of natural selection versus genetic makeup, I ask the Professor why she chose to work with sea urchins as a model organism. She turns to me for the first time that evening. With a hint of impatience, she explains that she works with sea urchins because they're simple and easy to work with, and they help her elucidate some general biological principles – not because she has any particular interest in them. Another graduate student chimes in, explaining that he tried to work with sponges, which he ultimately decided were a terrible model because they proved incredibly difficult to maintain, especially without established protocols for keeping them in a laboratory setting. As he eloquently puts it, “Making a new model organism is a pain in the ass.”

Yet my interlocutors are undertaking exactly such a project. At the Marine Biological Laboratory (MBL) in Woods Hole, Massachusetts, neurobiologist Dr. Josh Rosenthal is spearheading an institute-wide initiative to make certain species of coleoid cephalopods (octopuses, squid, cuttlefish) into viable model organisms for biological research – what I will refer to as the “cephalopod initiative” for lack of a better term.

I arrived in Woods Hole at the beginning of October 2017 and spent roughly a month with the various MBL researchers and staff who work with and on cephalopods in various ways. Throughout my fieldwork, I would see that graduate student's statement manifest first-hand through the elaborate, time-consuming, and costly operations of the cephalopod initiative. While the more common species of cephalopods are not particularly difficult to find and extract from

the sea, they are notoriously troublesome organisms to *keep* in a laboratory setting, illustrated by ubiquitous media coverage of piratical octopuses that escape from their tanks at night, pillaging fish from other tanks and escaping through drainpipes (Roy 2016), or tampering with equipment to flood (Dell’Amore 2009) or even shortcircuit (2008) entire aquariums. Further, their delicate developmental processes and short lifespan mean that most attempts to breed cephalopods over successive generations have historically failed (Sykes, Koueta, and Rosas 2014), greatly limiting any kind of biological work that requires precise control and manipulation of an organism’s genetic composition.

So, why then are Josh Rosenthal and a whole array of MBL staff going to such lengths to produce an infrastructure for establishing cephalopods as novel marine model organisms? Clearly, he and his associates have come to see this initiative as a worthwhile scientific venture, despite being an ostensible “pain in the ass,” in sharp contrast to the researchers that I met at the pub that night. This striking impracticality became a launching point for the present thesis. One can’t help but wonder: what is it about cephalopods in this particular context that makes them worthy of such trouble? During my time at the Marine Biological Institute, an alternative but parallel question emerged: what is it about the use of cephalopods as model organisms that invites scientific and conceptual trouble?

To contextualize these questions, Chapter I will introduce cephalopods as a centerpiece for pragmatic and conceptual upheaval on the backdrop of rapidly-evolving understandings of model organisms, but also a focus for hope and nostalgia. To start, I will outline some of the scientific discourse surrounding model organisms in marine sciences, namely a basic understanding of these organisms as useful tools that are selected for their ability to generate universal insights about the world, a premise which is increasingly undermined by recent

developments in genomics and scientific backlash toward the perceived artificiality of research on popular models. In the subsequent section, I will frame the cephalopod initiative from the institutional logic of the MBL, explaining how the initiative embodies a hoped-for return to the days of foundational discoveries that once established the MBL as an international hub for research, in what is now a time of institutional precarity.

Next, I trace Josh Rosenthal's discovery and subsequent study of a biological phenomenon in cephalopods called RNA editing, thought to be a possible genetic and evolutionary mechanism that enabled the cephalopod's remarkable intelligence. I argue that this discovery defies conceptions of model organisms as tools that come epistemically *after* a research question, but instead pose novel questions in their own right, suggesting a reconfiguration of "intelligence" as a form of genetic plasticity. The final section of this chapter raises the pop-science figure of the "alien," often conjured by my interlocutors as a rationale for studying the cephalopod. While the notion of an "alien model" inheres certain epistemic tensions, I argue that the fundamental indeterminacy of aliens, and associated failures to biologically map the cephalopod, have generated previously unthinkable questions that escape existing frameworks for model organisms and anthropocentric notions of intelligence.

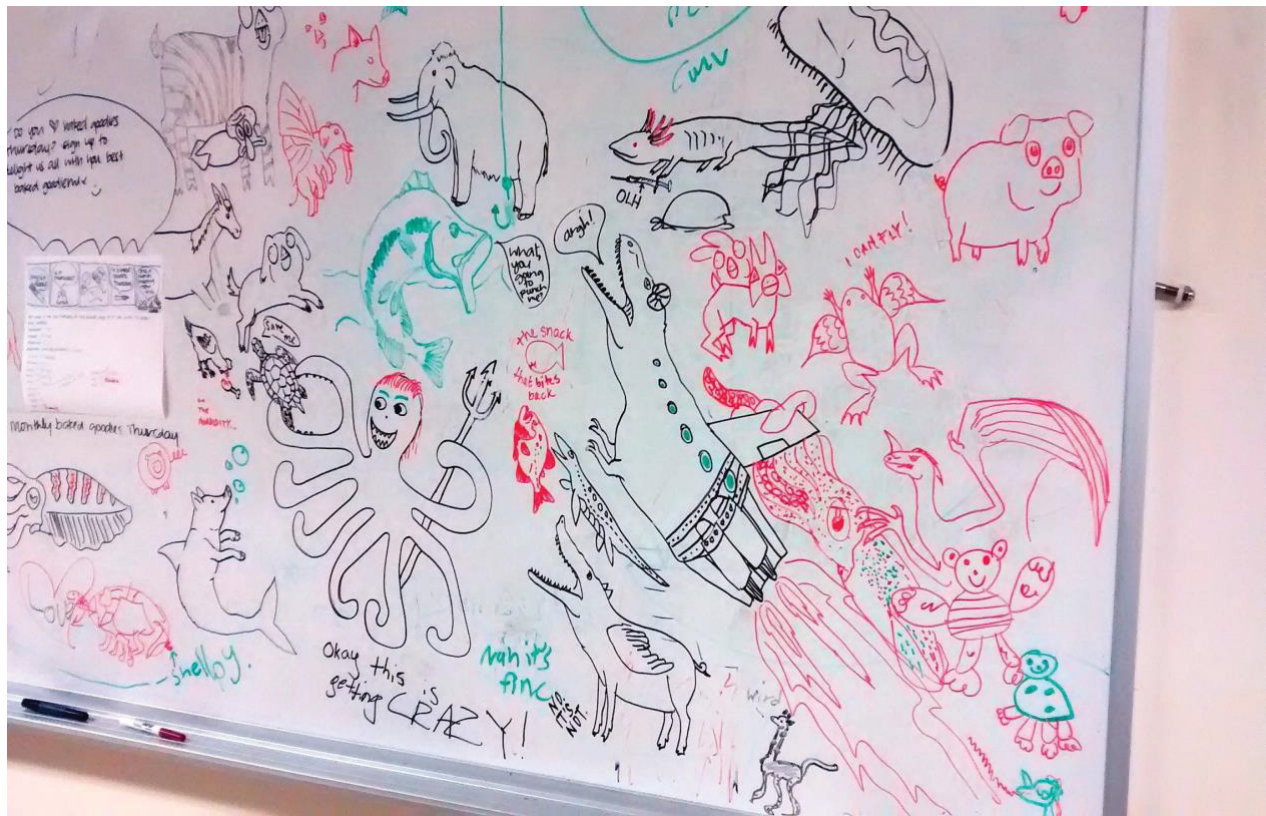
Chapter II explores these questions through an entirely different route, via a series of ethnographic vignettes depicting my time with cephalopods and cephalopod researchers at the MBL. I draw from anthropologist Ann-Marie Mol's notion of "enactment" to examine the various techniques that collectively constitute a squid as the site of RNA editing, rendering it a tangible, viewable phenomenon that takes on different forms at different moments as the researchers deal with various problems and protocols. Taken together, these techniques

operationalize important conceptual questions, such as: can “thinking” take place outside the squid’s brain?

My third and final chapter will use a conversation I had with one of the postdoctoral students as a launching point to consider possible intersections between the disciplines of marine biology and anthropology, which both traditionally engage with instantiations of radical difference. What does the recognition of “alien intelligence” mean for disciplines like anthropology and other social sciences that were largely founded on a notion of “the” human as a uniquely rational, cultural entity against a backdrop of unthinking nature? How could one conduct an anthropology from the perspective of cephalopod after “the” human? Although this thesis in no way conclusively addresses these questions, the field of cephalopod science opens up an epistemic space in which notions of “thinking” and therefore “the” human are in flux.

Writing about scientific models of the brain, anthropologist Nicolas Langlitz has said that “The choice of model establishes a paradigm... Whole cosmologies are folded into these models.” (Langlitz 2017, 16). In this thesis, I am not interested in firmly establishing a generalizable epistemic or ontological status of model organisms, so much as determining what imaginings the cephalopod as model possesses for my interlocutors at the MBL, and how these imaginings may sometimes upend fundamental notions about model organisms, cephalopods, and humans, even beyond the marine sciences. What paradigms does the cephalopod invoke or inaugurate in the context of model organisms research? What cosmologies does the cephalopod contain within it?

CHAPTER I



A whiteboard in the communal kitchen outside Dr. Josh Rosenthal's office.

The right animal for the job

On the top floor of the building where Dr. Joshua Rosenthal works, the physical space is organized not along social lines, in the human sense, but along organismal lines. A pale blue streak of tape runs along the floor next to my desk, demarcating the separation between Rosenthal's lab, whose occupants study a subclass of cephalopods known as coleoid cephalopods (cuttlefish, squid, and octopuses), and a neighbouring lab that investigates a viciously-toothed fish called the lamprey. If you visited the lab in October 2017, as I did, you might have noticed two whiteboards: one just inside the entrance of Rosenthal's lab that cheerfully wishes onlookers a "squidly day!" Over in the floor's communal kitchen, which is shared by at least three or four labs, a second large whiteboard is covered with drawings of various intermingling organisms, some fantastical combinations of marine and non-marine animals and others more biologically-accurate renderings of model organisms, including the octopus, squid, and cuttlefish that Rosenthal and his students investigate.

As I encountered more students and researchers in my daily wanderings around the MBL's facilities, I began to notice that their introductions typically followed a certain format:

My work is on RNA editing in cephalopods.

I study gene regulatory networks using sea urchins.

My research? It's on spinal regeneration in lampreys.

I investigate the visual system of a fish species called the skate.

Or similar. It became clear that model organisms are the fundamental tools of these researchers' daily work. A classical anthropologist might comment that the researchers claim a kind of totemic affiliation with their model organisms; they provide a backbone (though at the MBL, the organisms frequently lack one) around which to self-identify and collectivize. Or a more contemporary scholar might emphasize the particular socio-historical context surrounding the

construction of specific models. A philosopher of science may have noted that they almost always articulate their research in terms of a duality between a biological process or phenomenon and an organism that exhibits this phenomenon, thereby making it accessible to study.

Very soon after my arrival, I realized that I had taken for granted that I knew what a model organism was in even the most basic terms. A simple online search readily supplied a few standard definitions of model organisms. Merriam-Webster Dictionary defines an animal model as “an animal *sufficiently like humans* in its anatomy, physiology, or response to a pathogen to be used in medical research in order to obtain results *that can be extrapolated to human medicine*” (2018). Oxford Dictionary’s definition of an animal model is “An experimental model, especially of a disease or other pathological process, using animals *in place of humans*.” On Wikipedia, a model organism is a “*non-human* species that is extensively studied to understand particular biological phenomena, with the expectation that discoveries made in the model organism will *provide insight into the workings of other organisms*.” Notably, these definitions all tend to emphasize a degree of commensurability between the model organism and other organisms, usually humans, through which the organism could serve as a simplified proxy for demonstrating translatable principles. Model organisms, in my distinctly un-scientific understanding, seemed to occupy a vaguely-delineated territory of not-human, yet human-like enough to adequately represent aspects of the human.

How do the MBL students and researchers conceive of model organisms, the “bread and butter” of their day-to-day lab work? Unsurprisingly, some were taken aback by my basic and perhaps naïve questions about such a fundamental aspect of biological research. Indeed, their interest seemed to concern less what a model organism *is* than what it can be *good for*. When asked about their choice of model, many researchers extolled the virtues of their favoured

organism at length: the ease of capturing the organism in the wild and breeding it in the laboratory, rapid life cycles that shorten experiment times, transparent eggs allowing easy observation of the organism's development, eyes that function similarly to human eyes, or the sheer biological simplicity of their model organism. Many of the scientists I spoke with expressed that their choice of organism hinges on such pragmatic factors, a sentiment that I began to think of as “the right animal for the job” (Singer 2016, Ankeny and Leonelli 2011). As the professor I spoke with at the pub explained, her work with sea urchins was not driven by any particular interest in the organism itself, but with the general principles one can draw from their biology.

Configured in this way, the choice of model organism comes temporally and epistemologically *after* the choice of scientific question. In other words, the fundamental research question is of primary importance and then the most appropriate model organism is chosen, in the same way that someone chooses the most appropriate tool for a home repair.¹ Yet, even a brief stay at the MBL revealed the inadequacy of this analogy for researchers whose daily use of model organisms reflect a broader, thornier landscape of knowledge production.

Indeed, there are many situations where the organism comes first, in which pragmatic constraints guide epistemic decisions, or even become indivisible in the process. Perhaps one of the most important things that makes an organism a model is simply that “we already know a lot about them,” as one student put it. Biological research has traditionally centered around a

¹ This sentiment echoes the Krogh Principle, first introduced in a 1929 essay by physiologist August Krogh, who stated: “For a large number of problems there will be some animal of choice or a few such animals on which it can be most conveniently studied” (Lindstedt 2014, 1640). In an essay, Krogh joked about the constructivist implications of his principle, reminiscing that “[w]e used to say as a laboratory joke that this animal had been created expressly for the purposes of respiratory physiology” (Lindstedt 2014, 1640).

standard set of ubiquitous “supermodels,” such as the mouse, fruitfly, nematode worm, zebrafish, and African clawed frog, to name just a few (Maher 2009). Over the years, scientists have accumulated massive amounts of information characterizing these organisms on molecular, genomic, behavioural, and ecological scales. Global scientific infrastructures have emerged to facilitate data sharing and best practices for the use of individual supermodels. Whole careers and communities are built around one particular model organism. Whatever the original rationales for selecting these particular organisms,² they now act as powerful tools of social capital that, when employed, grant elevated political and economic credibility to projects (Ankeny and Leonelli 2011). Conversely, establishing new models outside of this infrastructure involves major time investment, career flexibility, ample funding, and significant institutional support (Gladfelter 2015). Even using a non-model organism in research requires extensive justification when applying for grant funding (Bolker 2012).³

Some argue that this hegemonic status has become highly problematic. It is a research assistant at the MBL who first informs me that a subset of the scientific community refuse to identify their work as model organisms research, preferring to adopt the philosophy of using “different animals to answer different questions.” These researchers are disturbed by what they perceive as the increasing homogeneity of model organisms, which capture just a tiny fraction of the earth’s biodiversity, yet are used to extrapolate fundamental biological laws (Bolker 2012,

² Some argue that these supermodels are in fact “models of convenience,” selected through a confluence of availability and historical accident, rather than intentional decision-making processes (Bolker 2012).

³ Philosopher Peter Godfrey-Smith takes scientific models as a kind of collective fiction that allows continuity and communication between scientists. This fiction can result in scientific “inertia” when researchers cling to particular models amidst surrounding changes in knowledge that render the original rationale for the model’s use null (Godfrey-Smith 2009).

Gladfelter 2015, Sullivan 2015). If the choice of organism determines many key aspects of research, including what questions can be asked and how they can be addressed, then using the same model organisms will result in a loop of self-contained, self-fulfilling knowledge.^{4, 5}

These critiques invoke a nostalgia for the pioneering days of model organism research, when scientists like Thomas Hunt Morgan, who founded the use of the fruitfly as a model organism, investigated at least 50 different organisms, producing a dizzying array of biological questions that remain unanswered today (Goldstein and King 2016). Biologists Goldstein and King underscore the need for more such fundamental “curiosity-driven” research: “If one reads cell biologist authors of that era, or if one follows his or her curiosity and thinks about fascinating questions from first principles, a very different landscape of ideas may emerge than does from reading modern cell biology textbooks—which necessarily focus mostly on the questions that have already been answered.” (Goldstein and King 2016, 819).

In many ways, the landscape of model organisms research is already in turbulence. During the “genomic era” of the 1990s, the landscape of model organisms research became deeply connected with the possibilities afforded by new genetic technologies. A new set of technologies called Next Generation Sequencing emerged that made it possible to produce

⁴ The notion that model organisms are more than generalizable representations of the world is not new. Social scientists have traced the histories of individual model organisms, showing how each possesses its own specific epistemological trajectory: different contexts have differently constituted them as the objects of knowledge production. Multispecies ethnography and Science and Technology Studies approaches, on the other hand, emphasize the complex entanglement of humans and non-humans, and the mutual constitutivity running through these assemblages.

⁵ These critics worry that the stakes of said epistemic loop go far beyond the field of biology: Amy Gladfelter, a Professor of Molecular Biology and occasional MBL researcher, argues that “work in nontraditional model systems is an imperative for our society to prepare for problems we do not even know exist” (Gladfelter 2015, 3687).

massive amounts of genetic data very rapidly and at a fraction of their previous cost (Ekblom and Galindo 2011). In particular, high-throughput sequencing has enabled relatively fast and affordable access to a diverse array of genomes, meaning that researchers are far less limited to the standard collection of model organisms, leading some scientists to predict that “an ever-expanding breadth of model systems may be a hallmark of future cell biology” (Goldstein and King 2016). The era of supermodels may be coming to an end.

These days, the ability to tinker with an organism’s genetic makeup has also rendered the notion of simply selecting the “right animal for the job” considerably messier. In earlier times, researchers might selectively breed certain organisms in order to produce offspring that possessed “natural” qualities that make them good models of certain phenomena (e.g. epilepsy) (2012). The advent of gene editing tools that can (sometimes reversibly) alter small sections of the genome with increasing precision, means that scientists can now manipulate organisms for specific purposes to an unprecedented degree. When I asked one of the postdoctoral students in Rosenthal’s lab for his definition of a model organism, he gave a less-than-straightforward answer:

Models evolve. The more they’re used, the more you know. Every year, more and more strains are developed that are useful for different aspects. If you knock out (colour) pigments, it’s easier to image them. So these strains of zebrafish with pigments knocked out are now their own little sub-model. Or you mutate some gene that makes them epileptic so now suddenly it’s a model for epilepsy whereas the original zebrafish wasn’t. So it’s nuanced.

The newfound ability to manipulate the genes of experimental organisms with ease and precision allows new “versions” of models can be cultivated through genetic manipulations that elicit an entirely novel or “unnatural” attribute of interest to researchers, like epilepsy in a zebrafish. These models can no longer be conceptualized as static representations of “nature”; they are flexible and emergent beings that complicate a simple tool/job dichotomy.

One can't help but think of the fanciful drawings of model organisms adorning the communal whiteboard between labs: the aquatic xenopus with bird wings, an octopus with red hair, the pig-dolphin and elephant-butterfly hybrids, and a T-rex whose lower half appears to be a turbo jet. In their own playful way, these images evoke the growing destabilization of conventional model organisms research, as well as a subversion of boundaries between different species and between living organisms and technologies, made possible by a growing understanding of genomics and its applications. Do these drawings contain an implicit vision of the future of model organisms research? If so, what is this imagined future?

A biology lab by the sea

Since its inception in 1888, the Marine Biological Laboratory has prided itself on the caliber of scientific discoveries produced by the many researchers who frequent the institution as a summer research centre and the relatively few who work there year-round. During my stay, a number of researchers proudly asserted that the MBL has historically set itself apart from other marine biological institutes by its contributions toward the elucidation of broader biological principles: over the years, researchers associated with the MBL have cumulatively won over 57 Nobel Prizes (2019a).

In the 1970s, immunologist Lewis Thomas rhapsodized about the golden age of basic discoveries that could only have taken place at the MBL. More than a mere laboratory, it was “a paradigm, a human institution possessed of a life of its own, self-regenerating, touched all around by human meddle but constantly improved, embellished by it” (Thomas 1978, 58). A continuous stream of scientists from around the world were drawn to the MBL's prestigious summer courses and the generativity that resulted from the collective intelligence of hundreds of

congregated scientists. From their improbable observations about the local wildlife, these scientists would ultimately lay the groundwork for the contemporary fields of visual physiology, developmental and reproductive biology, ecology, and neurobiology over decades of summers. Lewis proclaims: “If you can think of good questions to ask about the life of the earth, it should be as good a place as any to go for answers.” (Thomas 1978, 61). As almost every researcher I met assured me, the MBL’s historical importance as one of the first marine centres for world-class research in the biological sciences cannot be understated.

Take the example of the “Woods Hole squid” *Loligo pealeii*, a local species of squid and now the de facto mascot of the MBL (squid motifs are ubiquitous on campus and in the handful of tourist shops and restaurants that comprise “downtown” Woods Hole). Much of our current scientific understanding of how signals are transmitted through the nervous system was originally derived from studies at the MBL using this species of squid as a model. In the early 1930s, the now-famous biologist JZ Young ascertained that the transparent strands he observed in the “Woods Hole squid” were in fact enormous nerve fibers that conducted electrical signals (Young 1996). Shortly thereafter, researchers realized that they could exploit the large diameter of these giant axons to directly measure action potentials by inserting an electrode, which was impossible in the relatively tiny axons of humans. Scientists Hodgkin and Huxley would later receive the Nobel Prize in 1963 for their work on the biophysics of ion channels, headlining a legacy of research that would use the giant squid axon to uncover the basic functioning of the nervous system (Keynes 2005).

Despite the MBL’s continued popularity as a seasonal hub for scientists from around the world, recent decades have seen a decline in its importance as a site of major discovery. Marine organisms had seen their status wane amidst the hegemonic popularity of “supermodels” like the

fruit fly, mouse, and nematode worm. The MBL's operations became increasingly unsustainable from a financial perspective.⁶ This crisis came to a head in 2013, when the MBL was forced to become an affiliate of the University of Chicago, losing its status as an independent research institute for the first time in its lengthy history. Thus, the MBL's move to reinvent itself was not merely an opportunity to revitalize its historical status, but a practical necessity.

In one of our conversations, Josh explains that marine research institutes like the MBL have increasingly faced a choice between two diverging trajectories over the past decades. The majority of marine institutes have come to be dominated by environmental and ecological approaches within biology, a niche made possible by the diverse resources available to these oceanfront institutes. This type of research tends to focus on the holistic understanding of an organism within its geographic or ecological setting; hence, the setting is critical, but not so much the use of model organisms that provide universal information or direct applications for the human.

An alternative option, as Josh explains, is to move towards the use of standard model organisms, such as *drosophila* or mice: to become, essentially, a “biology lab by the sea.” Josh must sense my incredulity at the thought of a marine biology institute that predominantly researches non-marine organisms, because he doubles down on this assertion with an anecdote:

There's a biology institute in Maine – it's a small version of the MBL. They had a director that came in there and brought in all people who work on standard models. They're this little island

⁶ Until its affiliation with the University of Chicago, the MBL prided itself as an independently-functioning private research site without the kind of oversight or institutional entanglements that could potentially threaten the integrity of scientific research. The MBL's existence has been primarily funded through grants, 50% of which came from the federal government, and the rest from institutional fundraising and private donors (Reckford 2013). However, cuts to federal funding in recent years have made it increasingly difficult for independent research centres like the MBL to stay afloat (Gwynne 2014).

in the ocean. It kind of worked in the sense in that it got people more grant funding but it's not taking advantage of the local resources... You've got to ask yourself too, at a small institute, working on these mainstream systems, are you going to compete well with MIT and Harvard and Stanford, and all those places? With the resources they have, it's going to be hard to compete.

I am struck by the incongruity of the image: a biology institute that does not exploit its niche, but is instead fashions itself into an artificial “island in the ocean.” This is hardly the unbridled potential of the MBL's early days, when basic curiosity about the natural world ruled amidst concerns about limited funding and institutional support. On an institutional level, this notion of a “biology lab by the sea” arguably parallels scientific tension between the use of standard models and critiques that they have become so highly engineered and de-contextualized as to severely limit the scope of biological research, and perhaps more fundamentally, tension between the desire for new discovery versus the standardization, continuity, and precision that popular models may offer.⁷

Instead of distinguishing itself through one of these trajectories, the MBL has sought an alternative approach in order to revitalize its historical status. Rather than forsaking the basic sciences or absconding to popular model organisms, the MBL decided to simply create and popularize new model organisms: *marine* model organisms, to be exact, which would both take advantage of their seaside niche and reconfirm the MBL's importance as a seasonal hub for international research. This initiative would become the first of the MBL's four strategic research

⁷ This tension has been re-imagined in biologist William Sullivan's fanciful take on Italo Calvino's novel *Invisible Cities*. In a brief essay, Sullivan imagines a mythical “Institute for the Study of Non-Model Organisms” where researchers are provided with the funding and infrastructure needed to freely pursue their study of the most bizarre and overlooked creatures, with whole teams devoted to the cultivation of these organisms (Sullivan 2015). Like the growing demand for many varieties of exotic fruit and vegetables that are rarely stocked by Western grocery stores, a yearning for diversity is increasingly beginning to infect biologists, who wish to “taste the scientific delights of non-model organisms” (Sullivan 2015, 388).

themes published in April 2016: to access and exploit the “vast diversity of life” in the oceans, that represent “the next frontier of basic biological discovery” (2016). The mission statement calls for a “*renaissance* of biological discovery in marine organisms”; that is, a renewal of the fundamental breakthroughs and spirit of curiosity that characterized the MBL’s golden era.

A key figure in this initiative, neurobiologist Dr. Josh Rosenthal was recruited by the MBL as a full-time Senior Scientist in January 2017 to work towards their goal of producing the infrastructure for new marine model organisms, specifically the cephalopod. It is no coincidence that it is in this atmosphere of nostalgia for past exploits, spurred by a desperate institutional need for transformation, innovation, and adaptation, that the cephalopod initiative was conceived. It is also unsurprising that they would select Josh Rosenthal to lead this initiative, whose work up to that point perfectly embodied an ethos of basic discovery and was poised to vault the cephalopod back into its former eminence.

A thinking model

When we last left the Woods Hole squid in the 1960s, it was still in its glory days as a model organism, its giant axon becoming the site of one key discovery after another. By the 1990s, the squid was still by far the most important model for electrical excitability and Josh Rosenthal was just one postdoctoral student among many using its axon to investigate the biophysics of ion channels. Ion channels are like tiny gates studding the cell membranes of neurons, the basic units of the nervous system. They control the flow of charged particles (ions) in and out of the neuron, thus creating and regulating the electrical signals that transmit information through the nervous system (Huettner 2013). The basic functions of our nervous system –movement, sensation, thought– are all regulated by such electrical signals. Different

types of ion channels have different effects on nervous system signals, and many researchers had worked for years to characterize the specific ion channels in squid axons in order to better understand their equivalents in the human nervous system.

Scientifically-speaking, then, Josh was a direct heir to the work of Hodgkin and Huxley who first used the giant axon to model electrical signals in neurons, still chipping away at the many nuances of how ion channels regulate the nervous system. In fact, Josh's project was to clone and sequence the genome of the very same ion channels that Hodgkin and Huxley had famously worked with. Such a project had only recently become possible in the context of the "genomic revolution" and accompanying technologies that allowed long genetic sequences to be determined more cheaply and efficiently than ever before. Despite these breakthroughs, cloning a segment of DNA was still relatively slow and painstaking work at the time. In doing so, Josh encountered a complication: no matter how many times he carefully cloned the squid's DNA, he was unable to get a consistent sequence, which perplexed both him and his supervisor. After much head scratching, they gradually "put two and two together," realizing that they were observing a phenomenon called "RNA editing" that had only recently been discovered at the end of the 1980s.

In order to be expressed as a physical trait, the original DNA sequence that makes up a gene is replicated by a pathway of different molecules that actually enact the change. A segment of DNA is first "transcribed" into a complementary segment of the molecule RNA, which is then "translated" into a string of amino acids that collectively form a protein, which are the fundamental physiological actors and structures of life (2019b). This process constitutes perhaps the most fundamental doctrine of cellular biology: that DNA is a biological script, faithfully read and carried out by the intermediary RNA. In RNA editing, however, certain segments of RNA

are intercepted by enzymes called ADARs (Adenosine Deaminase that Acts on RNA), which enact a small but critical change to the genetic code that may drastically alter or even render the final protein product useless (Rosenthal 2015). Although minute, a single edit like this can mean the difference between having a devastating genetic disease like muscular dystrophy or not (Cross 2019). Thus, RNA editing contradicts a straightforward DNA → RNA → protein doctrine, showing that, far from a mere transmitter of genetic information, RNA itself plays an active role in the process of determining what kind of protein is created or whether a protein is created at all (Rosenthal 2015, 1814).⁸

RNA editing is a “natural” occurrence, in that potential sites exist that are vulnerable to editing exist in the genetic code of all organisms, vertebrates and invertebrates alike. In theory, RNA editing could impact up to 50% of all the proteins produced in an organism, the basic building blocks of life. However, until recently, RNA editing had rarely been observed in active parts of the human genome or among the standard model organisms for which there existed thorough genetic profiles (Rosenthal and Seeburg 2012). When Josh sequenced sections of the squid genome and noticed consistent discrepancies in transcriptomes (the entire collection of RNA sequences in a cell), he realized not only was the squid’s genome speckled with potential editing sites, but that that RNA editing was actively happening. Throughout the late 1990s to

⁸ RNA editing is just one phenomenon among many that characterize an era of “post-genomics,” a term indicating that the scope of scientific inquiry has transcended that of simple DNA sequences. While still focally concerned with genetics, we now understand that a variety of mechanisms and factors regulate gene function and expression, from the molecular level to environmental. This form of biology goes beyond the sequence, and beyond the dogma that DNA is faithfully translated into RNA. Gene editing, poly-genomics, epigenetics, symbiotic relationships involving a mixing of genetic materials all complicate genetic reductionism, hearkening “The reversal of the question ‘What is the genetic message?’ into its opposite of ‘What is the DNA being told?’” (Franklin 2006, 169)

early 2000s, new sequencing technology made it possible to catalogue the presence of editing in many non-model species. By analyzing genetic sequences from the squid's closest cephalopod relatives, the octopus and the cuttlefish, Josh and a team of researchers established that RNA editing occurs in unprecedented rates in these organisms (Alon et al. 2015). This suggested a set of new questions that would define the rest of Josh's career: why do coleoid cephalopods edit so much in comparison to other organisms? What evolutionary purpose does RNA editing serve?

In "conventional" Darwinian evolution, physical changes occur when a mutation occurs in a DNA sequence that codes for a gene, impacting the final protein product; RNA editing instead introduces a paradigm in which "organisms use RNA as a canvas to modify and enrich this flow of information" (Alon et al. 2015), thus introducing an alternative and even more powerful source of genetic diversity that serves as fodder for the evolution of novel traits. Moreover, RNA editing has several theoretical advantages over conventional evolution. For one, it is highly specific, capable of implementing fine-tuned adjustments to the production of proteins. Conventional evolution, on the other hand, may involve modifications to multiple areas of DNA that might result in a mixture of advantageous and disadvantageous traits. Second, RNA editing is incredibly fast. A useful physiological trait can take many generations to emerge through conventional evolution, whereas RNA editing can happen within a matter of hours. Thirdly, RNA editing is reversible, enabling a high level of flexibility in different situations. Unlike conventional evolution, RNA editing "enables the potential fitness of new mutations to be sampled gradually" (Liscovitch-Brauer et al. 2017, 1817). In other words, RNA editing has the potential to be a highly specific, speedy, and flexible technique that expands the range of physical characteristics that can emerge from the same set of DNA.

Several major findings have helped Josh and other researchers elucidate the biological significance of RNA editing in cephalopods. In both vertebrate and invertebrate organisms, RNA editing appears to be most common in the nervous system tissues (Rosenthal and Seeburg 2012). In the squid, almost 60% of all RNA sequences studied appeared to be subject to RNA editing, particularly in sites that are critical for controlling the excitability of neurons (Alon et al. 2015). As an example, in 2012, Rosenthal and collaborators found that cold and warm-climate octopuses possess similar genes encoding for ion channels; however, extensive RNA editing only appears to take place in the cold-climate octopuses, ostensibly for the purpose of adopting optimal neurological responses in response temperature fluctuations (Garrett and Rosenthal 2012). In these cold-climate octopuses, RNA editing allows certain ion channels to close rapidly and without a long refractory period, thus allowing neurons to fire efficiently even at colder temperatures, which would normally slow the speed of neural signals. Such an adaptation would be particularly important in cold-blooded organisms like the cephalopod that lack the thermoregulatory capacities of mammals (Garrett and Rosenthal 2012).

Another clue to the evolutionary significance of editing emerged in 2017, when Rosenthal and his collaborators measured the presence of RNA editing in a wider selection of cephalopod species. Cephalopods are divided into two distinct subclasses, the shell-less, behaviourally-sophisticated coleoid cephalopods (squid, cuttlefish, and octopuses) and their “primitive” shelled cousins, the nautiloid cephalopods (Schweid 2014). Along with researchers in Tel Aviv, Rosenthal found that RNA editing was employed extensively by the coleoids, but not at all by the nautiloids (Liscovitch-Brauer et al. 2017), RNA editing has played a key role in the evolution of the coleoid cephalopod’s “intelligence;” in other words, it appeared that only “smart” cephalopods edit their genes.

Intelligence, from this perspective, contains multiple conceptual layers. Physiologically, coleoid cephalopods possess nervous systems that are far larger and more complex than any other invertebrate, including specific lobes for learning and memory, whereas the nautilus has only a simple nervous system layout. Josh's paper notes that the common octopus nervous system contains roughly five times as many neurons as a mouse, for example (Liscovitch-Brauer et al. 2017). On a behavioural level, coleoid cephalopods are well-known for their wide repertoire of "intelligent" behaviours and advanced cognitive abilities, including memory, learning, personality ("inter-individual differences"), possible tool use, and the ability to play. (O'Brien, Roumbedakis, and Winkelmann 2018) (Nakajima et al. 2018). Tied to this is an evolutionary rationale for the coleoid cephalopod's intelligence, which emerged as a result of a trade-off between losing the protection of a shell and acquiring enhanced cognitive and behavioural flexibility. In fact, cephalopods and humans share a common evolutionary narrative: both were physically-vulnerable organisms (the human due its large brain and long developmental period, and the cephalopod due to the loss of its shell) that evaded major predators and bested competition through sheer intelligence.

By inviting yet another layer through which to conceptualize the cephalopod's intelligence, RNA editing suggests an entirely different evolutionary and genetic pathway to intelligence that is unique to cephalopods: as Josh's article concludes, "Extensive recoding is an invention of coleoid cephalopods (Liscovitch-Brauer et al. 2017, 191). Beyond the behavioural, cognitive, or physiological, the cephalopod's innovation occurs on a molecular, genetic level. Intelligence is reconfigured as a form of genetic plasticity.

Practically speaking, by serving as a simple model for all other axons, including those of humans, the squid's giant axon was the perfect tool for extrapolating toward universal biological

laws. Josh's initial work on the biophysics of ion channels employed the same logic as those of his predecessors, wherein the axon, and by extension the squid, was merely the "right animal" for representing the basic mechanisms of the nervous system. His discovery of RNA editing in the squid and other coleoid cephalopods, however, ran inverse to this logic. What was originally just the "right tool for the job" became the source of unexpected questions that could only be addressed through the cephalopod. Far from just a passive vessel, the cephalopod itself delimited a new area of research that imagines an alternate route to cognitive sophistication.

Arguably, then, cephalopods are *not* good model organisms in the traditional sense of the term. In the 1970s, a contemporary of JZ Young disparaged his attempts to use the octopus as a simple model for memory, saying, "Invertebrate brains are not necessarily simpler than vertebrate brains, they are merely different. Both are horribly complicated" (Kloot 1973). Instead of representing a simplified proxy of an equivalent human system, the cephalopod neural system defies most conventional scientific understanding of the basic genetic and nervous system functions that form the basis of the human's ostensibly singular "intelligence."

Aliens on Earth

In the octopus, man can recognize a stranger and a brother, a sapient being from another world.

- George O. Mackie (1972), Professor Emeritus of zoology at the University of Victoria

A general enthusiasm for exploring the uncharted territory of the bizarre and dramatically non-human seemed to prevail among those working on the cephalopod initiative. When I met with Bret Grasse one afternoon, the newly minted Manager of Cephalopod Operations at the MBL, he was full of superlatives about his favourite organisms. In fact, his career has centered

on promoting public interest and institutional investment in cephalopods – a cause that he genuinely believes in. In 2009, Bret managed to land his dream job as an aquarist at the Monterey Bay Aquarium in California almost directly out college. At a world-class aquarium like Monterey, every aquarist wants to make themselves indispensable by establishing a specialization or particular brand. To chisel out a niche among what he saw as “alpha personalities” like the “jellyfish guy” and “starfish girl,” Bret decided to hone his expertise in one of the most notoriously difficult marine organisms to culture.⁹ During his time at the Monterey Bay Aquarium, he invented a novel way to cultivate cuttlefish by running tubing through standard plastic soda bottles to provide their eggs with an optimal flow of oxygen bubbles and water depending on their developmental stage. The resulting contraption looks makeshift, but is very effective. Another innovation he calls the squid “cradle” resembles a mini-hammock on which pockets of closely monitored cuttlefish eggs are gently bounced up and down. When I dropped by the Marine Resources Center at the end of my stay in Woods Hole, Bret’s cuttlefish cradle had given rise to newly hatched flamboyant cuttlefish (*Metasepia pfefferi*), not even the size of my smallest fingernail and already displaying intense hues of deep orange and maroon.

⁹ Though cephalopods are hardly new to biological or neuroscientific research, wide-scale research on cephalopods has been stymied by the fact that scientists have never quite mastered the art of raising them through multiple lifecycles, from egg to adult to egg, and so on. One very well-respected researcher at the MBL maintains approximately 150 captive cuttlefish for his experiments, but they have proved almost impossible to culture. A lab member tells me that during the researcher’s past attempts to breed the cuttlefish, each successive generation lost fitness very rapidly; that is, they weakened and died. Why is a mystery. This means that the researchers have to order shipments of new eggs every year and start afresh. Rosenthal’s research, for instance, requires a constant supply of fresh cephalopods from the local waters or caught in their native habitats around the world and shipped to the MRC.

Bret's motivations clearly extend beyond the professional benefit of standing out in a competitive field. With relish, he informs me that the results of the first full genomic analysis of any cephalopod species (Albertin et al. 2015) concluded that they are genetically the most dissimilar to any other animal on the planet, possessing hundreds of cephalopod-specific genes that have never been observed in other organisms. In an interview on the MBL website, he expounds on this rationale for studying the cephalopod:

Cephalopods have many unique and exaggerated characteristics of interest to study. Their neurons are very large, which is useful to neurobiologists. They have the biggest brain-to-body ratio of any known animals. They can regenerate arms and other tissues very quickly. Physiologically, they are supremely weird. Octopuses have three hearts, blue blood, and neurological receptors at the base of each arm, so it's like they have eight brains in addition to a central brain... They are like aliens on earth. (Kenney 2017)

Conversely, some of the researchers in Josh's lab expressed that they had moved into cephalopod research precisely because the radical alien-ness of the invertebrate allowed them to dissociate from any potential empathy for their model organisms. A postdoctoral student admitted that one of his primary motivations for moving into cephalopod research was a budding distaste for his previous work with vertebrates, which involved the gristly process of breaking the spinal cords of salamanders in order to observe their regeneration. Josh, too, prefers not to use vertebrates for experiments. In the lunch room one day, he reminisced about his time at the University of Pennsylvania, where he could hear the bleating of sheep as they were wheeled into a cardiovascular lab down the hall every morning and silence as the cart was wheeled back out in the afternoon. Cephalopods do not possess spinal cords to break or warm flesh to cut into, nor do they scream shrilly when being carted to their execution. Even I, a first-time viewer of live dissection, was able to stomach (barely) the sight of a squid's head feebly propelling itself around post-mortem.

Near the end of my meeting with Bret, I asked if he foresaw an eventual career change or even a shift in marine animal focus (despite his accomplishments, the combination of tousled hair, loose T-shirt, and West-coast inflection made it difficult to believe that he could be much older than thirty). He replied, without hesitation, that it will always be cephalopods for him. He used to work with great white sharks, but felt they were overrated and over-studied. Why study something already known when you could study the strangest animal on the planet, a practically unlimited source of potential discovery?

Cephalopods have long been associated with the figure of the alien. Indeed, in recent years, they have dominated imaginings of the alien in science fiction and popular media, though to provide a comprehensive overview of the bidirectional influences between these realms and that of scientists is outside the scope of this thesis. In *Alien Ocean*, anthropologist Stefan Helmreich argues that the alien is most often conjured in contexts of conceptual ambiguity, arising as a result of failures to map biological understandings of “life forms” onto human systems of thought and meaning (“forms of life”) (Helmreich 2009, 16). This ambiguity unsettles assumptions that the realm of the biological can “unproblematically anchor” the human realm of meaning, or indeed that the two can be set apart at all (Helmreich 2009, 7). Aliens transect constructed boundaries between human and nature, self and other, like and unlike (Helmreich 2009, 17), and, as such, they remain necessarily indeterminate.¹⁰

¹⁰ Helmreich, who spent years studying and working alongside marine microbiologists, explores the multiple fluid identities that marine microbes take on in relation to humans. Like cephalopods, marine microbes may be “othered” as constituents of a vast and enigmatic ocean, resistant to human representation and control. On the other hand, the study of marine microbes may suggest the fundamental biological kinship and interdependence of all living organisms (Helmreich 2009, x).

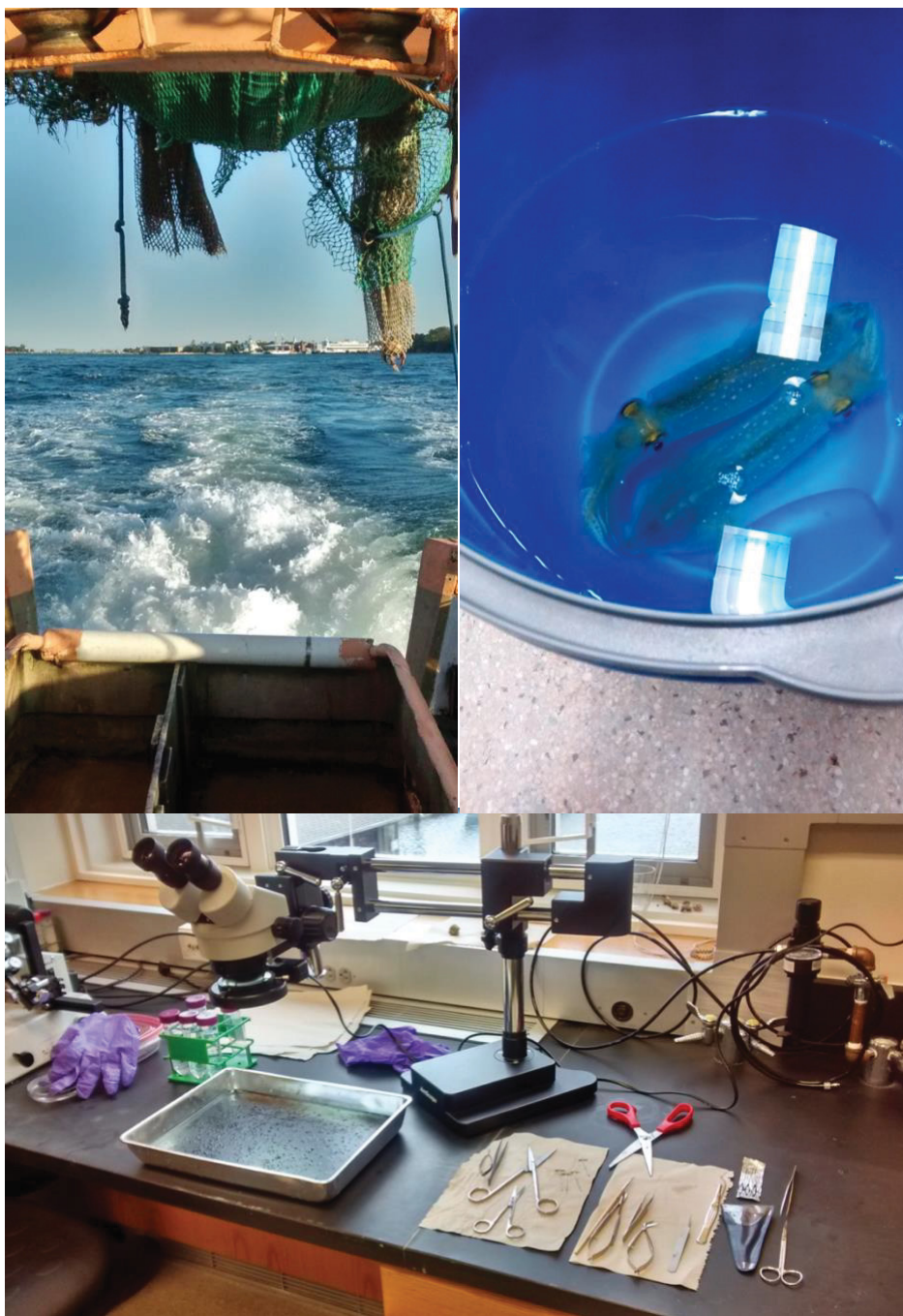
This indeterminacy would seem to pose an impossible barrier for researchers hoping to make the cephalopod into a model organism. As we have seen, model organisms are at least partly characterized by accumulated knowledge, infrastructure, and the ability to meticulously control the biological makeup and processes of an organism, to the extent that they can function as homogenized systems that reveal ostensibly universal laws of the natural world; they function, in other words, as a “test tube for achieving a full understanding of all biological processes” (Ankeny and Leonelli 2011). From this perspective, the notion of an alien model seems to involve a coupling of two contradictory poles.

As the case of the cephalopod demonstrates, however, it is exactly this “alien-ness” that affords them such epistemic appeal. Philosophers of science have remarked on the ability of poorly-understood model systems to generate surprising new lines of research that were previously inconceivable (Rheinberger 1997, Langlitz 2017, Morgan 2005). While simple (“transparent”) models lead to the resolution of scientific questions, (“opaque”) models that are equally or more complex than their targets may produce insights that derail and re-orient lines of research (Langlitz 2017). Josh’s repeated failures at mapping the cephalopod genome generated an unexpected offshoot to his line of research: one that propelled him to study the cephalopod for precisely those traits that distinguish them from all other living organisms, thereby inverting the conventional notion of a model organism as “the right animal for the job.” Alien models evade representation; they “think for themselves” and, in doing so, pose unthinkable questions.

Partly to justify their utility as model organisms, cephalopods have occupied a place of tension in scientific discourse: simultaneously configured as deeply alien, singularly innovative, unfathomable and indeterminate, they also must be subjugated to the scientific ideals of standardization and generalizability that make an animal into a “tractable” model organism. Josh

sometimes refers to the cephalopod as a “candidate” model organism. This adjective suggests as much an assessment of the current state of affairs in model organisms as it outlines expansive hopes for the future. In this context, the candidate organism occupies a liminal status of almost but not-quite; trying to demonstrate its qualifications for the “job at hand” in a space where the job itself has yet to be fully defined. It also points to the considerable work that must be done before the candidate can become a fully-fledged and accepted member of the scientific community. In the next chapter, I delve into some of this work by detailing the daily operations of the lab. What kind of practical labour is required to produce the cephalopod as a “thinking” model organism?

CHAPTER II



Upper-left: View from the back of the squid fishing vessel, the Gemma. Upper-right: two local squid that were selected for dissection. Bottom: the lab bench, prepared for dissection.

Enactments

Model organisms are at least partially constructed by their manipulators, an insight that MBL scientists would readily share with social scientists, who have detailed the numerous contingencies involved in the historical trajectories of many popular model organisms. Science studies scholars have described model organisms as simultaneously technical and social artifacts that occupy an ambiguous-yet-distinctive epistemic status; part exemplar of the “natural,” and part “artificial” construction of the researcher, they offer a unique “meeting point between knowledge and reality” (Ankeny and Leonelli 2011, 315). In the conventional dictionary definitions described in the first chapter, model organisms *must* be designated as “natural” to serve their epistemic purpose as a microcosm through which to make visible and explore the laws of “nature.” In the first chapter, I have also touched on the ways in which model organisms are widely construed as “artificial”: models are quite literally manufactured by researchers, in that they can be selectively bred, subjected to genetic tinkering or to environmental pressures that reshape their very materiality, allowing them to take on a socially-validated position as meticulously controlled and standardized tools that are replicable across different contexts.

The revelation that cephalopods are *not* good model organisms in the traditional sense of the term, however, problematizes such a distinction. What if, in the same way that model organisms cannot readily be mapped onto a tool/job dichotomy, the act of designating a model organism as a natural/artificial “hybrid” points to the insufficiencies of this dichotomy, rather than implying its universality? The notion of artificiality relies on a historically-contingent division between the “constructed” world of humans and “natural” world that stems back from the Enlightenment and continues to pervade Western scholarship (Lock and Nguyen 2018, 57). Accompanying that is an assumption that culture, symbolism, language, tool use, and other

products of human “rationality” are what render the human separate from its environment (Rees 2017).

How can one do ethnography in a way that does not take for granted a top-down human “construction” of scientific objects? In *The Body Multiple* (2002), anthropologist Ann-Marie Mol offers the term “enactment”¹¹ to describe how the disease atherosclerosis is practiced at a Dutch hospital. Mol evades the problematics of a socially-constructed body, disease, or reality, by arguing that atherosclerosis is inextricable from the material set-up and practices of healthcare providers. Taken in this sense, the medial-scientific object can be captured ethnographically as an accumulation of practices that comes into being at a particular location and moment in time: a good ethnographer “stubbornly takes notice of the techniques that make things visible, audible, tangible, knowable” (Mol 2002, 33). Prioritizing the pragmatics has important implications. This method implies that enactment is not solely a human performance, but in fact requires the participation of a whole troupe of non-human actors. The various organisms, technologies, and procedures employed in research are engaged in a process of mutual “instruction” in which each “object itself becomes an agent of the process of knowledge.” (Rheinberger 1997, 31).

As such, I am not interested in establishing a universal epistemological status of the cephalopod as a model organism, so much as documenting the technical and discursive prerequisites involved enacting the squid as a possibility of new knowledge. In his ethnographic exploration of the science of brain plasticity, anthropologist Tobias Rees has called attention to the labour required to translate a theoretical question into the technical-material apparatus of an

¹¹ Sociologist Charis Thompson has also used the term enactment in her 2005 book, *Making Parents: The Ontological Choreography of Reproductive Technologies*, which highlights the dynamic arrangement of numerous elements that collectively “choreograph” the production of individuals who employ assisted reproductive technologies.

experiment. In this sense, scientists can be thought of as “construction workers” in their attempts to “bring thought and technology together in such a way that new knowledge becomes possible” (Rees 2016b, 151). Despite the necessary role of researchers in organizing experimental apparatuses, Rees argues that experimental knowledge is ultimately produced via machines and technical procedures: a “technocentric” rather than “anthropocentric” means of actualizing reality (Rees 2016b, 180).

In this section, I present a series of moments that highlight my informants’ interactions with the squid, to tender just a few of the numerous practicalities that allow the squid to serve as a model organism for marine biological research, and that collectively enact RNA editing as a tangible, viewable phenomenon. I have placed these moments in a kind of step-wise temporal progression, from fishing the squid, to dissecting and viewing it as a specimen under a microscope.¹² In doing so, I examine the various techniques that determine the squid’s transformation from an animal into a scientific object that operationalizes “intelligence.”

We set off early one morning to go “jigging” for squid on the MBL’s research vessel, the mid-sized green and white fishing boat the Gemma. There are eight of us: myself, the research assistant Corbin, postdoc students Juan, Yisrael, and Eldad, a visiting PhD student named Matt, the Gemma’s captain, and the captain’s elderly dog. Josh has chosen to remain behind. He is skeptical of our chances on this rather windy day – better go another morning when the waters are calmer and the lures can more easily sink to the depth of a cruising squid. Today’s voyage is

¹² I have rearranged the order of events to present a more logical narrative of scientific procedure, as if from the perspective of a single squid. In fact, these events occurred across different days with multiple different squid. The steps for preparing the squid as a specimen follow a stringent, detailed protocol; thus, the scene depicted here is largely representative of how any squid would be dissected on any given day, for example.

mostly for the benefit of the visiting PhD student, who is running experiments to address a long-standing debate on whether squid can breathe through their skin in addition to their gills.

Normally, the researchers would use net-caught squid that the Gemma brings into the MRC most mornings, but Matt needs to run his tests with at least one hand-caught squid to establish that the damage nets can inflict upon squid is not affecting his results. So, this particular expedition is a first for not only myself, but also a few of the postdocs.

The captain steers us into the Atlantic for over an hour. Eventually, the heavy splashing of waves forces us to retreat into the small cabin, where we perch along wooden benches. At first, we talk jovially amongst ourselves; then, gradually, silence sets in. The elderly dog stands and takes one or two wobbling steps, then sinks back onto its bedding. I am the first to break the silence: "I might be sick." Juan shakes his head grimly. The visiting PhD student abruptly walks to the doorway and, ashen faced, pronounces that he might also vomit.

Once the boat finally slows (much to our relief), we set lures on our fishing rods and spread ourselves around the railings of the boat. Yisrael explains that the trick is to cast deeply into the water, where schools of squid swim, and gently bob the rod up and down to mimic prey. It is rather difficult to break through the waves, and my fishing line tends to rise back up until I notice it glinting on the surface of the water and cast it back down. After almost two fruitless hours, Yisrael manages to catch one squid, re-invigorating us for a short while until we collectively decide to head back.

Even though only a single squid was caught, the mood as we dock at the Marine Resources Center is ebullient. We call:

"Poor guy – he was the only one who came up to see what was happening."

"Brave squid!"

“What a martyr!”

On a different day, Corbin lets me tag along with him to the Marine Resources Center, and I watch him perform a dissection on two of the net-caught squid. He brings a pail with the two squid upstairs to his workbench. One is larger and more actively banging the sides of the pail, while the other is relatively placid, though pulsing gently. You can see right through the skin, with its blue-green iridescent markings, to the organs of the squid. The bench is laid out with a number of delicate metal implements (tweezers, scalpels, forceps), a deep tray half filled with cold sea water, bottles of formaldehyde, and exquisitely fine pins imported from the Czech Republic for mounting the samples. He cuts the head off the larger squid with a pair of ordinary scissors, and sets both parts into the tray. The severed head turns a subdued dark red, which Corbin has told me is a sign of agitation, and the tentacles continue to feebly propel the head around the tray. Seeing my grimace, Corbin archly adds, “I’d be upset too.” I watch as he gently cuts squares of the skin, stellate ganglion, and finally slices the head in half to delicately excise the two optic lobes, each of which resembles a tiny clove of garlic.

Corbin uses a large machine called a microtome to finely slice and mount the squid’s optic lobes onto wax slides. While doing so, he consults a booklet of detailed anatomical drawings of the squid that were published by the famous neurologist JZ Young in the early 1900s. Much of the basic information that he collected about cephalopods is still considered accurate, Corbin tells me. Once re-constituted as translucent pearl-sized circles, one can barely recognize the squid sections as originating from any living organism.

After an exacting multi-day process in which Corbin treats the squid sections with a fluorescent stain to reveal the presence of RNA editing, the post-doc student Yisrael lets me sit with him as he takes photographs of the slides under a microscope, occasionally narrating for my benefit. He is trying to use Photoshop filters to compare the distribution of an enzyme called ADAR that performs RNA editing with the distribution of cells. If the enzyme's location matches up with the cells, then it is likely that RNA editing is taking place in this area of the squid, the optic lobe. He expertly toggles the microscope settings to bring the stained sample into focus. Then there is a long interlude of at least twenty minutes in which we both struggle with the use of Photoshop settings, trying to get the best contrast so the cell outlines are visible against the purple stain.

Finally, a satisfactory result is achieved, and we take a moment to survey the screen. It's a visual problem. For a moment, I am disoriented, caught in the many layers of processes the squid endured to become the present object of our scrutiny—fished, dissected, sliced, mounted, soaked, buffered, treated with antibody and antigen, suspended overnight, dyed and counter-dyed, magnified, and now filtered through imaging software—that it's hard to tell exactly what we are seeing and what this has come to represent. In the end, that image alone cannot conclusively show the presence or absence of RNA editing in the optic lobe. Corbin and Yisrael will have to run this procedure many times with different samples of the squid.

In my brief sea voyage, it became evident that the squid does not start out as a model organism. For the researchers, the squid in its natural environment was a silly, brave, animal, something to be pitied and offered casual gratitude for its sacrifice to science. A number of my shipmates were unaccustomed to catching their squid live and, like myself, were unsteadied by

the turbulence of the expedition, but excited by its novelty. Usually Corbin the research assistant would act as a liaison between the live squid and the researchers. Armed with his pail, he would visit the Marine Resources Center on days when a fresh batch of squid was brought in by the Gemma's crew and select a few of the least damaged specimens for dissection. Even after performing the same dissection procedure countless times, Corbin offered some matter-of-fact empathy in response to the squid's apparent distress (though perhaps partly for my benefit). Indeed, it is difficult to pinpoint a single moment in which the squid ceased to be a squid, relatable to the researchers in some very fundamental respects, and acquired its status as a model with representative power.

In order to become the site of RNA editing, the squid had to be fundamentally processed through several technological and conceptual lenses. It was only after the lengthy material transformations of the living squid into an organ, a slide, a sample, an image of cells and enzyme activity, and then data, that RNA editing could be made visible. Only partially captured in the vignettes were the considerable technical preparations and requirements involved in this process. To name just a few elements: the efforts of researchers, technicians, and boat captains; various technologies, including fishing rods and lures, dissection tools, the microtome and wax, the microscope and imaging software; and specialized facilities that house the living squid and its subsequent forms. Underlying all of this was the highly detailed written procedure that Corbin religiously consults at each step of processing the specimen, refined by many decades of accumulated knowledge hearkening from the time of JZ Young.

As I was led through this process, one could say that I was taught to see the squid in a particular way; like Byron Good's medical students, whose immersive training taught them to interpret the anatomical and cellular "realities" of the human body, "Learning to make sense of

the confusion that appears through the microscope was largely a matter of learning to see” (Good 1994). What exactly was it that Yisrael I observed when we looked at the magnified, digitally-processed image of cells? The result was the visual rendering of a biological process: RNA editing. All of these daily procedures and pragmatics taking place in the lab accumulated such that the squid could become the condition allowing RNA editing to become a *visible* and *measurable* phenomenon – one that could literally be mapped onto the body of the squid.

What kind of conceptual questions are made materially accessible by such an endeavor? Corbin and Yisrael explained this particular experiment as an attempt to localize where RNA editing takes place in the neurons that run throughout the squid’s body. In general, the relatively large and complex nervous systems of coleoid cephalopods are composed of three structures: a large bundle of nerves called the central ganglion (the “brain”), which is flanked by two optic lobes that each connect to one of the eyes, and a peripheral nervous system that, in the octopus, makes up roughly two-thirds of the body’s 500 million-odd neurons (Hochner, Shomrat, and Fiorito 2006). Typically, we might assume that neural connections extending between the brain and the rest of the body (arms, tentacles, beak, and mantle) would reflect the brain’s conventionally-designated role as a decision centre, transmitting sensory information and motor directives (Hochner 2013). As an example, the squid’s remarkable camouflage abilities are activated when the nerves signal muscle in the skin of the squid to contract or dilate, either revealing or hiding millions of individual pigmented cells that reflect light in different combinations to form elaborate colour displays (Hochner, 2013). It was once widely accepted that this and other neural processes are largely “vertically controlled,” with motor directives generated in the “brain” and traveling through axons to initiate action in a target area of the body.

Through experiments like the one described here, Josh's team has found preliminary evidence that RNA editing may occur outside of the squid's central nervous system. The presence of neural bodies that are edited in the skin, for instance, could indicate that a form of "horizontal control," is taking place in which neural signals are self-generated and transmitted amongst neighbouring neurons in the skin. Such "self-organized" behaviour could be a possible mechanism for producing highly-complex and adaptive patterns of colour change that allow cephalopods to navigate their environment in a remarkably sophisticated manner: for instance, imitating poisonous species of fish to ward off predators and even using camouflage as a hypothesized means of "communication" with other cephalopods (Hochner 2013, 23). In Corbin's words, does squid camouflage amount to a kind of "thinking in patterns"?¹³ Where does "thinking" take place in the squid's body? Can "thinking" take place outside the brain, as it is typically defined? Of course, my informants would never make such broad extrapolations based on a few sets of slides from a single squid, but these are just a few of the questions that can be operationalized through such experiments.

Indeed, these questions are already being operationalized in such a way that inverts the typical relationship between model and target, by initiatives that attempt to re-model our basic understanding of "thinking" after coleoid cephalopods. Along with a number of scholars, neurobiologist Binyamin Hochner has spearheaded the use of the term "intelligent embodiment"

¹³ Corbin's off-handed comment may have been inspired by a book that was extremely popular at the time directly leading up to my fieldwork. In *Other Minds* (2016), Philosopher Peter Godfrey-Smith explores the possibility that coleoid cephalopod skin senses and reacts to light without central nervous system mediation, in line with the idea of a peripherally dispersed partially-independent nervous system. Most interestingly, he characterizes some of these changes as "an inadvertent expression of the animal's inner processes," even describing a particularly brilliant array he witnessed to be a result of "dreaming" in colours (2016, 127).

(originating in the field of robotics), which suggests that intelligence must be rooted in the very materiality of the organism and its surroundings: the malleable points of contact and oft-reciprocal modes of interaction between flesh and the environment (Hochner 2013, Hochner, Shomrat, and Fiorito 2006, Hochner 2012). Cephalopods are ideal models for locating “intelligence” in the physical realm, in that their behavioural complexity clearly arises from the inextricable co-adaptation of highly unique neural, anatomical, and physiological systems. Within Hochner’s framework, it follows that “intelligence” must be diffused throughout the body and its environment rather than contained within any single physical location (for instance, the brain, as cephalopod embodiment clearly demonstrates) or a metaphysical realm accessible to only the human. Further, if intelligence is body-specific, then would there not exist a plurality of different intelligences, each form specific to the organism? At stake in these questions is the notion of thought itself, as it is conventionally defined; through the science of cephalopods, the process of thinking becomes diffuse, decentralized, destabilized and, as I will suggest in the following chapter, de-anthropologized.

CHAPTER III



Corbin peers into squid tanks on the main floor of the MBL's Marine Resources Center.

Cephalopod culture

One day, after a morning of sparse conversation in the lab, I wandered into the small conference room where one of Josh's postdoctoral students was having his lunch break. A tanned, slight man with rimless glasses, Yisrael exudes the erudition of a scholar and the hardiness of someone who had spent much of his life outdoors. Raised in Australia, he had spent the last 15 years completing his university education and postdoctoral research at Bar-Ilan University in Ramat Gan, Israel. Most of his work has combined the behavioural study of marine organisms with large-scale genetic analyses; as such, his research often involves a mixture of techniques: collecting living organisms from their natural habitats, observing and experimenting with them in controlled environments, and then breaking down their biochemical properties in the lab.

Over lunch, Yisrael recounts how his research on a species of tiny Red Sea boxer crabs struck a major chord with the public earlier that year. These tiny crabs carry around a single pink sea anemone in each claw, which greatly resemble tiny writhing pom-poms, and are thought to be useful for food collection, chemical camouflage, and defending against potential predators. Yisrael's 2017 paper found that if researchers took a single anemone away, the crab would split their remaining anemone in half, causing both halves to regenerate via asexual reproduction (Schnytzer et al. 2017). When both anemones were removed, the crab would try to duel another crab to take or break off at least a re-growable piece of their anemones. In other words, anemones are important enough that, bereft of them, boxer crabs will either grow, scavenge, or steal a new set.

The image of an obsessive pom-pom wielding crab proved astoundingly popular in the media, spawning numerous pop-science publications, a National Geographic news item, and was

featured in a BBC program on “Nature’s Greatest Dancers.” Though pleased with this publicity, Yisrael was quizzical about the nature of public interest. Most news coverage anthropomorphized the crab behaviour for comedic effect (“Boxer crabs go to crazy lengths to keep a pair of pom-poms: They keep their friends close and their anemones closer”; Griggs 2017), but few explicitly touched on the possible implications of acknowledging this as a form of tool use. According to Yisrael, there are many probable examples of tool use in invertebrates: some octopuses, for instance, have been observed carrying the discarded halves of coconut shells, which they clamber into when in need of shelter or protection (Finn, Tregenza, and Norman 2009). However, such cases are often de-legitimized by scientists and journalists alike, who tend to refer to them as examples of instinctual behaviour or symbiosis (as they did in the case of the boxer crabs). According to Yisrael, primates are more likely to receive the assumption of intelligence or agency, while invertebrates are usually depicted as non-sentient automata in the Cartesian tradition. As Yisrael emphasized, it’s simply easier for most people to accept intelligence in animals that are closer to humans.

Our conversation moves towards the topic of travel. After serving in the Israeli army for five years, Yisrael used the money he had saved to spend seven months backpacking through Asia. Reflecting on this experience, he muses:

There’s something different about China. When you’re in Thailand and Cambodia, because it’s a little “third world” and sort of “less advanced” than where we come from, somehow the differences that you see in life and how things work – in your head, things aren’t quite as organized, so things work differently. And then you get to China and China’s surprising because everything in China is super advanced (in the big cities, not in rural areas) and super organized, and everything is working properly, yet working *differently*... One of the biggest lessons I learned is how there’s no such thing as normal. There’s no such thing as the *right* way to do something. There’s just different ways.

After a brief-but-thoughtful pause, he continues:

People are just really anthropocentric... traditionally, people are just uncomfortable with the thought that animals can do things that are somehow comparable to what we do. [using finger quotes] ‘We’re special. We’re different. We’re separate. We’re not animals. We’re not part of nature.’ We distance ourselves, and I think it makes us even more uncomfortable when we discover how close we are.

Hearing Yisrael’s analogy between “cultural” and “biological” difference, I wondered whether anthropologists and marine biologists in some ways undertake parallel projects, at least in their fundamental approach. Sociocultural anthropology and marine biology are both disciplines that traditionally seek to observe, engage with, and provide explanations for radically “alien” difference, whether embodied by the Trobriand Islanders of Papua New Guinea or a bioluminescent seabed-dwelling invertebrate. Historically, both disciplines have assigned their objects along temporal lines of evolution: gradations of difference on an axis that assumes fundamental commensurability between its units. Constructing these continuums ostensibly allows one to uncover universal laws of “human nature” (anthropology) or “living organisms” (biology), and to delineate the “self” or “human” in relation to an “other.”

In the nineteenth century, for example, classical anthropologists set out to explain the multitude of existing cultures by proposing what was essentially an evolutionary theory of society and culture. Thus began a project of situating societies along a spectrum of civilization, ranging from “lower tribes” possessing only rudimentary cultures, to then-contemporary Western nations, the pinnacle of so-called “modernity” (Morgan 1877, Tylor 1871). Foundational to this project was the notion that all human societies possess (in varying degrees of complexity) a set of traits that separate us from the natural world, afforded by a uniquely human capacity for “reason”:¹⁴ culture, language, meaning, art, history (Rees 2017). Thus, a historically-particular

¹⁴ René Descartes famously conceptualized the human as a thinking subject in a world of physical objects. His work was among the first in a long line of influential Western scholars to

conception of “the” human was borne out by anthropologists, founded upon basic dualities (nature/culture; human/non-human) that would dominate Western thinking for hundreds of years.

The discomfort of experiencing radical difference firsthand, as Yisrael pinpoints, lies in recognizing the failures of our universal explanatory categories. To conceptualize China as “super advanced” yet radically different from Western cities is allowance that “modernity,” in Yisrael’s eyes, equated with efficiency, organization, and complexity, can not only take on multiple forms, but that such anthropocentric axes of development need to be redrawn (“there’s no such thing as normal”). His anecdote asks: if the very notion of “modernity” can be extended, distorted, even cast away entirely, then what about “tool-use,” “agency,” “intelligence,” and all of those fundamental trappings that form the contours of “the” human?

In entertaining these intersections between the marine biology and anthropology, however, I run the risk of refashioning the cephalopod as a new iteration of the nineteenth century figure of the “primitive.” If we employ anthropocentric axes to argue that all organisms can “think” in some form, then we simply grant the cephalopod access to a lesser echelon of humanity; designating the cephalopod an “honorary vertebrate,” as I have sometimes heard it called. In other words, we might be tempted to conclude that the cephalopod does indeed think, but just not as well as the human. What would an anthropology of the cephalopod that refuses to measure along the “universal” axes drawn by humans/”the” human look like? A multitude of approaches have been proposed over recent decades, some of the most prominent movements including multispecies ethnography, science and technology studies (STS), and adherents of the suggest that the capacity for “reason” or “good sense” is what fundamentally separates humans from animals, who are reduced to mere biological machines (Descartes 1968).

“ontological turn” who seek to reframe the problem of multiple “cultures” into that of multiple “worlds.” Multispecies ethnographers, in particular, have delved into the sheer alien-ness of non-human organisms in their efforts to realize non-anthropocentric forms of anthropology. Notably, in her piece “Tentacular Thinking,” influential scholar Donna Haraway (2016) harnesses the metaphor of the cephalopod’s non-centralized nervous system as a rousing cry for multispecies approaches that revel in the chaotic intermingling of human and non-human, ushering in an epoch in which figures like the cephalopod render anthropocentric notions like bounded individualism and disembodied rationalism entirely untenable. At stake in multispecies work is our ability to comprehend and rehabilitate the urgently damaged worlds that we co-inhabit. Fittingly, the contours of this epoch cannot be illuminated through the work any single scholar, or indeed any organism: “Myriad tentacles will be needed to tell the story of the Chthulucene” (2016, 28). Though my fieldwork was brief, my hope is that this account will serve as a starting point through which RNA editing cephalopods prove generative additions to the tentacular provocateurs of the Chthulucene.

One interesting and highly speculative take on this question is offered by Czech philosopher Vilém Flusser’s fictionalized account of the *Vampyrotheuthis Infernalis*, a real species of cephalopod known as the “vampire squid.” Half pseudo-biological treatise and half philosophical musing, Flusser paints *Vampyrotheuthis* as an ultimate “other”: physiologically monstrous, hunting its prey through deceit, engaging in depraved behaviour like cannibalism, and inhabiting a land of eternal darkness thousands of meters below the surface of the sea (Flusser and Bec 2012). Like any good anthropological object, the existence of *Vampyrotheuthis* holds a mirror to the human, although Flusser insists that any attempt to reorient the vampire squid as human foil would be purely “dangerous romanticism” (Flusser and Bec 2012, 77).

Instead, he writes long sections of his treatise *from the perspective of the squid*, leading the reader through discussions of Vampyrotheuthian thought, social life, and art.

If culture is a “deliberate modification of the world by a subject” (Flusser and Bec 2012, 72), then culture in Vampyrotheuthian terms suggests a vastly different mode of existing-in-the-world from that of the human. Human culture, according to Flusser, is a continuous act of negotiating and removing objects that cross our path, whereas the vampire squid’s culture is one of ravenous consumption: the former an “emancipatory enterprise,” that attempts to purge “nature,” and the latter an “integrating enterprise” that incorporates “nature” within the self (Flusser and Bec 2012, 73). Objects in the human world are merely refracted rays of light from the sun; in the opaque blackness of the ocean floor, Vampyrotheuthis directs and modulates its bioluminescent organs at will in order to produce its own world (Flusser and Bec 2012).

Thought too must be revisited from the perspective of Vampyrotheuthis, who possesses a variety of mechanisms for acquiring, processing, and storing information, such as a glandular system that secretes ink and venom, the chromophores that regulate its camouflage capabilities, tentacles that mediate exploration of the world, and bioluminescent organs. For Flusser, these systems of information processing are modes of “reflection” that constitute a squid-centric form of history, the existence of which problematizes the object-driven history of the human:

Every reflection produces history. But we men have a certain difficulty in conceiving of “history” as a process of storing and sorting acquired information only in human memory. That is because we men store a great part of the acquired information in objects such as books, paintings, buildings and tools. We do not have a model for a history without objective culture ... But Vampyrotheuthis offers us the opportunity to elaborate such a model. He allows us to contemplate human history from his point of view, and to do a vampyrotheuthian critique of human history. (Flusser and Bec 2012, 84-85)

Following Flusser, could one seriously pursue an anthropology of cephalopod “thought,” cephalopod “culture,” or cephalopod “history,” that critiques these very notions? Although

Flusser himself admits the impossibility of ever fully comprehending the Vampyrotheutian world, his self-described fable opens a space in which to think do an anthropology after “the” human.

CONCLUSION

Beyond the marine sciences, cephalopods are already having a tangible impact on how research is conducted. Nakajima et al. (2018) have categorized cephalopods as “boundary objects” (a term originating in sociology) that serve as the focus of inquiry for multiple communities of knowledge production: in the case of cephalopods, transecting disciplines as diverse as neurobiology, genomics, robotics, art, history, and literature. This thesis itself is a testament to the potential of cephalopods to generate conversation and sustained collaboration between seemingly diverse disciplines. In this case, however, they might be better characterized as “super-boundary subjects” that actively displace perceived frontiers within and between the biological, the philosophical, and the anthropological.

In this thesis, I have traced just a few of the ways in which coleoid cephalopods escape from conventional boundaries of both marine biology and those social sciences that take as their foundation a singularly thinking human. As uniquely “alien” creatures, their indeterminacy is simultaneously troublesome for researchers that seek to standardize model organisms and full of latent epistemic potential to pose previously unthinkable questions. Instead of serving as a simple model through which to answer pre-set questions about universal (human) neurophysiology, the genetic plasticity afforded by RNA editing radically diverges from our understanding of “intelligence,” allowing the investigation of “alien” forms of intelligence that destabilize our own. These are just a few of the consequences of employing the cephalopod as a “thinking model,” in the dual sense.

Anthropocentric notions of intelligence and thinking have long-since served to prop up a modernist view of humans as separate from the natural world. Removing these buttresses would require anthropologists to challenge the conceptual foundations of what was traditionally the

field's object of inquiry: "the human." Such an endeavor would inevitably entail a "de-anthropologization" of anthropology itself (Rees 2016a). The philosopher and historian of science Hans-Jörg Rheinberger has argued: "An epistemology that sets out to grasp the dynamic nature of scientific thinking should accordingly be as plastic, mobile, fluid, and open to risk as scientific thinking itself" (Rheinberger 2010, 28). An anthropology of thinking from the perspective of the cephalopod, then, must model itself after their malleable, decentralized, embodied, and often slippery modes of thought. As with the science of cephalopods, this anthropology should orient itself toward that which is stubbornly unknown and un-reckonable within our existing frameworks, pursuing those foci that always generate a "surplus" of often accidental questions rather than answers (Rees 2015, 162). In the case of the cephalopod, anthropology must embrace the stakes of populating the world with thinking organisms and situate itself in the turbulent waters that ensue.

REFERENCES

2008. "Otto the octopus wreaks havoc." *The Telegraph*, Friday, October 31.
<https://www.telegraph.co.uk/news/newstopics/howaboutthat/3328480/Otto-the-octopus-wreaks-havoc.html>
2012. "Background on Mouse as a Model Organism." National Human Genome Research Institute, Last Modified May 23, 2012, accessed Jan 10, 2018.
<https://www.genome.gov/10005834/background-on-mouse-as-a-model-organism/>
2016. Life in the Oceans: Biological Discovery at the Marine Biological Laboratory. In *MBL Strategic Themes*. Woods Hole, MA: Marine Biological Laboratory.
2018. "Animal model." In *Merriam-Webster*. Online Dictionary: Merriam-Webster. accessed September 29, 2018. <https://www.merriam-webster.com/dictionary/animal%20model>
- 2019a. "Nobel Laureates Affiliated with the MBL." Marine Biological Laboratory, accessed April 13, 2019. <https://www.mbl.edu/nobels/>
- 2019b. "Unit 1: What Is DNA? What Does DNA Do?". Nature Education, accessed July 1, 2019. <https://www.nature.com/scitable/ebooks/essentials-of-genetics-8/contents>
- Albertin, Caroline B, Oleg Simakov, Therese Mitros, Z Yan Wang, Judit R Pungor, Eric Edsinger-Gonzales, Sydney Brenner, Clifton W Ragsdale, and Daniel S Rokhsar. 2015. "The octopus genome and the evolution of cephalopod neural and morphological novelties." *Nature* 524 (7564):220.
- Alon, Shahrar, Sandra C Garrett, Erez Y Levanon, Sara Olson, Brenton R Graveley, Joshua JC Rosenthal, and Eli Eisenberg. 2015. "The majority of transcripts in the squid nervous system are extensively recoded by A-to-I RNA editing." *Elife* 4:e05198.
- Ankeny, Rachel A, and Sabina Leonelli. 2011. "What's so special about model organisms?" *Studies in History and Philosophy of Science Part A* 42 (2):313-323.
- Bolker, Jessica. 2012. "Model organisms: There's more to life than rats and flies." *Nature* 491 (7422):31.
- Cross, Ryan. 2019. "Watch out, CRISPR. The RNA editing race is on." *Chemical and Engineering News (C&EN)*, March 25.
- Dell'Amore, Christine. 2009. "Curious Octopus Floods Aquarium." *National Geographic*, February 27. <https://www.nationalgeographic.com/animals/2009/02/curious-octopus-floods-aquarium/>
- Descartes, René. 1968. *Discourse on Method and the Meditations*. London: Penguin UK.

- Ekblom, Robert, and Juan Galindo. 2011. "Applications of next generation sequencing in molecular ecology of non-model organisms." *Heredity* 107 (1):1.
- Finn, Julian K, Tom Tregenza, and Mark D Norman. 2009. "Defensive tool use in a coconut-carrying octopus." *Current Biology* 19 (23):R1069-R1070.
- Flusser, Vilém, and Louis Bec. 2012. "Vampyroteuthis Infernalis: A Treatise, with a Report by the Institut Scientifique de Recherche Paranaturaliste." Minneapolis: University of Minnesota Press.
- Franklin, Sarah. 2006. "The Cyborg Embryo: Our Path to Transbiology." *Theory, Culture & Society* 23 (7-8):167-187.
- Garrett, Sandra, and Joshua JC Rosenthal. 2012. "RNA editing underlies temperature adaptation in K⁺ channels from polar octopuses." *Science* 335 (6070):848-851.
- Gladfelter, Amy S. 2015. "How nontraditional model systems can save us." *Molecular biology of the cell* 26 (21):3687-3689.
- Godfrey-Smith, Peter. 2009. "Models and fictions in science." *Philosophical Studies* 143 (1):101-116.
- Godfrey-Smith, Peter. 2016. *Other minds: The octopus, the sea, and the deep origins of consciousness*. New York: Farrar, Straus and Giroux.
- Goldstein, Bob, and Nicole King. 2016. "The future of cell biology: emerging model organisms." *Trends in cell biology* 26 (11):818-824.
- Good, Byron. 1994. *How medicine constructs its objects. Medicine, rationality and experience*. Cambridge: Cambridge University Press.
- Griggs, Mary Beth. 2017. "Boxer crabs go to crazy lengths to keep a pair of pom-poms." *Popular Science*, February 2, 2017. Accessed November 18, 2018. <https://www.popsci.com/boxer-crabs-thieving-cloning-anemones>.
- Gwynne, Peter. 2014. "Tight Finances May Spell the End of Independence for Research Centers." *NOVA Next*, November 14, 2013.
- Haraway, Donna. 2016. *Staying with the Trouble: Making Kin in the Chthulucene*. Durham and London: Duke University Press.
- Helmreich, Stefan. 2009. *Alien ocean: Anthropological voyages in microbial seas*. Berkeley and Los Angeles: University of California Press.
- Hochner, Binyamin. 2012. "An embodied view of octopus neurobiology." *Current biology* 22 (20):R887-R892.

- Hochner, Binyamin. 2013. "How nervous systems evolve in relation to their embodiment: what we can learn from octopuses and other molluscs." *Brain, behavior and evolution* 82 (1):19-30.
- Hochner, Binyamin, Tal Shomrat, and Graziano Fiorito. 2006. "The octopus: a model for a comparative analysis of the evolution of learning and memory mechanisms." *The biological bulletin* 210 (3):308-317.
- Huettnner, James. 2013. "Ion channel." In *Encyclopædia Britannica*: Encyclopædia Britannica, Inc, accessed February 11, 2019. <https://www.britannica.com/science/ion-channel>.
- Kenney, Diana. 2017. "Bringing Cephalopod Culture to New Heights at the MBL." The Marine Biological Laboratory, accessed May 22, 2019. <https://www.mbl.edu/blog/bringing-cephalopod-culture-to-new-heights-at-the-mbl/>.
- Keynes, Richard. 2005. "J.Z. and the Discovery of Squid Giant Nerve Fibres." *Journal of Experimental Biology* 208 (2):179.
- Kloot, William van der. 1973. "The Anatomy of the Nervous System of Octopus vulgaris. J. Z. Young." *The Quarterly Review of Biology* 48 (1, Part 1):46-47.
- Langlitz, Nicolas. 2017. "Opaque models: Using drugs and dreams to explore the neurobiological basis of mental phenomena." In *Progress in brain research*, 53-72. Elsevier.
- Lindstedt, Stan. 2014. "Krogh 1929 or 'The Krogh Principle'." *The Journal of Experimental Biology* 217 (10):1640. doi: 10.1242/jeb.095505.
- Liscovitch-Brauer, Noa, Shahar Alon, Hagit T Porath, Boaz Elstein, Ron Unger, Tamar Ziv, Arie Admon, Erez Y Levanon, Joshua JC Rosenthal, and Eli Eisenberg. 2017. "Trade-off between transcriptome plasticity and genome evolution in cephalopods." *Cell* 169 (2):191-202. e11.
- Lock, Margaret, and Vinh-Kim Nguyen. 2018. *An anthropology of biomedicine*: Chichester, West Sussex: John Wiley & Sons.
- Mackie, G. O. 1972. "The Anatomy of the Nervous System of Octopus vulgaris." *Science* 177 (4055):1183.
- Maher, Brenda. 2009. "Biology's next top model?" *Nature* 458 (9).
- Mol, Annemarie. 2002. *The body multiple: Ontology in medical practice*: Durham, Duke University Press.
- Morgan, Lewis Henry. 1877. *Ancient society; or, researches in the lines of human progress from savagery, through barbarism to civilization*: New York: Henry Holt and Company.

- Morgan, Mary S. 2005. "Experiments versus models: New phenomena, inference and surprise." *Journal of Economic Methodology* 12 (2):317-329.
- Nakajima, Ryuta, Shuichi Shigeno, Letizia Zullo, Fabio De Sio, and Markus R. Schmidt. 2018. "Cephalopods Between Science, Art, and Engineering: A Contemporary Synthesis." *Frontiers in Communication* 3 (20).
- O'Brien, Caitlin E., Katina Roumbedakis, and Inger E. Winkelmann. 2018. "The Current State of Cephalopod Science and Perspectives on the Most Critical Challenges Ahead From Three Early-Career Researchers." *Frontiers in Physiology* 9:700-700.
- Reckford, Laura. 2013. "Vote To Align MBL With University Of Chicago Next Saturday." *Cape Cod Wave*, May 26, 2013.
- Rees, Tobias. 2015. "Developmental diseases—an introduction to the neurological human (in motion)." *American Ethnologist* 42 (1):161-174.
- Rees, Tobias. 2016a. "On Deanthropologizing Anthropology—An Essay on Tarek Elhaik's "The Incurable Image""." *Somatosphere. Science, Medicine and Anthropology*.
- Rees, Tobias. 2016b. *Plastic reason: An anthropology of brain science in embryogenetic terms*: Berkely and Los Angeles: University of California Press.
- Rees, Tobias. 2017. "What is 'the' Human? Take, for Example, Culture." Lecture presented at ANTH 302 After "the" Human: An Introduction to the Conceptual Challenges of Contemporary Anthropologies of Medicine. Montreal, Quebec, January 12, 2017.
- Rheinberger, Hans-Jörg. 1997. *Toward a History of Epistemic Things: Synthesizing Proteins in the Test Tube*. Stanford: Stanford University Press.
- Rheinberger, Hans-Jörg. 2010. *An epistemology of the concrete: Twentieth-century histories of life*: Durham: Duke University Press.
- Rosenthal, Joshua JC. 2015. "The emerging role of RNA editing in plasticity." *Journal of Experimental Biology* 218 (12):1812-1821.
- Rosenthal, Joshua JC, and Peter H Seeburg. 2012. "A-to-I RNA editing: effects on proteins key to neural excitability." *Neuron* 74 (3):432-439.
- Roy, Eleanor Ainge. 2016. "The great escape: Inky the octopus legs it to freedom from aquarium." *The Guardian*, Wednesday, April 13.
<https://www.theguardian.com/world/2016/apr/13/the-great-escape-inky-the-octopus-legs-it-to-freedom-from-new-zealand-aquarium>.
- Schnytzer, Yisrael, Yaniv Giman, Ilan Karplus, and Yair Achituv. 2017. "Boxer crabs induce asexual reproduction of their associated sea anemones by splitting and intraspecific theft." *PeerJ* 5:e2954.

- Schweid, Richard. 2014. *Octopus*. Edited by Jonathan Burt, *Animal*. London: Reaktion Books Ltd.
- Singer, Emily. 2016. Biologists Search for New Model Organisms. *Quanta Magazine*. Accessed December 2, 2018. <https://www.quantamagazine.org/biologys-search-for-new-model-organisms-20160726/>.
- Sullivan, William. 2015. "The Institute for the Study of Non-Model Organisms and other fantasies." *Molecular biology of the cell* 26 (3):387-389.
- Sykes, António V, Noussithé Koueta, and Carlos Rosas. 2014. "Historical review of cephalopods culture." In *Cephalopod Culture*, 59-75. Springer Aquatic Sciences.
- Thomas, Lewis. 1978. *The lives of a cell: Notes of a biology watcher*. London: Penguin.
- Tylor, Edward Burnett. 1871. *Primitive culture: researches into the development of mythology, philosophy, religion, art, and custom*. Vol. 2: J. London: Murray.
- Young, John Z. 1996. "John Z. Young." In *The History of Neuroscience in Autobiography*, edited by Larry R Squire, 556-586. San Diego: Academic Press.