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The Lobster NEWSLETTER

3rd ANNUAL SEA GRANT SYPOSIUM HONOURS J. STANLEY COBB

On July 14, 2005, over 70 scientists and students gathered at the University of Rhode Island's Graduate School of Oceanography for a daylong symposium on lobsters to honor the lifetime achievements of J. Stanley Cobb. The symposium titled "Lobsters as Model Organisms for the Intersection of Fisheries, Behavior and Ecology" was arranged to honor the life's work of J. Stanley Cobb, the recently retired URI biological sciences professor. Cobb is an international leader in lobster research and, over the years has gained the respect of his fellow biologists. Barbara Somers and Kathy Castro give their version of events.

Scientists came from Australia, Portugal, Norway, Canada and throughout the United States to pay their respects to Cobb, whose soft-spoken and polite manner have endeared him to so many. While many scientists attending the symposium were former students of Cobb's, a seemingly equal number joked that he didn't accept them and they had to pursue their advanced degrees with other professors.

Barbara Somers (right) and Kathy Castro read letters of congratulation sent by Stan's colleagues unable to attend the symposium.

Bruce Phillips of Curtin University of Technology in Perth, Western Australia, a long-time colleague and friend of Cobb's, was the keynote speaker and gave a fitting tribute to all of Cobb's accomplishments over the years. Phillips co-authored with Cobb the definitive text on lobsters that is used around the world and is considered be many to be the "The Lobster Handbook".

Phillips noted Cobb's career could be measured by the fact that he had papers published in more than 40 different scientific journals, he had 35 graduate students go on to successful careers in science, and he was regularly invited to deliver papers at international conferences. He also explained his hypothesis of correlation between lobster abundance and Stan Cobb's career.

Cobb, in a presentation, said he is concerned about shell disease and the effects on lobsters of rising water temperatures and pollutants in bottom sediments. "In the 30 years I've been working with lobsters, nothing has given me as much concern as this recent phenomenon". The severity is the difference. "Severe cases are those in which 50% or more of the carapace is infected and it makes one wonder whether the net result is a lower threshold to disease. A new disease would change natural mortality rates, and impact what fishermen can take out of the population. So to me, that's a real challenge to lobster biologists. The emergence of disease is an important population leveling factor." Over the last year, scientists and fishermen have been lobbying to raise federal funds to pay for research into the shell disease that has been killing and sickening lobsters in coastal Rhode Island.

The day also included two synthesis talks, summarizing recent multi-collaborator fisheries ecology research programs on the American clawed lobster, *Homarus americanus*, and the Caribbean spiny lobster, *Panulirus argus*. The talks were presented by Dr. Lew Incze of the University of Southern Maine and Dr. Mark Butler of Old Dominion University. There was a poster session.

Cobb wanted the afternoon sessions to include all those who had traveled so far to share in this day. The format included discussions regarding current and future challenges for the lobster fishery. The challenges, identified by Cobb, related to disease and population level impacts, metapopulations and links to fisheries management and cooperative research. As the afternoon progressed the international importance of the challenges that had been presented became very obvious. Discussions involved scientists from all corners of the globe with a concern for lobster populations being the common thread. Discussions revealed that worldwide environmental changes may be at the root of many of these challenges and the need for collaboration concerning the lobster resource is becoming more and more important.

The proceedings from the symposium will be included in an issue of the *Journal of Crustacean Biology*.

After all the serious discussion, the evening's main event was the lobster dinner and the J. Stanley Cobb roast. Person after person took the mike and explained the contribution Stan had made in their organization and for their lives: RI Department of Environmental Management, RI Sea Grant, Darden Foundation, Ocean State Fishermen's Association, and former students. In addition to the many gifts he received, he was awarded the coveted Humes award from the Crustacean Society. The highlight of the evening was the movie premiere produced by Win Watson featuring Stan's little known sports career.

We will miss your day to day presence Stan, but we won't be surprised to see you at the next International Lobster Meeting with more ideas!

RESEARCH NEWS

Lobster shell disease: priorities for further research

From: Michael Tlusty, Roxanne Smolowitz & Harlyn Halvorson

American lobsters are the single most economically important species being fished in the Northeastern United States. The 2003 value of catches exceeded $285 million dollars, even with severely reduced harvests in the south from Cape Cod to Long Island Sound. With healthy stocks in this area, the value of the industry could likely reach $350 million dollars. Fewer lobsters were caught in the south because of several health issues including shell disease. Shell disease results from bacterial invasion of the carapace, but the reasons for this increase in the ability of bacteria to penetrate the carapace are unknown. This disease is reportedly increasing in prevalence into the more productive waters off northern Massachusetts, New Hampshire, and Maine (which accounted for 88% of lobster landings in 2003). Shell disease presents a threat in that its presence can have economic impact through devaluation of the product (shell diseased lobsters are not marketable as a live product) as well as through a reduction in fishery output. Thus it is imperative to understand why shell disease has become epizootic and if it can be transferred up the coast thus affecting American lobster throughout their entire range.

While numerous meetings have addressed shell disease, there has yet to be a dedicated meeting of scientists solely exploring the causes, correlations, and priorities for furthering our understanding and potential mitigation of shell disease. Thus, in March, 2005, the workshop *State of lobster Science 2005: Lobster shell disease – assessing research priorities for understanding how lobster biology and health issues impact productivity* was convened by representatives from the New England Aquarium, the University of Massachusetts at Boston, and the Marine Biology Laboratory at Wood's Hole, and funded by Darden Restaurants and the Sudbury Foundation to gather scientists to examine shell disease in American lobsters. This instructive workshop included a large number of participants that demonstrated many active and diverse lines of research involving: information from directed study of epizootic shell disease, research that is applicable to the continued study or understanding of shell disease, and important information concerning disease monitoring in lobsters fished along the northeastern U.S. coastline. What became obvious from this meeting was the lack of information about epizootic shell disease of American lobsters and why it is occurring.

Discussions during this workshop did conclude that the disease results from the interaction of several factors and, importantly, in order to understand this disease, we need to conduct investigations of these factors. In many cases, we will need to develop a better understanding of normal processes in order to understand what process is abnormal and how that results in disease. To further understand shell disease, an urgent need is to develop a laboratory-based model of lobster carapace formation as well as to be able to control the onset of the disease. This model could be used by many laboratories to standardize research procedures and would allow for controlled laboratory experiments that would result in elucidation of the various factors influencing the onset of shell disease, as well as examining potential treatments and remedies.

Necessary investigations

The priorities for further investigation of shell disease in American lobsters, as discussed within this workshop, can be divided into 4 main categories.

I. Bacteria

The Flavobacteriaceae clade of bacteria appears to be very important in the occurrence of disease. However, to better understand how this clade of bacteria influences shell disease in American lobsters, the lobster science community needs to:

1) determine if all or only a few Flavobacteriaceae are important in the disease
2) fulfill Koch's postulates. Ultimately, the routes of bacterial transfer need to be understood, and the relative contributions of transfer between animals compared to environmental transfer (through the sediment or water column) need to be understood
3) define to what extent the Flavobacteriaceae are present in the bio-film (the thin biologically active layer at the water-lobster interface) on the lobster and how this relates to increased amounts of shell disease
4) determine if shell disease is due to a change in occurrence or quality of the Flavobacteriacae on the animal's carapace
5) understand how environmental changes may affect the population of Flavobacteriacea in the environment
6) evaluate the relationships between the microorganisms community, and how the predator-prey interactions on the lobster's carapace (i.e. amoebic grazing on bacteria on the carapace surface) influence the onset of shell disease.

II. Carapace Formation

Microscopically the carapace of a lobster affected with shell disease appears normal in areas distant from the diseased carapace. Additionally, histologically, the inflammatory responses of these lobsters to erosions appear appropriate and good, indicating that many parts of the innate immune system appear to be functioning well. However, molecular changes may occur within discrete sections of the carapace as it is formed, reducing its overall effectiveness in resisting the erosive bacteria. Additionally changes in the innate immune system may make the animal less able to react at a molecular level when erosions occur in the carapace.

Specifically, the lobster scientific community needs to:

1) understand if shell disease is promoted by a decrease in the quality of epicuticle production (the first line of defense of the cuticle)
2) evaluate the effect of nutrition on cuticle formation. Specifically we need to know what the role nutrients such as astaxanthin, proteins and calcium have in shell formation and strength, and if shell formation can be compromised by fishing practices (through a change in nutrition via bait composition) or pollutants such as alkyphenols (which may affect the

melanizing abilities of the outer carapace or ability of the hemocytes to respond to erosions of the inner carapace at the molecular level)
3) evaluate the level of calcification of the carapace in animals from affected areas compared to unaffected areas
4) understand how signals from the diseased areas of the carapace are received in the underlying tissues and how these signals stimulate the inflammatory responses originating at the cuticle base
5) examine the population structure of lobsters to determine if some potential strains are more susceptible to shell disease than others.

III. Increased Temperatures

Increased temperatures have been correlated with the increase in shell disease in eastern Long Island Sound and Rhode Island and the Massachusetts coast lines. This area is the most southern extent of the American lobsters range. The American lobster scientific community needs to:

1) know if increased temperatures are coincidentally associated with epizootic shell disease or if there is a causative relationship
2) determine the reason for an apparent lag between higher temperatures and higher levels of shell disease along the coast of MA
3) if the number of days of temperature over some threshold is important in shell disease occurrence
4) investigate temperature effects on new cuticle formation and the molt cycle
5) determine how increased temperatures affect lobster behavior, molting season, egg production, and larval movement and settlement.

IV. Innate Immune Systems

Lobsters possess an innate immune system. Unlike vertebrates, this system does not have "memory." In order to understand how a deficient innate immune system might affect the occurrence of shell disease, the lobster scientific community needs to:

1) determine if shell disease is promoted by a defective innate immune system and if a poorly functioning innate immune system affects the molecular composition of the shell as it is formed
2) evaluate protein levels (total protein, hemocyanin or molting cycle proteins) in the hemolymph and determine if altered levels can affect the susceptibility of individual lobsters to epizootic shell disease
3) investigate the role of the hemocytes (the innate immune system cells) using function tests or hemocyte quantification and qualification tests.

Actions

Experiments in each of the above categories need to be conducted. The methods used to investigate these subjects will include both field and laboratory work. Much of the information could be determined with the use of both a laboratory-based model of shell formation, and a model shell disease system. The shell formation model would be used to establish normal values of lobster functioning as well as to examine the effect of how the various factors influence not only shell formation, but the development of erosions. The model of shell disease could then be used to examine how environmental perturbations and changes in health or stress status of lobsters affect the progression of the disease.

Without a model system for understanding shell disease, progress in advancing our scientific understanding of shell disease, and ultimately determining an appropriate managerial response, will be greatly limited.

In addition to the laboratory investigations of shell disease, fishery observer based monitoring of the progression of the disease is paramount, as these data are critical to fully understanding the spread of the disease. Along with the detailed spatial and temporal data on the incidence of the disease, environmental factors (salinity, oxygen, temperature) need to be simultaneously collected to be able to determine correlates and potentially contributing factors. Finally, in a larger context, it is critical to understand how shell disease impacts the natural mortality of lobsters. Current stock assessments assume constant natural mortality rates. With increasing incidence of shell disease in the southern extent of the lobsters' range, this is not a safe assumption.

To initiate the necessary research described here, two objectives need to be fulfilled – first is the organization of the scientists into a consortium, coalition, or working group; and second, funding needs to be made available for the work to be accomplished. Some of the delay in response by the scientific community is because of a lack of communication between scientists. As a group, the scientists were not aware of the variety of work being conducted on shell disease. The individuals meeting at this workshop represented well a cross section of the scientific community, from numerous institutions. The priorities set forth in this document are a good step toward the organization of the group. Ultimately, it would be best to have this group formally organized to assure that goals and priorities are met and progress is being made. The Lobster Institute formed the Lobster Health Coalition, with a successful first meeting. However, there has been little follow-up, as there was no money to assist the coalition with their goals.

Thus, funding for research is a major factor to assure that the progress made in this workshop carries through. To initiate the necessary research described here, significant funding is needed to continue any research or monitoring of this disease. It is clear that the economic importance of lobsters in the northeast creates a priority of funding this initiative, as understanding lobster shell disease will not only ultimately prevent decreases in value of the resource, but may also assist in increasing its economic value. Support of lobster fishermen and the lobster shellfish associations is essential in any funding request, and that support was evident by the participation of lobster fishing associations and fishermen at this meeting. The foundations, particularly Darden and Sudbury, were also very helpful in beginning this initiative, but it is clear from the amount of work that needs to be done that significant government funding will have to be allocated to this problem. Above all else, it is clear that without significant funding, appropriate action to understand shell disease will not be initiated, perhaps until a significant problem occurs in the fishery and it is too late. At the time of this writing, Senators Snowe (ME), Gregg (NH), Kerry (MA) and Kennedy (MA) have initiated a senate appropriation to provide $3 million towards shell disease. It has not been determined how this money would be appropriated, or if the money will be allocated.

While shell disease is not the only disease impacting lobster health, it is a key disease to understand. It appears the prevalence and severity of the disease can be influenced by the pathogen (type, density, pathogenicity), internal lobster factors (shell quality, nutritional status), and the environment (ocean temperatures, current patterns, microbial communities). Only by concomitantly assessing these three areas will researchers full understand how this and other diseases will affect lobster populations, and the management methods necessary to control the spread of these lobster diseases.

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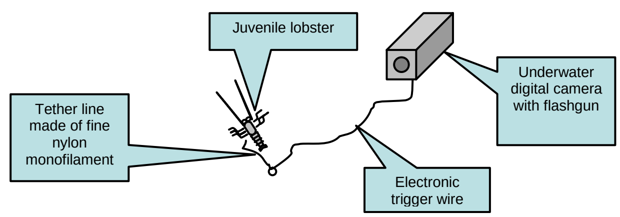
Shedding light on nocturnal lobster predators

From: Andrew Jeffs, Daniel Bassett & John Booth

Identifying the predators of early juvenile spiny lobsters is extremely difficult, despite the importance of predation in dramatically reducing recruitment. Field observations by divers are not effective because individual predation events are infrequent, many occur during darkness, and divers attract and scare many potential predators. Identifying lobster predators through gut content analyses of potential predators is also problematic, in that it involves sampling large numbers of potential predators in order to find lobsters in gut contents. Tethered juvenile lobsters have been used in a number of studies to identify spatial and temporal patterns of predation, but they are of limited use in determining which culprits are involved. This difficulty has been overcome by using remote underwater video with infra-red lighting, however, the equipment is expensive, complex, and the artefacts of highlighting a tethered lobster with infra-red lighting are unknown. To attempt to overcome some of these difficulties we have developed an underwater digital still camera system which only records images when the tethered lobster is removed from the trigger.



Photograph taken at night with the camera system of an octopus (Octopus maorum) *taking a tethered juvenile* Jasus edwardsii.

The system is relatively simple to operate, and is effective at night through the use of a small flashgun. The digital camera also records precisely the time when the photographs are taken and the relative size of the predator can be assessed from the photograph.

The novel camera system is now being used to identify predators and the timing of predation events on <1 year-old *Jasus edwardsii* juveniles in New Zealand and already the system has recorded a variety of predators, including wrasses, blue cod, long-tailed stingray, and octopus.

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FISHERIES & AQUACULTURE UPDATE

Hatchery production of southern rock lobster in Tasmania

From: Arthur Ritar and Greg Smith

Scientists at the University of Tasmania have recently produced Australia's first hatchery-reared rock lobsters from eggs, an important achievement in the move towards sustainable farming of lobsters. In the laboratories of the University's Tasmanian Aquaculture and Fisheries Institute (TAFI), phyllosoma larvae of southern rock lobster (*Jasus edwardsii*) were grown for about one year through the 11 morphological stages of development and more than 20 moults. The final-stage larvae (Figure 1) attained a total length of around 40 mm prior to metamorphosing over a 15-minute period into colourless, deep-bodied pueruli (Figure 2). This transitional stage between the planktonic phyllosoma and the benthic juvenile lasts three weeks, during which time animals gain colour. Production of pueruli in the laboratory has only been achieved previously by research groups in Japan (led by Professor Jiro Kittaka and Dr Hirokazu Matsuda) and New Zealand (led by Dr Len Tong and Mr Graeme Moss).

Fig. 1. Final-stage phyllosoma larva shortly before metamorphosis to the puerulus

Lobsters are Australia's most important fisheries, worth more than $450 million Australia-wide, and in Tasmania have an estimated annual value of about $50 million. These fisheries, like most around the world, are fully exploited with little opportunity for expansion. This has led to growing worldwide interest in the farming of lobsters, to increase production and to exploit new and lucrative market opportunities. Lobsters have several attributes that make them suitable for aquaculture. They are highly sought after and achieve a premium price in the market. Juveniles are hardy, suffering few diseases in captivity, and tolerate relatively high stocking densities whilst exhibiting little aggression or cannibalism. Whereas the current Tasmanian legal size for lobsters is around 600 g, markets exist in Asia and elsewhere for smaller 200–300 g animals. Cultured lobsters appear well suited to these markets and the southern species grows to the required size in around 30 months.

Early attempts to develop aquaculture of southern rock lobster in Tasmania started in 1997 with special initiative funding from the State Government. Later, TAFI was selected by the national funding agency, Fisheries Research and Development Corporation, to lead the national project on lobster propagation, with funding from their Rock Lobster Enhancement and Aquaculture Subprogram. Initial efforts were concentrated on the capture of lobster pueruli and juveniles from the wild and their grow-out for farming in land-based tanks. However, it quickly became apparent that while lobsters survived and grew well in captivity, large-scale aquaculture could not rely on exploiting the wild resource because supply was highly variable from year to year and the postlarvae were difficult to capture in sufficiently large numbers. To ensure a sustainable lobster farming sector, seedstock needed to be produced in the hatchery. The long-term goal of commercially producing hatchery-reared pueruli may also provide an opportunity to enhance the wild fishery.

Egg-bearing females collected from the wild, as well as animals held out-of-season using light and temperature manipulations, are used to produce a ready supply of newly hatched phyllosoma larvae. Prior to hatch, females are isolated into hatching containers supplied with flow-through seawater. Females hatch their eggs at dawn on 4–7 consecutive days producing a total of more than 100,000 phyllosoma larvae. Larvae are removed from the hatch containers and assessed for competency using a unique stress test developed at TAFI. Only phyllosomas of high quality are chosen for culture. A number of systems have been investigated for phyllosoma culture including upwellers and kreisels (cylindrical tanks) but, at present, the most appropriate is a circular basin. All culturing is conducted using treated flow-through water.

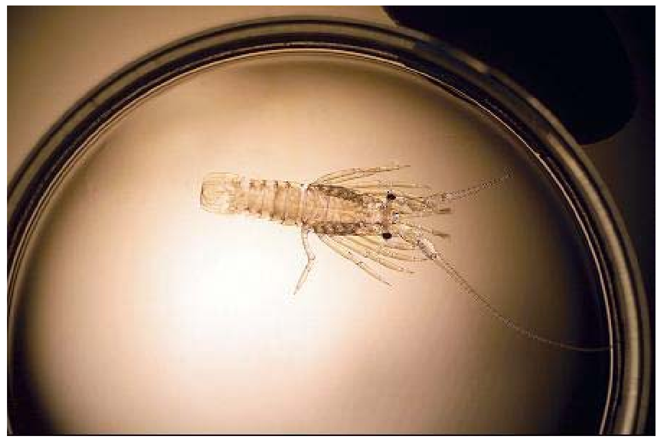

Fig. 2. Recently metamorphosed puerulus

The larval rearing program funded by FRDC is well ahead of schedule. We attribute this to a better understanding and control of larval health. Minimising bacterial diseases has been crucial to our success and has significant applications for the intensive hatchery rearing of other crustaceans, and aquaculture in general. Over the past 12 months, we have adopted a monitoring program to identify potential sources of pathenogenic bacteria, particularly *Vibrio* species, in our culturing systems. The result of this has been a focused approach in dealing with phyllosoma health issues. By far the greatest source of bacterial load in larval rearing stems from the use of *Artemia* as live food. To circumvent the issue of bacterial contamination, we developed a protocol for disinfecting *Artemia* prior to their introduction into the phyllosoma culture systems. As well, we minimised the proliferation of disease by ozonating the water to oxidize and destroy pathogens.

Significantly, the hatchery larval period was only 12 months and we are expecting to further reduce this in future with improvements in husbandry, nutrition and system design. In addition, our colleagues at the Australian Institute of Marine Science are examining the possibility of shortening the larval period through a better understanding of the moult cycle and the hormones that control it.

Our previous studies showed that lobster juveniles performed well in the laboratory when fed various diets. The research examined growth rate, feeding efficiency, survival and pigmentation. Rapid growth was achieved when animals were fed mussels, provided with brick shelters and floor substrates, and maintained at 18°C. Survival rates were very good. Nearly all mortalities occurred at the moult due to cannibalism as animals were vulnerable in the soft-shell stage. Lobsters also grew 15% faster at 18°C compared to ambient (mean 16°C). Prawn pellets and the experimental moist diet showed promise for further development, which would reduce the cost of farming lobsters. This research will be invaluable for growout of lobsters when large numbers of pueruli can be produced in the hatchery.

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TOPICAL TOPICS

This is a new section in *The Lobster Newsletter* in which often contentious topics of the day are discussed by invited contributors. The topic considered in this issue is:

Where does metamorphosis to the puerulus stage mainly take place among the shallow-water palinurids, and what factors - internal and/or external - are implicated in its progression?

Opinions were sought from those parts of the world with a good field record of larval data, with either a generic approach to the issue, or a local one, being taken. Sadly, we were unable to obtain any contribution from Western Australia, where the most work on larval distributions has been done.

The Editors welcome feedback on the topic.

The topic for the next issue will be announced shortly on *The Lobster Newsletter* website, the best contribution receiving a significant book prize (see page 22).

If you have suggestions for a topic for a future issue, let one of the Editors know.

Metamorphosis in spiny lobsters

From: Andrew Jeffs

The pelagic phase of the lifecycle of spiny lobsters is very poorly understood and this is largely due to their cryptic morphology (transparency) and behaviour, as well as their extensive dispersal over large areas of ocean and their low abundance in the pelagic environment. As a consequence there is very little hard evidence that would serve to identify the location and possible triggers for metamorphosis from the phyllosoma to the puerulus. The common occurrence of late-stage phyllosomas near the shelf break has led to the assumption that metamorphosis takes place in this vicinity and that features of the shelf break region, such as contact by final-stage phyllosoma with the seafloor or seawater of different chemistry, is responsible for triggering metamorphosis (Phillips 1981, Pollock 1986, Booth & Stewart 1992, Bruce et al. 1997, McWilliam & Phillips 1997, Phillips & Pearce 1997, Yoshimura et al. 1999). In some ocean regions, the shelf break has at times been associated with higher primary productivity and therefore it is feasible that there is greater food abundance at the shelf break which may also trigger the final-stage phyllosoma to metamorphose. It has been suggested that the final-stage phyllosoma may need to reach a critical level of stored energy in order to trigger metamorphosis (McWilliam & Phillips 1997).

The only hard evidence for the location of metamorphosis in spiny lobsters suggests that metamorphosis may not be entirely associated with the shelf break. The location of metamorphosis of the Western Australian rock lobster, *Panulirus cygnus*, was inferred from the capture of 19 cast exuviae of final-stage phyllosomas at more than 161 km (ranging from 215 km to 400 km) from the shore of Western Australia and well beyond the continental shelf which only extends to about 45 km offshore (Ritz, 1972). Three metamorphosing final-stage phyllosomas of *Panulirus japonicus* were caught in the Kuroshio Current at 54 and 63 km from the coast of Japan in water more than 400 m deep, i.e., beyond the continental shelf (Yoshimura et al. 1999). Jeffs et al. (2001) inferred the location of metamorphosis of *Jasus edwardsii* based on the presence of soft carapaces in 33 out of 260 pueruli caught in an extensive offshore survey east of New Zealand. These recently metamorphosed pueruli were captured between 24 and 216 km offshore (mean of 92.4 km ± 7.8 S. E) and all were well beyond the shelf (740–3622 m deep). Statistical comparisons indicated that there was no relationship between the distribution of the recently metamorphosed pueruli and their stored energy levels, water depth, distance offshore, phytoplankton biomass, sea surface temperature, salinity, or the distribution of late-stage phyllosomas. However, there was a suggestion that metamorphosis could be associated with the inshore margins of oceanic eddies which are a dominant oceanographic feature of this region (Jeffs et al. 2001).

Where phyllosoma have been cultured their metamorphosis appears to occur spontaneously and varies widely in its timing between individuals of the same clutch of eggs and reared under the same conditions (Jeffs et al. 2001). Metamorphosis does not appear to depend on nutritional status, as many cultured phyllosoma appear to be nutritionally compromised due to poor knowledge about spiny lobster larval diet and feeding. The larval period in cultured phyllosomas varies substantially in relation to many factors including water temperature, food and lighting. Overall, metamorphosis in culture, and indeed instar moulting of phyllosomas, appears to occur earlier and at a smaller larval size in culture, than in the wild. The reasons for this are unclear, although this phenomenon has never been examined in great detail. Likewise, there has been relatively little work on the processes responsible for controlling metamorphosis in other closely related crustacean species such as slipper lobsters, shrimps and crabs (Knowlton 1974). With advances in phyllosoma culture, and the development of more powerful biochemistry and genetic tools, it is likely that our understanding of metamorphosis in spiny lobsters will develop quickly over the next decade.

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The Florida spiny lobster

From: Cynthia Yeung

The stock of the Florida spiny lobster (*Panulirus argus*) is concentrated in the tract of barrier reef off the Florida Keys archipelagos. Metamorphosis from the final phyllosoma stage into puerulus is believed to take place offshore. The puerulus then swims inshore to settle, taking perhaps 2–3 weeks in the process. The main supporting arguments for this theory are that (1) late-stage and particularly final-stage larvae are extremely rare inshore, and (2) pueruli have been caught offshore.

The first obstacle to a scientific evaluation of this theory is the murky definition of “offshore”. It seems that researchers who addressed this question defined “offshore” relative to their respective sampling area. In the Keys, it could mean “offshore of the reef tract”, “ relatively far offshore compared to where the samples nearest shore are”, “further than a small boat could safely sample”, or some other location.

A consensus is needed as to what “offshore” and “inshore” mean in measurable terms in order to answer *where* metamorphosis occurs. I propose that in the region of the central West Atlantic we use the nearshore front of the Gulf Stream system to define the boundary between “inshore” and “offshore” waters. It highlights the significance of physical processes associated with this dominant current system in spiny lobster recruitment. Oceanographers usually trace this front by the 20^{o}C isotherm at 100 m. If this information is not available, then the perpendicular distance from an isobath, or just from shore, can also give a spatial reference. I will use the frontal boundary definition of “offshore” in my opinion. While it is probable that metamorphosis occurs offshore based on the arguments mentioned before, we simply have not been catching enough of these late stages and pueruli in the pelagic environment for a quantitative assessment. In, say, one hundred plankton samples offshore of the reef tract, final-stage phyllosoma larvae and pueruli would only number in the single digits. The low catch rate could have resulted from true absence based on ecology, or false absence because of sampling/systematic deficiencies.

Assume that late-stage larvae are indeed mainly distributed offshore near the front of or within the Florida Current. This section of the Gulf Stream that flushes the Straits of Florida offshore of the Florida Keys has a mean axial surface velocity exceeding 150 cm s^{-1}, and the mean axis comes as close as 25 km from shore at some locations. Conservatively estimating the horizontal swimming speed of a puerulus at 10 cm s^{-1}, that of a final-stage phyllosoma must be lower. Without metamorphosing into a swimming puerulus, can a final-stage phyllosoma cross the turbulent front and escape the dominant downstream flow of the Florida Current to settle in the inshore reef and seagrass habitats?

I found from simulating larval trajectories in a circulation model of the Florida Keys that under certain wind conditions and at certain locations it is possible for even passive drifters in the Florida Current to move inshore. By swimming on the order of several cm per second directed shoreward, a larva can reach settlement habitat within as fast as a day. The model has not yet accounted for the frequent mesoscale eddies and meanders at the front that may further enhance onshore transport. This suggests strong swimming ability is not a requisite to onshore transport & settlement, so metamorphosis need not precede these processes.

Where and when metamorphosis occurs is tied to questions of what triggers metamorphosis and how long stage transitions can be delayed. Is it triggered internally by a biological clock or externally by environmental stimuli? If timing is internal, recruitment can be hit-or-miss – not being at the right place within a time window would debunk survival. My interest in the role of coastal eddies in larval transport lead me to speculate more along the lines of external stimuli. In addition to the potential of eddies for facilitating the cross-shore transport of particles, the eddy environment may also contain stimuli for metamorphosis. Larvae entrained into this mesoscale environment with different chemistry, biology, and hydrodynamics from the ubiquitous surrounding ocean would then metamorphose, and in doing so further increase their chances of migrating and settling inshore.

Although it is commonly opined that metamorphosis from phyllosoma to puerulus occurs offshore in the Florida Keys, I maintain that the case is very much open. Clever and careful experiments in the laboratory and in the field are needed to solve this mystery. In the end, we might find that requisites for metamorphosis are variable among species, environments, or regions.

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Coral Sea *Panulirus ornatus*

From: Darren Dennis

Several exhaustive, well planned field studies have provided insights into where the metamorphic moult mainly occurs in shallow-water palinurids, and the cues that initiate it (McWilliam & Phillips 1997, Jeffs et al. 2001, Yoshimura et al. 1999). Whilst it is generally accepted that the early-stage and mid-stage larvae are essentially passive particles transported by prevailing currents, the more near-shore distribution of late-stage larvae and pueruli indicates a more pro-active role in transport to the adult habitat. By apparently locating themselves near-shore the final-stage larvae give the subsequent non-feeding pueruli a fighting chance of surviving their inshore migration. However, unfortunately our understanding to date does not preclude the alternative that metamorphosis is simply part of a deterministic development.

The final gilled stages of *Panulirus ornatus* occurred along the shelf break in the NW Coral Sea in May 1997, just prior to peak settlement time, but they were almost as numerous 300 km east of the shelf in the South Equatorial Current which flows onto the coast (Dennis et al. 2001). It is likely metamorphosis only took place once the final-stage larvae were nearer shore, since pueruli were found almost exclusively on the shelf break. However, some pueruli were found up to 600 km east of the shelf, indicating the stimulus to metamorphose is not restricted to the shelf break. The vast majority of *Panulirus* spp. pueruli and final-stage larvae sampled in the Coral Sea were caught at depths less than 25 m, and most were caught near the surface. Hence, these larvae would be transported on-shore by surface currents produced by the prevailing south-east trade winds. In the case of *P. ornatus*, therefore, it is likely most metamorphosis occurs near the shelf break and near the surface.

The distribution of pueruli recorded in the Coral Sea in 1997, and recent advection modeling of *P. ornatus* larvae in the Coral Sea, suggest that most settlement occurs away from preferred adult habitat (e.g. Torres Strait)(Pitcher et al. 2005). Hence, metamorphosis does not take place mainly in the vicinity of adult habitat and it is not likely that conditions preferred by adult *P. ornatus* (including generally turbid, river influenced reefs) might instigate metamorphosis.

For most shallow-water palinurids the generally restricted near-shore distribution of final-stage phyllosoma larvae and pueruli and more developed swimming appendages, relative to the earlier stages suggests an active migration. However, whether their near-shore distribution is a result of active directed propulsion towards the shelf or a specific change of behaviour to utilize on-shore currents (e.g. increased time spent at the surface to make use of wind-driven currents) is unknown. The results of laboratory experiments on penaeid prawn larvae indicated an abrupt behavioural change that increased their chances of settlement in the Gulf of Carpentaria, Australia (Vance & Pendrey, 1997). Whilst early-stage penaeid larvae migrated vertically in response to day-night cues, once in depths less than ~10 m post-larval penaeid became responsive to tidal cues (emerging on flood tides), facilitating inshore movement. The cue in this case was shown to be the pressure differential in shallow water (highly unlikely to be the cue for metamorphosis in palinurids given the depth of the open ocean). However, a similar cue related to surface wind-driven currents might explain their near-shore distribution.

In terms of other possible external cues that might instigate metamorphosis in shallow-water palinurids, many have been proposed, including water depth, salinity, temperature, turbidity and appropriate food availability associated with the shelf habitat. The range of distribution (24–216 km offshore) and lipid reserves of recently-metamorphosed pueruli of *J. edwardsii* off New Zealand suggested food availability was not a likely external cue to metamorphosis (Jeffs et al. 2001). Limited success in rearing palinurid larvae in the laboratory has precluded the chance of experimenting with possible cues, although cultured pueruli likely metamorphosed under stable conditions suggesting a more deterministic process.

Given the wide geographic extent of most palinurid larvae and the logistic constraints of field studies, it is unlikely that future field sampling will provide definitive answers on where and why metamorphosis occurs in this commercially and ecologically important group. Perhaps future culturing success may help answer these questions. In the case of *P. ornatus* in the Coral sea at least, simply spending more time at the surface pre- and post-metamorphosis, possibly in response to wind-driven currents, appears to ensure transport onto the shelf.

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Food is the factor

From: John Booth & Steve Chiswell

The context

Our context is the red rock lobster, *Jasus edwardsii*, off the southeast North Island of New Zealand. Here the Wairarapa Eddy—anticyclonic, about 200 km across and well-established through geostrophy (e.g., Heath 1985)—helps retain phyllosomas near the coast (Chiswell & Booth 1999). Plankton sampling shows that phyllosomas enter the eddy within about 4 months of their spring hatching, and it takes a full year from hatching for them to develop through all their 11 stages. But metamorphosis does not take place immediately after moulting to the final stage, the final-stage larvae being present in the eddy for up to another year.

There is reasonably good evidence that the final-stage phyllosomas—at least those near shore—swim shoreward before metamorphosis (Chiswell & Booth 1999); the quite well-developed pleopods could effect this. The puerulus appears to be essentially non-feeding (Nishida et al. 1990). It swims towards shore, active at night throughout the water column and apparently taking refuge on or near the seafloor during the day. Settlement is mainly at depths <20 m.

Where does metamorphosis take place?

Most pueruli of *J. edwardsii* taken in plankton sampling have come from close to shore out to a little beyond the shelf break (around the 1000-m depth contour) (Booth 1994, Chiswell & Booth 2005); for the southeast of the North Island, this is within about 50–100 km of the coast. Rarely are late-stage phyllosomas taken this far inshore, implying that metamorphosis takes place near the shelf break.

But even in directed plankton sampling it is difficult to accurately pin down the exact 'normal' location for metamorphosis because there is no way of knowing how long the puerulus had been swimming towards shore when it was caught. Furthermore, from time to time pueruli are taken well beyond the shelf break: for example in February 1998, a particularly warm February, whereas most pueruli were caught within and about 50 km seaward of the shelf break, some were taken up to 330 km from shore (Chiswell & Booth 1999, Jeffs et al. 2001).

Since the puerulus is non-feeding, it needs to metamorphose fairly close to shore, otherwise it could well run short on fuel and not make it to the coast. Jeffs et al. (2001) estimated that a *J. edwardsii* puerulus off the southeast coast of the North Island in February 1998 had on average enough stored energy to swim up to 200 km. But this includes vertical movements too.

So we'll settle for the typical location of metamorphosis of *J. edwardsii* along the southeast coast of the North Island being within 75–100 km of the coast.

When does metamorphosis take place?

Settlement of the puerulus stage has been observed at several sites along the adjacent coast for 20 years or more (Booth 1994): most settlement is in winter, but it can start as early as early summer. It appears that settlement takes place in the second year after spring hatching: for example, larvae hatched in September–November 2000 start to settle in December 2001, with highest numbers settling in May–July 2002, settlement falling off markedly by October 2002. Higher annual settlement tends to be associated with more frequent than average southerly conditions (Booth et al. 2000).

Thus metamorphosis can take place at any time between 12 and 24 months after hatching, but most phyllosomas metamorphose in winter, about 20 months after hatching.

What brings about metamorphosis?

Whatever controls metamorphosis has to explain both when and where metamorphosis takes place. So, is the onset of metamorphosis brought about by exogenous factors ('relating to, or developing from, external factors'), endogenous factors ('of or relating to an internal cause or origin'), or a mixture of the two? If endogenous factors are implicated, then metamorphosis might also be deterministic in time ('from determinism—the doctrine that all events and actions are ultimately determined by causes regarded as external to the will' (Oxford)).

Moulting in adult *J. edwardsii* is essentially endogenous and deterministic: males are going to moult in spring, females in autumn! Similarly, endogenously controlled moulting through the phyllosoma larval stages (though perhaps still cued to day length or similar) seems likely. But there is strong evolutionary pressure for metamorphosis to the *non-feeding* puerulus to be non-deterministic because if metamorphosis were to take place at a certain time no matter what, the final-stage phyllosoma might very well be so far from the shore that the stored energy resources are insufficient for the puerulus to swim the distance. Non-deterministic metamorphosis is supported by the settlement record described above—metamorphosis can occur at any time of the year. Thus it seems unlikely that the progression of metamorphosis is entirely endogenous and deterministic.

If metamorphosis is exogenously controlled, what external factors might be implicated? It has been suggested for *J. edwardsii* that triggers for metamorphosis might include contact with the lower temperature and/or salinity associated with the shelf or contact with the seafloor (for examples, see Jeffs et al. 2005). The inshore current, the Wairarapa Coastal Current, is cooler and fresher than the offshore waters (Chiswell 2000) . However, we can discard temperature and salinity as external triggers for metamorphosis because data from larval tows show no relationship between metamorphosis location and either temperature or salinity. Also, pueruli can often be caught well offshore of the coastal current.

A believable 'normal' scenario?

Another possibility is that metamorphosis occurs simply when individual *J. edwardsii* phyllosomas, at the right phase of their moult cycle, have attained sufficient energy levels to fuel the puerulus swim to shore—similar to that suggested by McWilliam & Phillips (1997) for *Panulirus cygnus*.

Satellite colour imagery shows that the coastal waters off the southeast of the North Island are much more productive on average than the offshore waters of the Wairarapa Eddy. For much of the time final-stage larvae are well offshore in oligotrophic waters of the eddy, where predation levels are low but so too is prey abundance. We hypothesize that phyllosomas exist here on a low-energy diet, accumulating little reserve energy. However, every now and then some are transported by the eddy inshore into more productive waters. Here, where prey abundance is higher, the phyllosomas can stock up on food to reach some critical energy reserve level, and hence metamorphose. The external factor implicated in metamorphosis is therefore the encounter by phyllosomas of productive waters inshore of the eddy. The trigger is the accumulation of sufficient stored energy reserve.

This trigger may explain the 'normal' location of metamorphosis—the productive regions are inshore of the Wairarapa Eddy, right where most metamorphosis occurs. (From time to time, final-stage larvae can accumulate sufficient energy further out to sea, leading to metamorphosis there.)

This trigger can also explain the timing of metamorphosis. Advection of late-stage phyllosomas into the coastal zone occurs throughout the year, so metamorphosis can occur throughout the year. But chlorophyll in the region shows a strong annual cycle, with peak values occurring during April–May. Peak settlement occurs about 1–2 months later. This lag could be explained by the delay between primary and secondary production, time for phyllosomas to amass energy, and time for the pueruli to swim to the coast.

Shoreward-directed swimming by the final-stage phyllosomas into the coastal waters to feed would help. During southerly winds the shoreward movement of the final-stage phyllosomas, and of the pueruli after metamorphosis, is assisted by Ekman drift. The frequent northwesterly winds would take larvae offshore, back into the eddy—to wait their turn for transport towards shore again.

Summary

We propose that the main thing initiating metamorphosis in the final-stage phyllosoma of *J. edwardsii* is the uptake of fuel to a critical level, which happens after the larva has encountered areas of high production. Is this an exogenous or endogenous mechanism?—that's semantics. What is important is that although the actual time of moult will be controlled by the phyllosoma's internal physiology, it will usually occur near shore, in the region of the shelf break, after the uptake of sufficient food. Any other exogenous trigger(s) may not be necessary: after all, phyllosomas fed to excess in the hatchery metamorphose without any such cue, as far as we know.

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The final-stage phyllosoma metamorphoses to the puerulus while caught up in the flow of the Kuroshio?

From: Yoshimura Taku

The Kuroshio Current that flows northeast along the south coast of Japan is the largest western boundary current in the world: its depth extends to over 1000 m and the maximum current speed at the surface reaches 5 kt. Since ancient times the

Kuroshio has brought not only marine organisms and resources but also human beings and cultures to Japan—from tropical and subtropical regions—attracting a great deal of attention from cultural anthropologists and linguists in addition to oceanographers, ecologists, and biologists. The route of the Kuroshio sometimes shows dynamic change, alternating between two main patterns, a meander and the straight route. This change in route remarkably influences marine resources and fisheries. For the Japanese spiny lobster, *Panulirus japonicus*, for example, when the Kuroshio is more than 100 miles from the shore virtually no settlement of pueruli occurs.

Because of its high current speed and great volume, many people believe that it is impossible for a planktonic organism within the current to make it to the coast before being swept northeastward and away from Japan. But there must be mechanisms that allow organisms within the Kuroshio to reach the coast of Japan: for example, a lot of tropical and subtropical juvenile fishes appear every summer on the Pacific coast of Japan. Direct contact of the Kuroshio with the shore, and branch flows produced by frontal eddies on the northern side of the Kuroshio, are mechanisms that could bring about transport across the Kuroshio to the coast.

The adult population of *P. japonicus* is distributed mainly along the Pacific coast of Japan and northern Taiwan. My recent studies indicate that phyllosoma larvae are transported south of the Kuroshio within a few months of hatching. Based on the duration of the larval stage in rearing experiments, they must spend more than half a year at sea before returning as pueruli to settle in the coastal nursery grounds. They must progress across and north of the Kuroshio in order to return to the coast, probably by swimming and making use of currents such as those mentioned above.

Thus far, four metamorphosing final-stage phyllosomas of *P. japonicus* have been caught during the five cruises conducted by the Fisheries Research Agency. Three of them were caught in and around the Kuroshio axis (Yoshimura et al. 1999). The sampling position of another, from the two research lines during the 2000 cruise of R/V Kaiyo-maru, is shown in the figure, at the northern edge of the Kuroshio. Sampling details for all four are shown in Table 1: metamorphosis was occurring at the surface or within 40 m of the surface in the Kuroshio, just after sunset or midnight, and between full moon and the last quarter.

We have caught 51 free-swimming *P. japonicus* pueruli (including the 43 referred to by Yoshimura et al. 1999) off Japan. Of these, 35 were taken near shore, 13 in the Kuroshio, and the other 3 south of the Kuroshio. Figure 1 shows the sampling site of pueruli during the 2000 research cruise. Because the mid- and late-stage larvae are in the open ocean south of the Kuroshio, but most of the final-stage larvae caught have been within the Kuroshio (Yoshimura et al. 1999, 2002), then the role of puerulus seems to be to swim out of the Kuroshio, to shore.

Given the above scenario, the final-stage larva and the puerulus must experience two characteristic environments: that of 1) the open waters south of the Kuroshio, and 2) the Kuroshio itself or waters inshore and north of it. In general, neither the horizontal nor vertical variation in the subsurface environment south of the

Kuroshio is large compared with the variations that exist where oceanic and coastal waters mix. If the final-stage larvae of *P. japonicus* daily migrate vertically between 100 m and the surface, then the differences in temperature and salinity that the larvae are exposed to are about twice and 10 times respectively compared with those south of the Kuroshio. This is why Yoshimura et al. (1999) suggested that temperature or salinity changes may provide a stimulus for metamorphosis.

But the recent larval rearing of *P. japonicus* have shown that no change in water temperature is needed for metamorphosis: two laboratories have succeeded in producing over 200 pueruli at a constant 24°C (Matsuda Hirokazu and Murakami Keisuke, pers. comm.). The diet and light-dark cycles were also constant, these results suggesting that an external stimulus is not necessarily required for metamorphosis. Instead, some internal stimuli such as time elapsed since molting or hatching, growth condition, or the amount of stored energy, may exist for metamorphosis. However, since the rearing experiments have always used coastal water it is difficult to entirely dismiss the possibility that some external stimulus such as a chemical, or salinity change, originating from coastal waters is present.

Which one then benefits most the recruitment of pueruli to the coastal region in nature, internal or external stimuli? The region south of the Kuroshio is made up of meso-scale eddies that propagate westward at about 7 cm/s (Hanawa & Ebuchi 2002), and Yoshimura et al. (2002) suggested that the mid and late phyllosomas are transported westward by these eddies. Because of the complicated nature of this flow, made up of high and low pressure eddies of varying scale, I think that there must be large variation in individual development times to reach final stage. This being the case, if internal stimuli exist for metamorphosis, then there is always the danger of ineffectual metamorphosis taking place far from the Kuroshio and the coast of Japan.

On the other hand, if some external cues exist in/around the Kuroshio, such as sound, chemical, magnetic field, and so on—as reviewed by Jeffs et al. (2005) —then the final-stage larvae can metamorphose in the Kuroshio with greater certainty of surviving to reach the coast. In order to maximize the chance of finding a route or branch current that transports pueruli to the coast, it is advantageous to stay in the Kuroshio for as long as possible within the time and energy constraints of the puerulus. Therefore I cannot eliminate the possibility that some external cues exist in/around the Kuroshio.

More research is essential in order to understand metamorphosis and shoreward orientation. Suitable sampling methods and mtDNA identification techniques for phyllosoma larvae around Japan are now available. It is my perception that our understanding of the ecology of the larvae and postlarvae of the Japanese spiny lobster is still at a basic stage—but has begun to gather momentum. The new Japan MAFF project "Development of seed production of the Japanese sea eels and spiny lobsters" continues until 2008, giving great opportunity for real progress. Both field and laboratory researchers belonging to the national and prefectural fisheries institutes participate in this project and it is expected that the biological and ecological studies will progress at the same time as mass rearing techniques are achieved.

Within this project, I plan to further research the role of the Kuroshio in *P. japonicus* recruitment. Collaboration between laboratory researchers with advanced rearing skills, and field researchers, should help to soon solve the remaining mysteries surrounding the dispersal of phyllosomas and the return of pueruli.

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Sampling data of 4 metamorphosing final-stage phyllosomas of *P. japonicus* caught by 3 research cruises.

Date	Time	Net depth	Lat N	Long E	Lunar face
1993/ 6/ 17	20 :29- 20 :54	surface	29.0	129.3	27
1995/ 7/ 26	2 :41- 3 :33	surface	30.1	129.2	28
1995/ 7/ 28	1 :18- 2:02	surface	30.1	129.2	0
2000/ 9/ 6	18:48- 20:49	40- 0m oblique	33.0	136.3	8

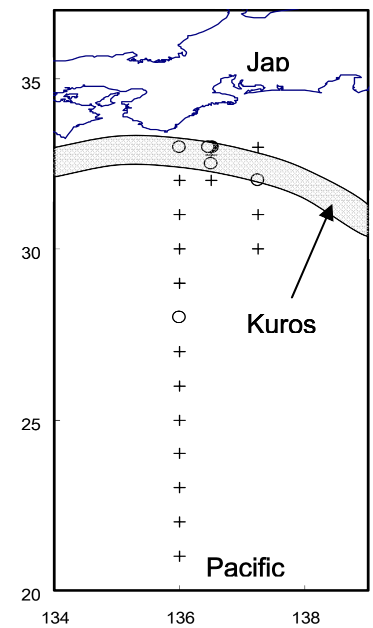

Fig. 1 Horizontal distribution of metamorphosing final-stage larvae and free-swimming pueruli sampled in Sep. 2000 by R/V Kaiyo-maru.
● : metamorphosing final-stage larvae
○ : free-swimming puerulus
+: no catch

ANNOUNCEMENTS

Slipper lobster book

The book covering the biology and fisheries of the slipper lobster (with Kari Lavalli and Ehud Spanier as chief editors) is currently being prepared for submission to CRC Press. Further information will be available on its publication date and other details in the next issue of *The Lobster Newsletter*.

For more details, contact either Ehud Spanier at spanier@research.haifa.ac.il or Kari Lavalli at klavalli@yahoo.com .

Normally The Lobster Newsletter *does not publish advertisements, but on this occasion the Editors have welcomed the following ad. We think that the book will be very useful to most readers. Further, the publishers have made available to the Editors of The Lobster Newsletter two copies of the book. One has been earmarked as prize for the best contribution to the Topical Topic in the next issue of the newsletter. The second will go to the best paper in the next issue from a new contributor from a still-developing country.*

Editor resigns

This is the last issue of *The Lobster Newsletter* I will produce. I started editing, and taking my turn producing issues, in 1993. Now it's time for something else.

A replacement editor—probably from the Southern Hemisphere—is sought (any volunteers?). In the meantime, production continues in the capable hands of Mark Butler and Peter Lawton.

Apparently there is reluctance among some researchers to contribute because their articles end up being quoted in primary papers. I say, good oh! if contributions are made use of. *The Lobster Newsletter* has—in my mind—never sought to be anything more than what people make of it at the time. During my tenure I have viewed it as being, among others, a vehicle for describing what people are up to, spreading 'news', and providing an opportunity to 'publish' material that might not otherwise have had a spot. If other people, in turn, want to use that information in their scientific papers, then—properly cited—that's fine! I'm just sorry that not everyone else agrees.

Also, the newsletter is the only place we hear about some work—particularly of researchers from still-developing nations. I hope the newsletter continues in that role.

Thanks to all contributors, particularly those who I have leant on for articles more often than was fair—many of you are New Zealanders and Australians. This needs to change, with other researchers from elsewhere contributing more.

E haere ra

John Booth

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