Volume 14, No. 2

OCEAN
Challenge

Volume 14, No. 2, 2004
(published Autumn 2005)

SCOPE AND AIMS

Ocean Challenge aims to keep its readers up to date with what is happening in oceanography in the UK and the rest of Europe. By covering the whole range of marine-related sciences in an accessible style it should be valuable both to specialist oceanographers who wish to broaden their knowledge of marine sciences, and to informed lay persons who are concerned about the oceanic environment.

***Ocean Challenge* is sent automatically to members of the Challenger Society.**
For more information about the Society, or for queries concerning individual subscriptions to *Ocean Challenge*, please see the Challenger Society website (www.challenger-society.org.uk) or contact the Executive Secretary of the Society (see inside back cover).

INDUSTRIAL CORPORATE MEMBERSHIP

For information about corporate membership, please contact the Executive Secretary of the Society (see inside back cover).

ADVERTISING

For information about advertising, please contact the Executive Secretary of the Society (see inside back cover).

AVAILABILITY OF BACK ISSUES OF OCEAN CHALLENGE

For information about back issues, please contact the Executive Secretary of the Society (see inside back cover).

INSTITUTIONAL SUBSCRIPTIONS

Ocean Challenge is published three times a year. The subscription (including postage by surface mail) is £80.00 ($US 152) per year for libraries and other institutions. New subscriptions, renewals and information about changes of address should be sent to Parjon Information Services, PO Box 144, Haywards Heath, West Sussex, RH16 2YX, UK.

Cover printed by Trade Winds, London.
Text printed by Halstan & Co. Ltd, Amersham.

OCEAN Challenge

The Magazine of the Challenger Society for Marine Science

SOME INFORMATION ABOUT THE CHALLENGER SOCIETY

The Society's objectives are:

To advance the study of Marine Science through research and education.

To disseminate knowledge of Marine Science with a view to encouraging a wider interest in the study of the seas and an awareness of the need for their proper management.

To contribute to public debate on the development of Marine Science.

The Society aims to achieve these objectives through a range of activities:

Holding regular scientific meetings covering all aspects of Marine Science.

Supporting specialist groups to provide a forum for discussion.

Publication of a range of documents dealing with aspects of Marine Science and the programme of meetings of the Society.

Membership provides the following benefits:

An opportunity to attend, at reduced rates, the biennial five-day UK Marine Science Conference and a range of other scientific meetings supported by the Society.

A monthly newsletter (*Challenger Wave*) which carries topical marine science news, and information about jobs, conferences, meetings, courses and seminars.

The Challenger Society Website is
www.challenger-society.org.uk

MEMBERSHIP SUBSCRIPTIONS

The subscription for 2005 costs £40 (£20.00 for students in the UK only). If you would like to join the Society or obtain further information, contact the Executive Secretary, Challenger Society for Marine Science, Room 251/20, Southampton Oceanography Centre, Waterfront Campus, Empress Dock, Southampton SO14 3ZH, UK; Fax: +44(0)23-80-596149; Email: jxj@noc.soton.ac.uk

COUNCIL FOR THE CHALLENGER SOCIETY

President
Duncan Purdie
Southampton Oceanography Centre

Honorary Secretary
Rachael Shreeve
Southampton Oceanography Centre

Honorary Treasurer
Sarah Cornell
QUEST, University of Bristol

Gary Fones

Yolanda Foote

Ruth Parker

Jennifer Pike

Roland Rogers

Andy Rees

Jonathan Sharples

Toby Tyrrell

Phil Williamson

Editor, Challenger Wave
Louisa Watts

Executive Secretary
Jenny Jones
(For address see below left)

ADVICE TO AUTHORS

Articles for *Ocean Challenge* can be on any aspect of oceanography. They should be written in an accessible style with a minimum of jargon and avoiding the use of references. If at all possible, they should be well illustrated (please supply clear artwork roughs or good-contrast black and white glossy prints). Copy may be sent electronically.

For further information, please contact the Editor:
Angela Colling, Department of Earth Sciences,
The Open University, Walton Hall, Milton Keynes, Bucks
MK7 6AA, UK.

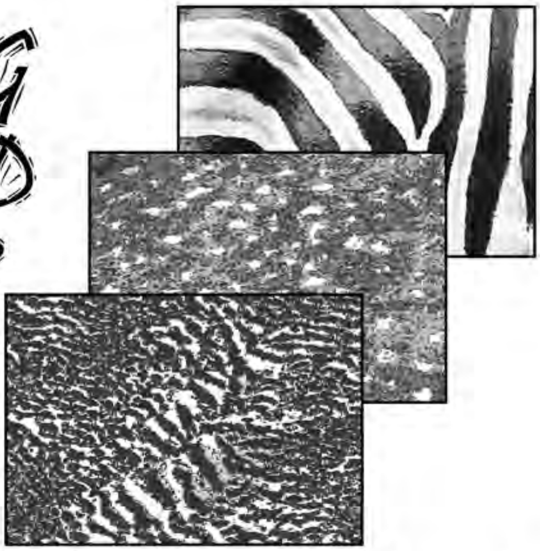
Tel. +44-(0)1908-653647

Fax: +44-(0)1908-655151

Email: A.M.Colling@open.ac.uk

CONTENTS

PATTERNING IN ATTACHED ORGANISMS



from Tiger Bush to Mussel Beds?

Jo Gascoigne and Johan van de Koppel

Distributions of plants and sessile organisms (i.e. those that live permanently attached to a particular substrate (sand, rock, soil etc.) can be extremely patchy. In fact, patchiness is so ubiquitous that most of us are not likely to ask ourselves why it exists or what consequences it might have. Usually, it is assumed that such patchiness reflects patchiness in the underlying environment – perhaps there are areas which have more nutrients, water or food, trap more seeds or larvae, or are more appropriate for attachment or germination sites.

The beds of mussels (*Mytilus edulis*) in which we work, in the Menai Strait in North Wales and in the Dutch Wadden Sea, occur on apparently uniform mud- and sandflats with no apparent variation in any of the factors mentioned above. Nonetheless, they are extremely patchy (Figure 1, overleaf), with areas of very dense mussel cover alternating with bare patches of mud. We started to ask ourselves why this should be. If there is little variation in the underlying environment, what is causing this patchiness?

The patchiness turned out to be even more intriguing than we thought, when spectral analysis of aerial images taken of the mussel beds showed that the patches were regularly spaced rather than random. The mussels had spontaneously formed bands, somewhat similar to the stripes of a zebra, about three metres apart in the Menai Strait, and six metres apart in the Wadden Sea. To find out more about regular patterning in ecological systems, we looked at studies that describe similar phenomena.

It turns out that sorting into regular spatial patterns is commonplace in a particular group of ecosystems that include arid vegetation in the African, Australian and Mexican deserts, peatlands in Siberia and Canada, and diatom biofilms on intertidal mudflats in Dutch, French and British estuaries. These ecosystems have a number of characteristics in common, including: (1) a uniform, flat substrate (soil or sediment) and (2) an environment strongly shaped by physical factors.

Most ecological work on self-organized patterning in ecosystems has been done in terrestrial vegetation systems such as the widespread 'tiger bush', found for instance in Niger and Burkina Faso. In these arid systems, water availability is too low for an even coverage of vegetation to persist. The local vegetation, however, has developed a clever 'water harvesting' strategy. Established plants increase the infiltration of rainwater in their immediate vicinity because their roots penetrate and break up the soil, and their leaves shade the ground, thereby reducing surface evaporation. This means that on a small spatial scale, plants are more likely to establish and thrive in the immediate vicinity of other plants. Rainfall in these arid countries typically drops in short but very intense showers that quickly saturate the uppermost layer of soil. As a consequence, water flows over the surface, and clumps of vegetation can 'harvest' water that has fallen in the surrounding area. However, as competition between plants for soil water is very strong in this environment, plants living at some distance from such a clump of vegetation are deprived of water. This combination of local facilitation between plants growing in clumps, but inhibition of growth at larger distances, leads to plants arranging themselves in patches (on flat surfaces) or bands (on slightly sloping surfaces), with bare ground in-between.

In other ecosystems, the dynamics of small-scale facilitation/large-scale inhibition can be driven by other limiting factors, such as nutrient supply in peatlands, for example (cf. Table 1), but the overall principle is the same. It turns out that this same mechanism for pattern formation has also been proposed for a number of non-ecological situations, such as the stripes of a zebra, the pigmentation of sea shells and the chemistry of embryo development! The principle that interaction between processes acting at different spatial scales can cause regular patterning was first suggested by the British mathematician Alan

Mussel beds may show patterning, even when the underlying substrate is fairly homogeneous

Figure 1 *A patterned mussel bed (*Mytilus edulis*) in the Menai Strait, North Wales.*

Turing back in 1952. (He is better known for breaking German codes during World War II.)

In order to test whether this 'Turing' mechanism could explain the patterning that we observed in our mussel beds, one of us (Johan van de Koppel) developed a mussel bed model. He assumed that large-scale inhibition arose as a consequence of competition for algae while short-range facilitation arose because mussels on soft sediment benefit from attaching themselves to each other to avoid being washed away by the strong tidal currents which occur both in the Wadden Sea and in the Menai Strait.

This model did indeed predict patterning, both in the mussels and in their algal 'prey' in the overlying water (Figure 2), with patterns in the mussel beds which look strikingly similar to the patterns that we actually observed in the field (cf. Figure 1). One particularly exciting outcome from this model was the prediction that self-organized patterning in mussel beds increases mussel productivity, relative to that of a homogeneous bed structure. Furthermore, patterning allows mussels to persist at algal concentrations that would be too low for mussels to survive in a homogeneous arrangement. Thus self-organized patterning may have great ecological importance for mussels in soft sediment systems.

The next stage was to test for the hypothesized interaction between small-scale facilitation and large-scale competition in mussel beds in the field. To do this we looked at growth in relation to density in replicate mussel beds on a large scale (20 m × 20 m squares of different densities of mussels) and on the small scale (0.25 m × 0.25 m

In the model, interaction between the effects of competition for food, and the advantagous effects of mussels attaching themselves to one another, results in a mussel bed pattern very like that observed in reality

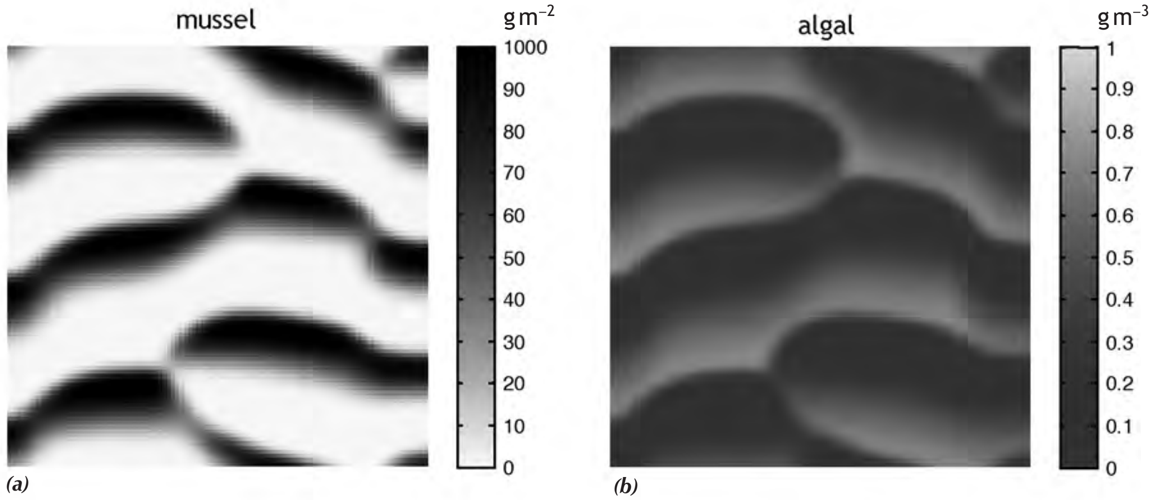


Figure 2 *Patterning which arises out of a spatial competition–facilitation model for* ***(a)*** *mussels and* ***(b)*** *their algal 'prey'; the area represented is* 25 m × 25 m *Note that in (b) the darker areas are depleted in algae compared with the lighter areas. In (a) the mussel patterning looks strikingly like patterning we observe in the field (cf. Figure 1).*

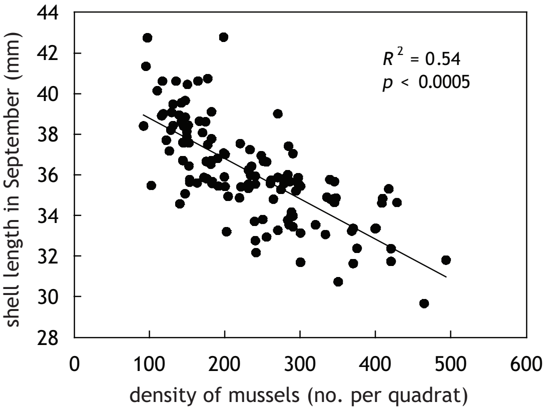


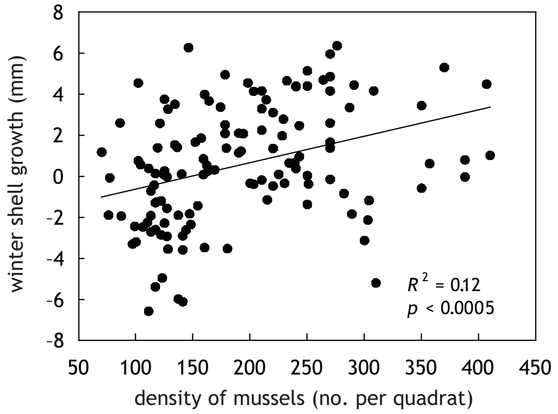
Figure 3 *Shell length in September, plotted against mussel density. Mussels sampled from higher density quadrats (0.25 m × 0.25 m) had less shell growth over the summer than mussels sampled from lower density quadrats (meat growth was also less where mussesls were at high density). The experiment started in April with mussels of equal mean length throughout the experimental mussel bed, so differences in length in September reflect differences in growth over the course of the summer.*

High densities of mussels have a strong negative effect on summer shell growth

squares of different densities). We started the experiment in April with mussels of equal mean size throughout the experimental bed. We divided the data into summer and winter datasets, to allow for underlying differences in mussel growth rates with season.

The results of the analysis were surprising. In the summer, it was very clear that competition dominated interactions between mussels, at both large and small scales. High density always had a negative effect on mussel growth, both at the large scale and at the small scale (Figure 3). We corrected growth over the winter using the relationship between growth and density observed for September, so that the effect of growth over the previous summer was removed. For this winter growth increment there was no significant effect of large-scale density. However, small-scale density had a strong positive (facilitative) effect on winter growth increment, both for growth in shell length (Figure 4, $p < 0.0005$) and meat dry weight (not shown). This means that mussels in high density clumps or patches (with lots of near neighbours) grow better over the winter than mussels with fewer near neighbours – a surprising result. Overall, we did indeed have large-scale competition and small-scale facilitation in our

Figure 4 *Shell growth over winter, plotted against mussel density. Here, winter shell growth has been determined by subtracting the growth over the previous summer (calculated using the September length–density relationship shown above) from the total growth. For this winter shell growth increment, the effect of small-scale density is reversed, with mussels in denser quadrats growing more on average over the winter. The same relationship is seen for meat growth.*



By contrast, at the small scale, high densities of mussels mean more shell growth in winter

Table 1 *Examples of facilitation of growth in relation to physical stress in various sessile biota.*

System	**Mechanism**	**Relation with physical stress or resource limitation**	**Regular patterning?**
Mussel *Geukensia demissa*	Protection from high summer temperatures in dense clumps	Change from competition in low intertidal zone to facilitation in high intertidal zone	Not reported
Mussel *Brachidontes lemilaevis* and barnacle *Chthalamus anisopoma*	Dense barnacles protect each other and small mussels from high summer temperatures	Barnacle survival and mussel recruitment increases with barnacle density after exposure to high summer temperatures at low tide	Yes
Acorn barnacle *Semibalanus balanoides*	Protection from thermal stress in dense clumps	Strong competition in low intertidal zone, facilitation in high intertidal zone	Not reported
Salt marsh plants	Amelioration of soil salinity and O_2 content	Change from competition to facilitation along gradient of increasing soil salinity	Not reported
Intertidal algae on silt	Reduction in sediment shear stress by algae	Bimodal distribution of sediment silt content and chlorophyll-*a* in areas of high bottom shear stress, unimodal where low shear stress	Yes
Alpine plants	Amelioration of effects of low spring temperatures	Change from competition to facilitation up altitudinal gradient	Yes
Semi-arid ecosystems (tiger bush)	Increasing soil water content by shading and root penetration	Facilitation strongest in driest habitats	Yes
Peatlands	Increased nutrient supply where transpiration rate highest	Model predicts patterning where nutrient concentrations low, continuous vegetation where nutrient concentrations high	Yes

patterned mussel bed – but the competition and facilitation were separated in time as well as in space, with competition dominating at all spatial scales in summer, but facilitation being strong at the small spatial scale in winter.

It is interesting to ask why there should be a switch from competition to facilitation at the small scale on a seasonal basis. It is plausible that competition should be reduced in winter since lower water temperatures mean that the mussels are metabolically less active. But why should there be positive benefits from a high local density in winter? We believe that the answer lies in the physical and mechanical stresses imposed on mussels by the stronger winds and larger waves during the winter. It is well known that mussels produce greater numbers of attachment (byssal) threads when wave energy is greater, and also that byssus production can take up a significant amount of a mussel's energy budget. It seems likely to us that on soft sediment, where the only form of hard attachment substrate is other mussels, mussels in dense clumps may save significant amounts of energy by benefiting from each others' byssal attachments.

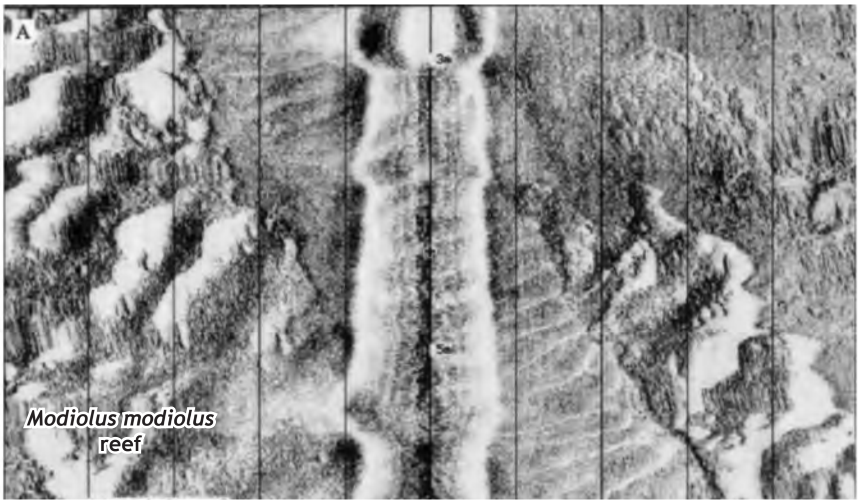
More generally, our research fits in well with the literature on facilitative interactions in other systems of attached organisms. It provides further support for the idea that facilitation is most likely in environments that are physically stressful, and that interactions may change from competition to facilitation up a gradient of physical stress (as found in the transition from summer to winter in the Menai Strait). We have compiled a table which shows some examples of these types of interactions (Table 1).

What now? We are looking for other systems which might show similar dynamics, as the principles put forward in our studies are turning out to be more common than we thought, in both the intertidal zone and the subtidal zone. For example, an intriguing image of subtidal horse mussels beds (*Modiolus modiolus*) off the Lleyn Peninsula was kindly provided to us by the Countryside Council for Wales (Figure 5). This picture seems to show regular patterning in these organisms as well – we can't wait to have a closer look!

Figure 5 *A side-scan sonar image of subtidal beds of horse mussels* Modiolus modiolus *on a sand/gravel substrate. These beds have a distinctive wave-form pattern, similar to the patterning of the mussels in the Menai Strait. (The band down the middle is the ship's track; the diagonal band may be a trawling scar.)*

Image by courtesy of Bill Sanderson (Countryside Council for Wales) and Ivor Rees and Jim Bennell (University of Wales Bangor).

Patterning may be common below the low-tide mark as well as in the intertidal zone



Acknowledgements

Thanks to Helen Beadman of NERC, Camille Saurel, Michel Kaiser, Gwynne Parry-Jones and Ivor Rees of University of Wales Bangor and Kim Mould of Myti Mussels Ltd.

Figure 2 is from J. van de Koppel, M. Rietkerk, N. Dankers, and P. M. J. Herman (2005) Scale dependent feedback and regular spatial patterns in young mussel beds. *American Naturalist* **165** (3).

Figures 3 and 4 are from J. Gascoigne, H. Beadman, C. Saurel and M. Kaiser (2005) Density dependence, spatial scale and patterning in sessile biota. *Oecologia* (in press).

Jo Gascoigne* is a postdoc at the School of Ocean Sciences, University of Wales Bangor. Her special interests are population dynamics, Allee effects, extinction risk and conservation and the interface between biology and physics.

Johan van de Koppel† is a theoretical ecologist at the Netherlands Institute of Ecology. His interests focus on the implications of positive feedback for the dynamics and spatial structure of ecological communities. He currently integrates mathematical models and empirical investigations in order to understand the spatial structure of estuarine ecosystems.

*Menai Bridge, Wales, LL59 5AB.
†Centre for Estuarine and Marine Ecology, Netherlands Institute of Ecology (NIOO–KNAW), PO Box 140,
4400 AC Yerseke, The Netherlands.

DEEP-SEA FISH

how researchers are tackling the challenge of decompression

Alan Jamieson

Since the early days of deep-sea biology during the pioneering HMS *Challenger* expedition (1872–76), it has been apparent that bringing deep-sea fish to the surface results in their death. The reason for this is the effect of decompression: fish living in the deep ocean have evolved to survive at pressures several hundred times greater than those on land. This high pressure inhibits simple laboratory experiments and impedes attempts to answer the most basic biological questions. Scientists are therefore left with a dilemma: do we study these animals in the deep sea at great expense, or do we bring them to the surface dead? Both paths create immense technological challenges, many of which have been solved with great innovation and imagination, with the aim of furthering our understanding of the deep-sea community. Discussed here are some of the reasons our knowledge of deep-sea fish lags behind that of shallow-water species, and some of the tools that the research community have developed to narrow the gap.

The largest component of the world's ocean is the deep sea (2000–6000 m deep). Much of this overlies the vast abyssal plains, characterized by gently undulating landscapes with an average depth of 4000 m. Inhabiting the abyssal plains are the grenadiers or 'rat-tails' (*Coryphaenoides* spp. of the family Macrouridae), known to continually forage, swimming immediately above the sea floor in search of food (Figure 1, overleaf). Rat-tails are the most abundant fish in the deep sea, and play a fundamental role in the dispersal of organic matter on the deep sea floor by consuming and scattering animal carcases. For these reasons they have been the subject of many studies, particularly in the last 30 years.

Researching these fish is technically problematic because of the remote and (to us) hostile nature of their environment, which is characterized by low temperatures, absence of light and – in particular – extremely high hydrostatic pressure. When rat-tails are brought up from their natural habitat they are killed by the rapid changes in pressure and temperature. As a result, our knowledge of these deep-sea fish is considerably lacking compared with that of their shallow-water counterparts, for which sophisticated laboratory experiments are easily undertaken. Described here are some of the technical solutions that have had to be developed to allow us to answer even the most basic biological questions about them.

Effects of decompression

In the relatively food-scarce environment of the deep sea, grenadiers have a low metabolic rate and, to optimize energy-use, achieve neutral buoyancy by means of a well-developed swimbladder. The bladder is filled with gas by diffusion from the blood via a biochemical mechanism. For neutral buoyancy, the internal gas pressure is typically equal to the ambient pressure (400 bar on average). In contrast to oil (used in shark buoyancy regulation), gas is extremely compressible, and the nature of high-pressure gas swimbladders does not easily accommodate the expansion of gas which results when the fish are brought to the surface. Grenadiers have no opening in the swimbladder, and there is no connection between the swimbladder and throat. Therefore, when they need to rise in the water column, they must resorb swimbladder gases, if the volume of the swimbladder is not to increase. The rate of gas expansion versus the resorption rate determines the severity of the effects of decompression. At the ascent rates typical of conventional sampling gear, a pressure decrease of 50 bar induces uncoordinated movement and tremors, at 100 bar convulsions occur, and higher rates still result in paralysis and nearly always death. As their gas bladders expand with decreasing pressure, deep-sea fish frequently suffer stomach eversion, which often pushes other internal organs out through their mouths (Figure 2) and induces internal bleeding. Similarly, internal eye fluid expands, forcing the eyes out of the head (cf. title graphic). However, it is thought that if the decompression period is long enough (e.g. several days) fish could survive at atmospheric pressure. With most deep-water sampling techniques (e.g. trawling), slow ascents would be impractical: ascent rates are typically 50 m per minute (a pressure decrease of ~5 bar per minute). Along with the effects of rapid decompression, fish also suffer thermal shock as a result of the the temperature change between the cold deep sea and surface waters.

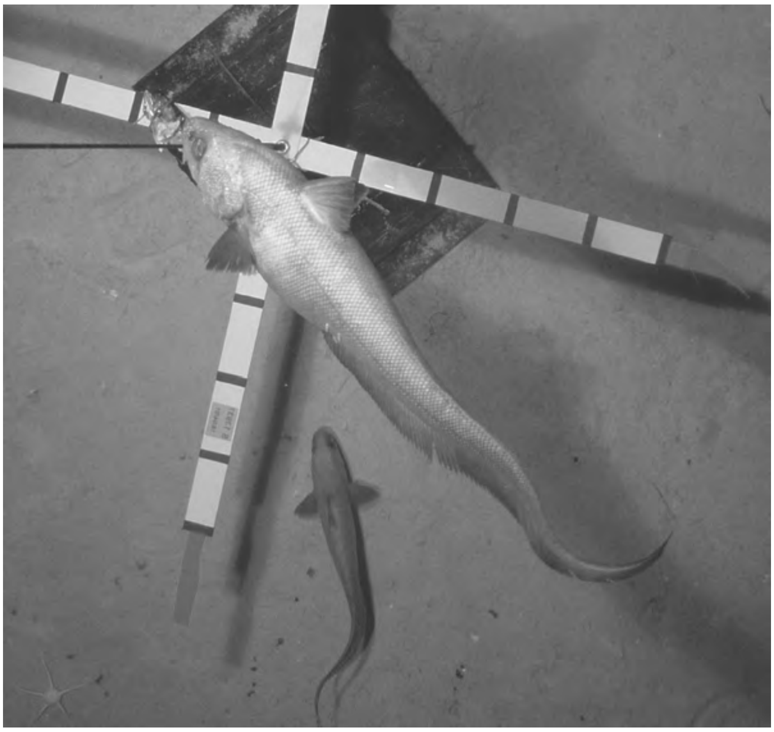
To understand the biology and ecology of deep-sea fish, specimens must be studied alive as well as dead – although in both cases there will be side-effects of capture. There are basically three ways to counteract the problems of fish decompression. The first is to observe deep-sea fish in the deep sea; the second is to decompress the fish and manage the effects of capture; and the third is to bring the animals to the surface under pressure.

In situ research

Many types of investigations, such as behavioural research, require that deep-sea fish be studied alive. This currently restricts sampling and observation to *in situ* studies. Observations and limited experimentation can be undertaken using autonomous observation platforms, manned submersibles or remotely operated vehicles. Autonomous observations are made possible by the use of landers or free vehicles (i.e. ROVs). Landers are not attached to the ship, and free fall to the sea floor with pre-programmed photographic or video equipment mounted inside a frame. They return to the surface by jettisoning ballast weights in response to an acoustic command from a surface vessel. In the study of fish, bait is typically positioned in the field-of-view of the camera to attract scavengers. Information on abundance, depth distribution, species assemblages, and interactions between different species, is readily obtainable. Longer-term platforms have been deployed to investigate the consumption of larger food sources such as dolphin carcases, or of bait introduced periodically in the study of seasonal patterns and migration.

Baited lander experiments have been deployed all over the world for many years, most frequently during the last 10 years, and were pioneered using the Scripps Institute of Oceanography FVV lander (FVV = Free Vehicle Video) and the University of Aberdeen AUDOS lander (AUDOS = Aberdeen University Deep Ocean Submersible) in the 1980s (cf. Figure 3). Unbaited long-term systems have also been used, such as Bathysnap, developed at the Institute of Oceanographic Sciences in the early 1980s.

Unbaited systems offer an insight into the natural occurrence of animals travelling across the sea floor. Although the number of fish observed may be far smaller than in a baited experiment, there is the advantage that the animals recorded are not restricted to scavengers.



Rat-tails are the most abundant scavenging fish in the deep sea, and can grow up to nearly 1 m long

Figure 1 *Deep-sea grenadiers photographed by a camera on a baited lander in the north-east Atlantic, at a depth of 4200 m. A small rat-tail is approaching the bait, while the large fish in the foreground is exploring the lander. (The scale bars shown are 10 cm apart, and the camera is 2 m above the sea floor.)*

Decompression invariably results in death for deep-sea fish brought up by conventional sampling gear

Figure 2 *The effects of decompression on deep-sea fish (mainly rat-tails) taken from a depth of 4000 m in the north-east Atlantic. The fish surrounding the dolphin carcase have internal organs protruding out of their mouths, as a result of swimbladder gas expanding during the ascent to the surface.*

A major limitation of landers, however, is that they remain in one site throughout the deployment, and it is not possible to respond to events, or manipulateh experiments in real time. Manned submersibles and remotely operated vehicles do, however, have such facilities, albeit at far greater cost and with limited availability. These piloted and/or remotely controlled vehicles can survey large areas of sea floor, locate particular areas of interest, and sample and manipulate experimental equipment on the sea floor. A great deal of information can be obtained using these techniques, which are non-destructive and, compared with trawling for example, are a relatively non-invasive sampling method.

Metabolic studies

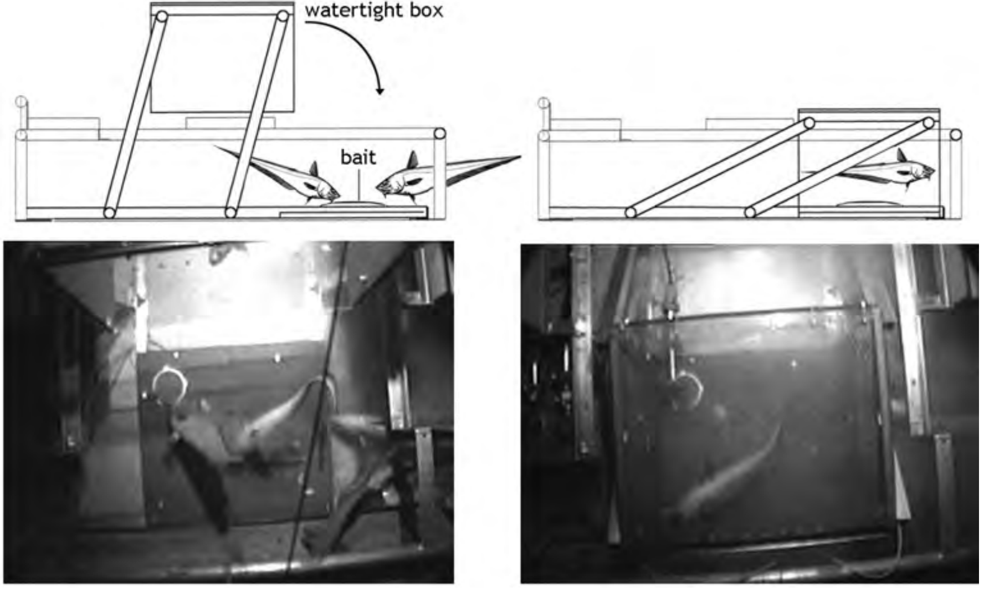
It is not possible to answer the question 'What is the metabolic rate of a deep-sea fish?' using conventional laboratory experiments, because the fish die during capture. In 1978, Dr Ken Smith Jnr from Scripps Institute of Oceanography in San Diego, designed an experiment to measure the oxygen consumption of grenadiers from a manned submersible. A cylindrical device sucked individual rat-tails into a watertight chamber. This allowed the oxygen consumption of the fish to be measured while the animal was at its natural pressure, proving for the first time that deep-sea fish have a much slower metabolism than their shallow-water counterparts.

Building on the idea of measuring oxygen consumption *in situ*, the University of Aberdeen's Oceanlab developed a more complex experimental lander called the Fish Respirometer or FRESP. The FRESP attracted grenadier into an area in view of a camera and, on the basis of existing knowledge of when peak numbers occurred at the bait, a watertight box was dropped over the bait capturing fish inside (Figure 4, right). Just three years ago, this technique achieved the first completely autonomous capture and measurement of oxygen consumption of deep-sea fish, and at a far lower cost than using a manned submersible. To complement the findings on metabolic rate, Aberdeen scientists asked 'What is the maximum energy output of a deep-sea fish?', i.e. 'How fast can it swim?' Simply observing the fish does not provide such information, as in the food-scarce environment of the deep sea they often conserve energy by swimming very slowly; and again conventional lab experiments are not possible. The Sprint lander was developed by Oceanlab to answer such questions.

Figure 3 *Deep-sea grenadiers observed* in situ, *feeding on a dolphin carcase at 4000 m depth in the north-east Atlantic. While foraging close to the bait, the fish adopt a head-down–tail-up orientation, and use their sensitive tactile and gustatory senses to locate their food. (This video image was obtained during the Large Abyssal Food Fall (LAFF) project, which investigated how large cetation carcases are 'processed' in the deep sea.)*

Images from baited landers have provided useful information about how organic matter (food) is found and dispersed on the deep sea-floor

Figure 4 *The FRESP lander triggers a watertight trap to capture grenadiers and measure their oxygen consumption on the deep sea floor.*



***The FRESP lander allows the oxygen consumption of deep-sea fish to be measured* in situ**

The Sprint experiment used two 1.5-metre electrodes placed around bait. At 60-second intervals an electrical pulse stimulated a 'fast start' in the fish. This electric shock was not enough to harm the fish but enough to trigger an escape response. By filming these sudden 'sprints' with a high-speed camera we obtained further information on deep-sea fish physiology. The sophistication of experiments that can be undertaken from landers, manned submersibles and remotely operated vehicles is increasing all the time.

Ex situ research

Imperative as such research surveys and *in situ* observation and experimentation are, it is often scientifically necessary to physically obtain specimens. Photographic and video observations do not permit analysis of chemical composition, diet composition, genetics or morphology. Trawling is currently the most common method of capturing deep-sea fish, but trawling at abyssal depths is no trivial task. Thousands of metres of warp are required to reach these depths, which limits the number of vessels capable of undertaking such operations. In shallow waters, trawling gear 'herds' fish into the mouth of the trawl where they are captured when they tire. In deep water, where there is no light, herding is thought to diminish and so-called 'filter trawling' occurs, with almost every animal in the path of the oncoming trawl being collected. Fish and other animals captured in a trawl are drawn into the cod-end where their delicate scales, fins and protruding features, some of which are required for identification, are often damaged.

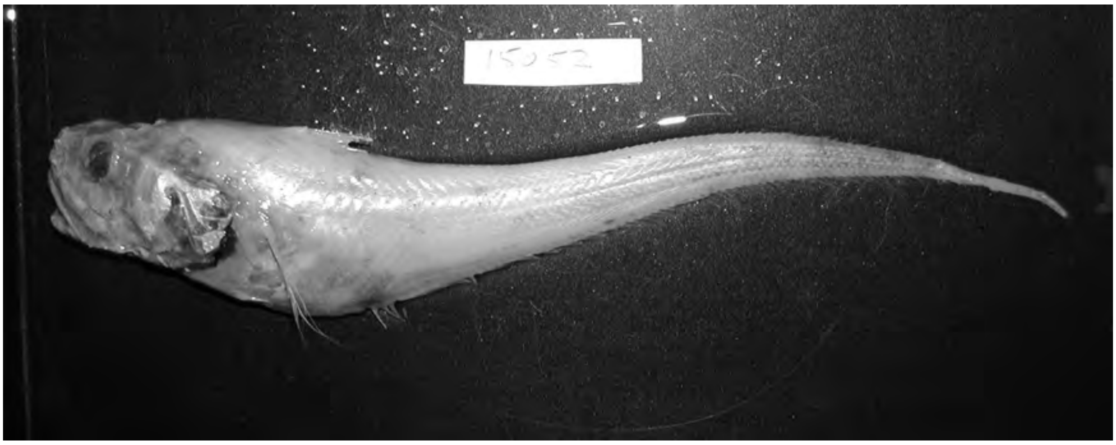
In the absence of a large vessel, fish can be captured without damaging them by using moored fish traps deployed in the same manner as landers. Fish traps are baited cages with one or more funnel entrances, which are elevated above the bottom and protrude into the trap. Once inside the cage, fish tend to explore the interior structure seeking an escape route, but are unable to locate the funnels again. Fish traps do not sample in the same quantities as trawling but they can be deployed from small vessels, are relatively cheap, and require very little ship-time to operate. Traps also have the advantage that they limit bycatch, and eliminate accidental damage to coral mounds, sponge fields or other biological communities, which is occasionally caused during deep trawling for scientific purposes.

Both trawling and funnel traps provide material for genetic, morphological and chemical composition analyses, but specimens are still subjected to the effects of decompression. Stomach eversion during decompression makes it difficult to answer the basic question 'What do deep-sea fish eat?' Furthermore, although we know that scavengers consume bait placed on lander vehicles, these are not typical natural events and there are species of grenadier that rarely approach bait and probably search for live food in the form of other fish or small crustaceans in or on the sea floor. Diet composition provides insights into predator–prey interactions and foraging patterns, and their influences on community dynamics. Such analysis is only possible by removing fish from the deep sea without loss of their stomach contents.

A series of novel fish traps were designed by Jeff Drazen at Scripps Institute of Oceanography to solve these problems. The traps consist of long plastic tubes with an open door at one end and a piece of bait at the entrance, connected to the trap interior via a fishing hook on a tensioned bungee cord. As the fish takes the bait, and then pulls at it when it snags, the bungee cord is released, the fish is pulled into the trap, and the door shuts behind it. The traps are recovered in the same way as landers, and the fish are subjected to typical decompression effects. However, the traps are fitted with extremely fine mesh filters on either end to retain the stomach contents after eversion. This technique provides a relatively cheap way of retrieving stomach contents.

Figure 5 *A rat-tail whose scales have been stripped off in the cod-end of a trawl. (The fish is about 50 cm long).*

Fish captured in a trawl often lose scales, fins etc., needed for identification



Hyperbaric research

An alternative to *in situ* and *ex situ* research is to bring deep-sea animals to the surface under high-pressure conditions. This raises the big question: can deep-sea fish be acclimatised to low pressure? This is perhaps the most technically challenging task of all. Just as camera systems and electronic instrumentation are housed in strong metal pressure vessels to resist the ambient external pressure, similar technology can be used to retain internal pressure. The technique involves lowering an open pressure vessel to the sea floor, closing it, and returning it to the surface whilst retaining the pressure at closure, i.e. making a hyperbaric chamber. This was first done using a small vessel for studying bacteria and plankton in deep seawater. The idea progressed by incorporating baited funnels into the open vessel; small crustaceans such as scavenging amphipods would swim inside the funnels (similar to those described above, but smaller) to locate the bait. The vessel would then close and return the amphipods to the surface under high pressure. Using this technique, physiological experiments were undertaken on the effects of decompression/recompression and metabolism. Similar traps developed by IFM-GEOMAR in Germany are still in use, and now incorporate temperature regulation.

In the 1970s, the basic principles of this technique were developed further by Scripps Institute of Oceanography in larger, more elaborate traps for capturing grenadiers, and the baited bungee method of capture was again used successfully. The trap design incorporated high-pressure viewports to observe the behaviour and health of captured specimens, and had certain limited experimental capabilities, such as measurement of the oxygen concentration of the water. However, difficulties in totally sealing the chamber autonomously have led to many failures of the trap. Also, the compressibility of the equipment as dictated by the material properties typically results in some loss of pressure.

The hyperbaric fish trap has recently been redesigned, and the current design, operated by Monterey Bay Aquarium Research Institute (MBARI), has been used with success on Pacific grenadiers. The new trap ascends to the surface very slowly to allow for any minor decreases in pressure within the equipment. During preliminary deployments of the trap a deep-sea fish was kept alive for 48 hours, but later deployments have managed to sustain a live fish for 80 hours.

Simultaneously, another hyperbaric chamber design was developed in Japan by JAMSTEC.* The Japanese capture method involved the use of a manned submersible. A small zoarcid fish (also known as an eelpout) was captured and placed into a pressure-resistant sphere and returned to the surface. The sphere was coupled to a re-circulation and feeding system in the laboratory, and the small fish was kept alive at a pressure of 200 bar for 64 days. The hypothesis driving this technique is that deep-sea fish can acclimatise to low pressure if slowly decompressed over days to weeks, and it is hoped that, one day, deep-sea fish can routinely survive in an aquarium or laboratory environment.

Discussion

The more we study the deep sea, the more it throws out new questions that need to be answered – a challenge that the marine science community is always eager to explore. A recurring theme associated with providing answers to deep-sea biological questions is the immense engineering input required. Experiments often make use of advanced technology, devised in response to biological questions. This multidisciplinary approach has benefited the science community in general, and in particular has improved our knowledge and understanding of the deep-sea environment. It is the ambition of deep-sea scientists and engineers alike that soon the deep sea will not be seen as such a hostile and problematic area of research, but an accessible and readily studied environment.

Further reading

Bailey, D.M., A.J. Jamieson, P.M. Bagley, M.A. Collins, I.G. Priede (2002) Measurement of *in situ* oxygen consumption of deep-sea fish using an autonomous lander vehicle, *Deep-Sea Research*, **49**, 1519–29.

Drazen, J.C., T.W. Buckley, G.R. Hoff (2001) The feeding habits of slope dwelling macrourid fishes in the eastern North Pacific, *Deep-Sea Research*, **48**, 909–35.

Koyama, S., T. Miwa, M., Horaii, Y. Ishikawa, K. Horikoshi, M. Aizawa (2002) Pressure-stat aquarium system designed for capturing and maintaining deep-sea organisms. *Deep-Sea Research* Part I, **49**, 2095–2102.

Phleger, C.F., R.R. McConnaughey, P. Crill. (1979) Hyperbaric trap operation and deployment in the deep-sea. *Deep-Sea Research*, **26A**, 1405–09.

Sebert, P. (2001) Fish at high pressure: a hundred year history. *Comparative Biochemistry and Physiology*, Part A, **131**, 575–85.

Alan Jamieson is a postdoctoral research fellow specializing in deep-sea technology at the Oceanlab, University of Aberdeen*, UK. He is primarily involved in the design of high-pressure lander technology for the study of deep-sea fish.

Email: http://www.abdn.ac.uk/oceanlab

*Main St, Newburgh, Aberdeenshire, Scotland AB41 6AA.

---

*JAMSTEC = Japan Marine Science and Technology Centre, now the Japan Agency for Marine–Earth Science and Technology (Independent Administrative Institution).

Sea Lice and Sea Trout

Are salmon farms causing increased parasitism on wild salmonids in Scotland

Philip Gillibrand
David Hay
Michael Penston
Alexander Murray

Over the past three decades, the development of salmon farming into a major industry in the Highlands and Islands of Scotland has been of huge benefit to employment opportunities in these rural communities, and to the Scottish economy as a whole. However, with the expansion of the industry has come rising concern about potential adverse environmental consequences for the marine ecosystems in which the industry is based. Possible impacts range from those on local scales (e.g. the export of carbon-rich fish wastes and chemicals used on fish farm sites) to wider regional-scale effects (e.g. a hypothesized link between dissolved nitrogen emissions from caged fish and increased risk of algal blooms). Over the past twenty years or so, considerable research effort has been invested in understanding local impacts, and developing appropriate predictive tools, and considerable progress has been made. More recently, scientists have been turning their attention to less tangible regional-scale effects. One such effect is a hypothesized, but as yet unproven, link between the sea lice populations that have been endemic on salmon farms, and infestations of lice on wild salmonids (salmon and sea trout). Declines in wild salmonid populations in Scottish rivers over the past few decades have been attributed by some to extreme sea lice parasitism caused by the expanding aquaculture industry, although the declines have been widely observed in salmonid populations throughout the North Atlantic region.

Sea lice are naturally occurring parasitic copepods, part of the marine zooplankton community. The species *Lepeophtheirus salmonis* and *Caligus elongatus* of the Caligidae family are particularly prevalent on salmonids in the Northern Hemisphere and, in the past, their occurrence on wild salmon has been taken as a sign that the fish have recently been to sea. However, the large numbers of farmed salmon kept closely confined in marine cages have provided abundant hosts for sea lice, leading to enhanced lice populations in inshore waters. Sea lice feed on host mucus, tissues and blood, and high numbers of parasites on individual fish can lead to reduced growth, secondary infections, unsightly lesions and loss of market value, and ultimately death (Figure 1). Such consequences of sea lice infestations have been estimated to cost the Scottish fish farming industry about £15–30 million per annum.

A key question is whether the sea lice populations found on salmon farms have caused increased parasitism on the wild salmonid populations found in the rivers and streams that enter the same coastal waters in which the salmon farming industry is located. Or, alternatively, are sea lice retained on the farms where abundant hosts are readily available? To answer that question, we need to understand the life cycles and behavioural traits of both sea lice and wild salmonids in order to assess how the two may interact.

Atlantic salmon (*Salmo salar*) are migratory fish found in the temperate and Arctic regions of the North Atlantic and the Baltic Sea. Atlantic salmon spawn in rivers and the young fish remain in fresh water for their first 1–5 years, before entering the marine phase of their life cycle. The smolt run, when the young fish (smolts) migrate to sea, typically occurs in late spring, from April to early June. Once at sea, the smolts immediately begin to head for feeding grounds in the open ocean; feeding grounds in the Norwegian Sea and off south-west Greenland are known, and others may exist. After usually spending several (1–4) years at sea, salmon return to their home river to spawn.

For this study, our main interest was in the sea trout population indigeneous to the River Shieldaig. Sea trout (*Salmo trutta*) are a migratory form of the common brown trout. The life cycle of a sea trout is similar to that of the Atlantic salmon: following a period of freshwater residence, sea trout migrate to sea as smolts. However, unlike

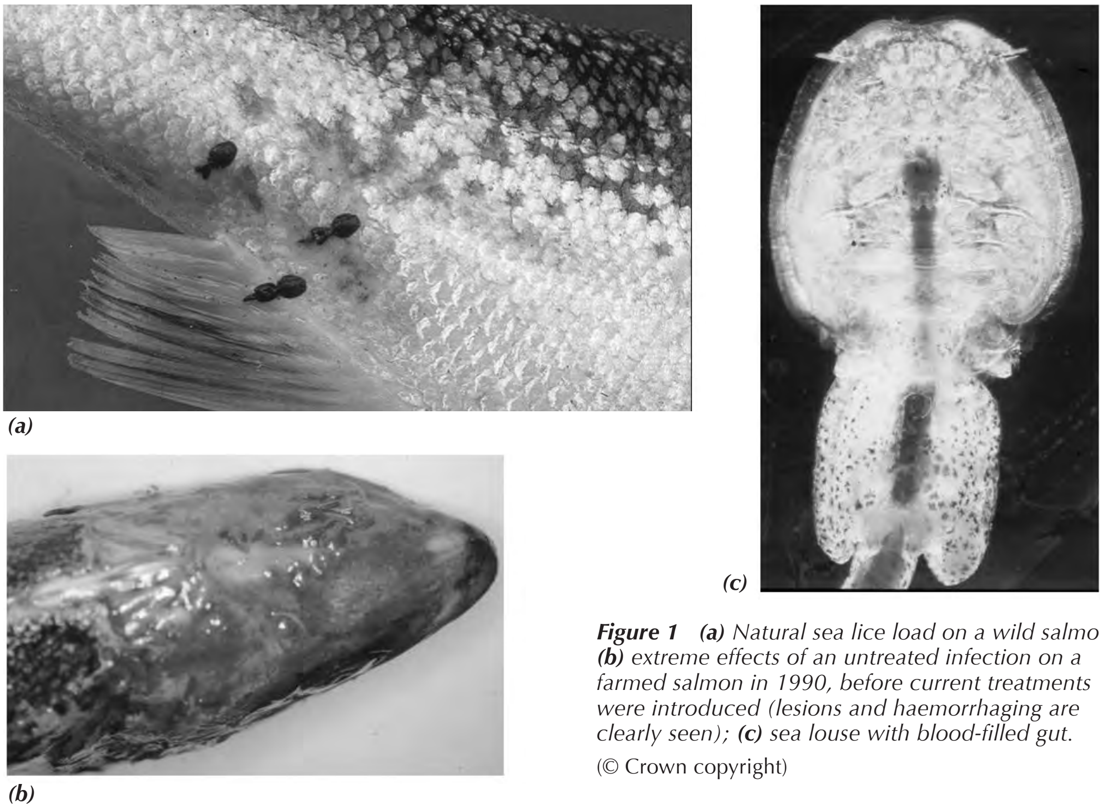


Figure 1 ***(a)*** *Natural sea lice load on a wild salmon;* ***(b)*** *extreme effects of an untreated infection on a farmed salmon in 1990, before current treatments were introduced (lesions and haemorrhaging are clearly seen);* ***(c)*** *sea louse with blood-filled gut.*

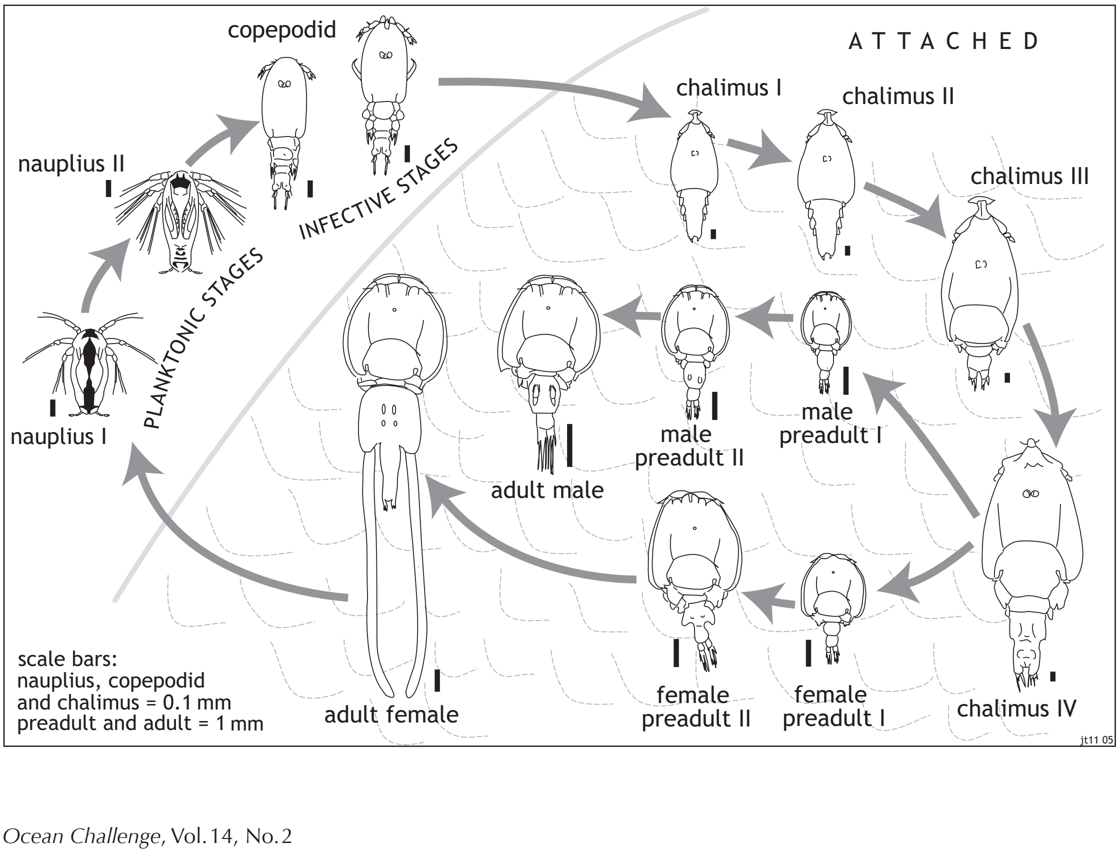
(© Crown copyright)

Sea lice affect the health of farmed salmon, and reduce industry profits

salmon, sea trout appear to remain largely in coastal waters, although in truth little is yet known about their patterns of movement along the coast. The tendency to inhabit inshore waters may make sea trout particularly susceptible to sea lice infestation from salmon farms. Like salmon, after a period at sea (usually a year or so), sea trout return to their native river to spawn.

Sea lice, like most caligid copepods, have a life cycle consisting of typically ten stages: two free-living planktonic naupliar stages, one infective free-swimming copepodid stage, four attached chalimus stages, two preadult stages and one adult stage (Figure 2). Female adults attached to fish release eggs into the water column which hatch into the first nauplius stage. These larvae are planktonic and drift with the prevailing

Figure 2 *Sea-lice life cycle. The eggs hatch into planktonic nauplii, which develop into copepodids which search for fish on which to live for the remainder of their lives. The different stages are separated by moults of the hard exoskeleton.*



Only the copepodid stage of sea lice is able to infect fish

water currents. The naupliar stages quite quickly (about three to four days at 10 °C) transform into copepodids, which are still planktonic but have some swimming capability. Copepodids typically survive for 2 to 8 days at 5–15 °C in full seawater, during which time they must locate and attach to a host fish. The planktonic phase of the sea lice life cycle may therefore last around three weeks (although older lice may become senescent), during which time the larval lice may disperse over a wide area, depending on the prevailing water circulation. The key to their survival is to find and attach to a host during this planktonic phase, either a farmed or a wild salmonid.

The role of larval dispersion in the sea lice quest to find suitable hosts has received little attention previously. During sampling programmes in Irish coastal waters during the 1990s, sea lice larvae were only found consistently within and close to salmon cages, but were also found sporadically close to river mouths. The researchers found a significant inverse relationship between distance from a fish farm and larval numbers, and concluded that there was a very high retention of sea lice within the fish farm cages, and that the lice found close to river mouths were a separate population associated with wild salmon and sea trout. This conclusion was also reached by other researchers who argued that lice larvae developing on fish farms would immediately attach to the readily available reservoir of hosts present in the cage. Thus it seemed that sea lice from fish farms were not related to parasites found on wild fish. More recently, however, new studies have begun to suggest that the presence of salmon farms in long narrow fjordic inlets may result in increased infection pressure on wild migrating salmonids.

Observations of sea lice larvae

Our field work concentrated on Loch Shieldaig, part of the Loch Torridon system in the north-west of Scotland (Figure 3). River Shieldaig supports a fish trap in its lower reaches, which has been established to monitor the local sea trout population in the river. The monitoring established that sea trout, heavily infested with sea lice, were returning early to the river without having spent significant periods of time at sea. Some of these fish exhibited very high lice burdens, enough to cause eventual mortality. This observation suggested that the fish were infected with lice very soon after descending the river. Acoustic tracking studies have shown that in the period shortly after they enter the sea, post-smolt sea trout move in and out with the tide, swimming in the intertidal zone for much of the tidal cycle. It seemed possible, therefore, that it was here that sea trout were encountering sea lice in significant numbers.

Sampling for sea lice larvae in coastal waters is not straightforward. Typically, low larval densities mean that in order to catch a significant number of lice, large volumes of water have to be sampled. The traditional method of sampling zooplankton is to tow a plankton net through the water from a research vessel. In order to catch sea lice larvae, a relatively fine mesh size is required for the plankton net, and given that large volumes of water have to be sampled, the nets tend to get clogged up with other plankton and detritus in the water. However, we found that the best method was to tow a small plankton net behind a slowly moving rigid inflatable boat.

Because it was hypothesized that sea lice might be infecting sea trout in the intertidal zone, plankton tows were first performed in the very shallow

Lice concentrations were sampled at site S in the intertidal zone at the head of the loch, plus seven other deeper sites

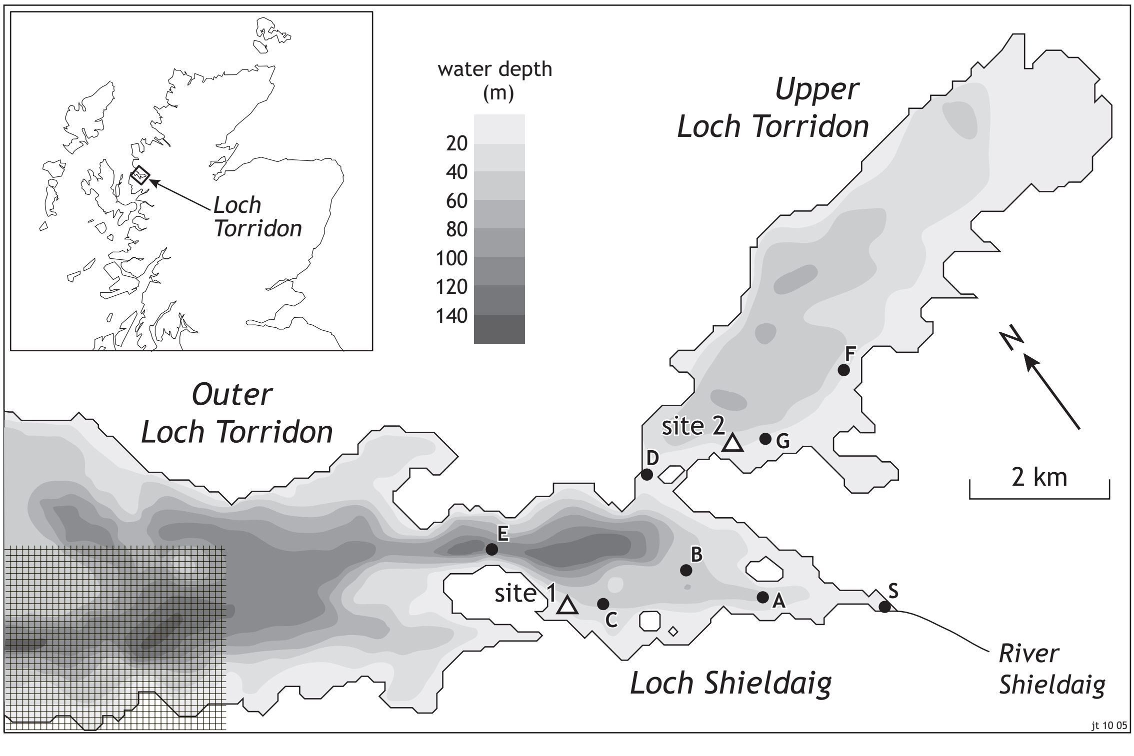


Figure 3 *Our study site, Loch Torridon on the north-west coast of Scotland. Lice sampling sites are identified as A–G and S. The locations of two fish farms (site 1 and site 2) and River Shieldaig are indicated. The model domain covers the entire area shown at a resolution indicated by the grid in the lower left corner.*

waters at the head of the loch, near the mouth of River Shieldag (site S on Figure 3), with the plankton net being towed either from a small boat or by wading. Sampling along the shoreline began in 1999 and has continued until the present day, with sampling typically performed weekly during the spring and summer, and monthly during the winter, although this has varied. Samples were collected from four 'sweeps' at different locations at the head of the loch.

The results from the shoreline sampling from 1999 to 2003 are shown in Figure 4. The first striking feature of the data is the strong biannual signal. Sea lice larvae were found in the littoral zone at the head of Loch Shieldaig in 1999, 2001 and 2003, but were not found in 2000 or 2002. The number of samples collected at this site each year and the number of days on which samples were taken are given in Table 1 below. The highest estimated densities recorded were 33, 94 and 143 lice m^{-3} in 1999, 2001 and 2003 respectively. The same biannual cycle was also observed at another river mouth site in Upper Loch Torridon when sampling was conducted there during 2001–2003.

A second key feature of the data was that no naupliar stages were detected at site S. All sea lice larvae sampled were the infectious copepodid stage of *L. salmonis*.

Following the early success in sampling sea lice larvae at the river mouth, sampling in the open waters of Loch Shieldaig and Upper Loch Torridon started in autumn 2001. Here samples were collected by towing a plankton net behind a rigid inflatable boat at five sites (A–E), with sites B and D soon being replaced by F and G. Repeat tows at each site were performed with the net being towed at different depths to provide some vertical resolution in the results. The open water sampling was conducted weekly unless adverse weather conditions made small boat work impossible.

Analysis of the 2001–2002 data showed that peak densities in the open water were typically much lower than those observed at the shoreline; average larval densities were less than 1 lice m^{-3} compared with almost 60 lice m^{-3} at the shoreline (Figure 5(a)). Also, in notable contrast to the shoreline data, both naupliar and copepodid stages of sea lice have been identified in the open water samples. Analysis of the ratio of nauplii : copepodid stages at each site suggests that the ratio decreases with increasing distance from a fish farm (Figure 5(b)).

Table 1 *Plankton sampling at site S in Loch Shieldaig: dates, numbers of samples collected (n) and numbers of days on which samples were collected.*

Year	Sampling dates	*n*	No. of days
1999	03/05/99 – 02/08/99	24	8
2000	22/03/00 – 19/06/00	42	14
2001	15/03/01 – 10/09/01	54	18
2002	01/04/02 – 09/09/02	17	6
2003	07/01/03 – 16/07/03	42	14

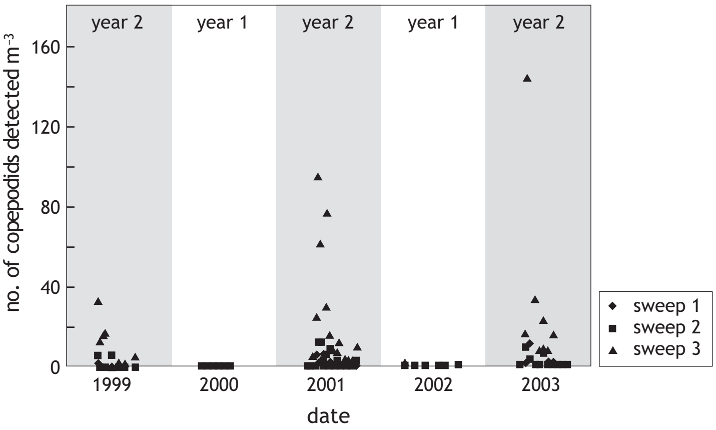
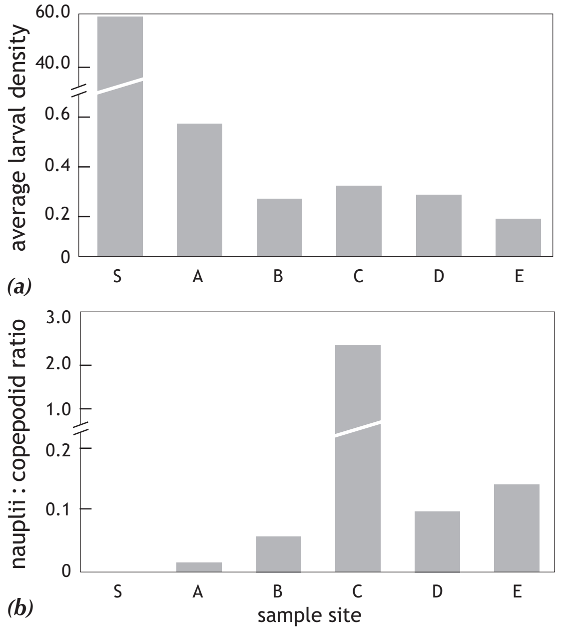


Figure 4 *Results of the sea lice sampling at the shoreline of Loch Shieldaig (site S), showing numbers of copepodids detected per cubic metre of water for 1999–2003. The samples were collected from three 'sweeps' along the shoreline at the head of the loch. The 'Year 1' and 'Year 2' labels at the top of the plot refer to years in the fish farm production cycle (see text).*

Sea lice abundance in intertidal waters follows the two-year salmon production cycle

Interpreting the observations

The biannual cycle of sea lice abundance observed at the shoreline site (Figure 4), and hinted at in the open water observations, closely matches the production cycle of local salmon farms in Loch Torridon. In Scotland, salmon production typically occurs over a two-year cycle. Empty cages are stocked with young lice-free salmon smolts, typically in early spring. Over the following 14–22 months, the smolts grow to full size marketable adults, which are then harvested over a period of a few months. The cages are then allowed to lie 'fallow' (empty) for a period of time (typically 6–8 weeks) before restocking takes place and the production cycle resumes. Statistical studies of lice burdens on productive salmon farms in Scotland, carried out at Strathclyde



Open water samples typically contained lower densities of lice larvae than site S; sites close to fish farms contained relatively more nauplii and relatively fewer infective stages

Figure 5 *Calculated **(a)** average larval densities (lice m^{-3}), and **(b)** nauplii : copepodid ratio, from samples collected during October 2001 – February 2002. Note that the average larval density at the shoreline (site S) was two orders of magnitude higher than values in the open water (A–E).*

University, have demonstrated that numbers of *L. salmonis* are relatively low during the first year of production and relatively high during the second year, when the fish reach adulthood. The years of 1999, 2001 and 2003, when high larval lice numbers were observed during our study, all coincided with the second year of the production cycle on local salmon farms.

The shoreline data from 2001 and 2002 were cross-correlated with a range of time lags against records of the lice burdens on the nearest local salmon farm. These results showed a significant ($p < 0.001$) correlation coefficient of $r = 0.39$ for lags of 1 and 3 weeks, suggesting that the appearance of lice at the shoreline lagged behind farm lice levels by this period. It is important to note, however, that this positive association between farm and shoreline lice levels is not regarded as evidence of causality, since both may have been driven by external factors.

As shown in Figure 5, analysis of the open water samples revealed two interesting features: first, that the average densities of larval lice initially decreased with increasing distance from the local salmon farms but then increased toward the head of the loch (sites C, B, A and S); and second, that the ratio of nauplii : copepodid stages decreased with increasing distance from the local farm, falling from about 2.5 at site C to zero at site S. This could be interpreted as suggesting that site C, with larger numbers of naupliar relative to copepodid stages, was closer to the source of the lice, and site S further away.

These data raised as many questions as they answered. Why do larval lice numbers appear to be highest at the mouth of the river, particularly if the source is not immediately local? What drives the aggregation of lice at the river mouth? Are behavioural traits involved, or is it purely the result of physical transport processes? Are lice larvae released by adult females to coincide with the spring smolt run, or has the year-round presence of farmed salmon facilitated continual breeding? What triggers the release of egg strings by female adult lice?

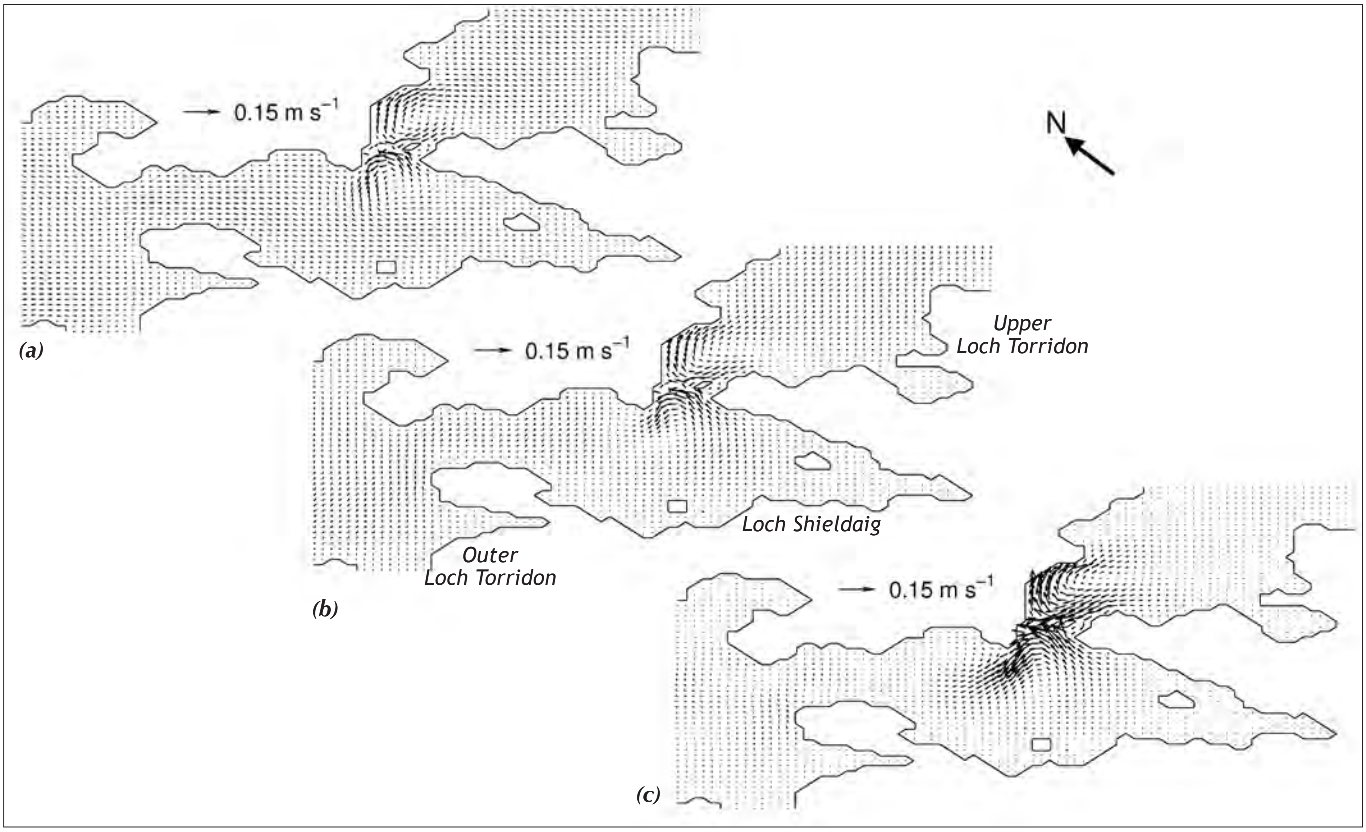
One way of beginning to address some of these questions is through computer modelling, which can help us to interpret the observations.

What do the models show?

Previous researchers had concluded that sea lice larvae released from adult lice on farmed salmon were likely to be retained within fish cages and were unlikely to disperse far enough to form populations at the mouths of rivers. We wanted to test that conclusion in the Scottish context, and therefore investigated the dispersion of lice larvae from salmon cages. We used a three-dimensional hydrodynamic model to simulate the water circulation throughout Loch Torridon for periods of interest during 2001–2003, when lice sometimes appeared at the shoreline sample site and sometimes did not. In this way, we could try to understand what factors were involved in the appearance of lice larvae at the river mouth. The model calculated water currents at a horizontal

Computed surface current patterns formed the basis for the lice transport model

Figure 6 *Surface flow fields (averaged over a tidal cycle) predicted by the numerical model for the Loch Shieldaig region (note key arrow for current speed).* ***(a)*** *A steady north-westerly wind of 5 m s*$^{-1}$ *gives rise to weak landward surface currents in Loch Shieldaig;* ***(b)*** *a steady south-westerly wind of 5 m s*$^{-1}$ *results in weak transverse surface currents across the loch; and* ***(c)*** *observed winds produce a gyre-like circulation in the Loch Shieldaig basin, enhancing the residual tidal currents generated at the sill between Loch Shieldaig and Upper Loch Torridon.*



resolution of 100 m and at 15 different depths in the vertical; these current fields were saved every half-hour. The water currents were forced by the tide and wind.

The computed current fields (Figure 6) were used to drive a lice transport model. This model simulated the release and dispersion of sea lice larvae from specified locations in the loch. The sea lice, which were assumed to be buoyant and remain in surface waters, as indicated by the observations, are carried around the loch by the prevailing currents, and also disperse as a result of eddies and horizontal mixing (diffusion). We used real observed wind speeds and directions in order to try and reproduce observed events. However, some of the most revealing results to date have come from simpler tests using steady wind speeds from fixed directions. These simulations allow us to asses how lice may disperse from various release points under different environmental conditions.

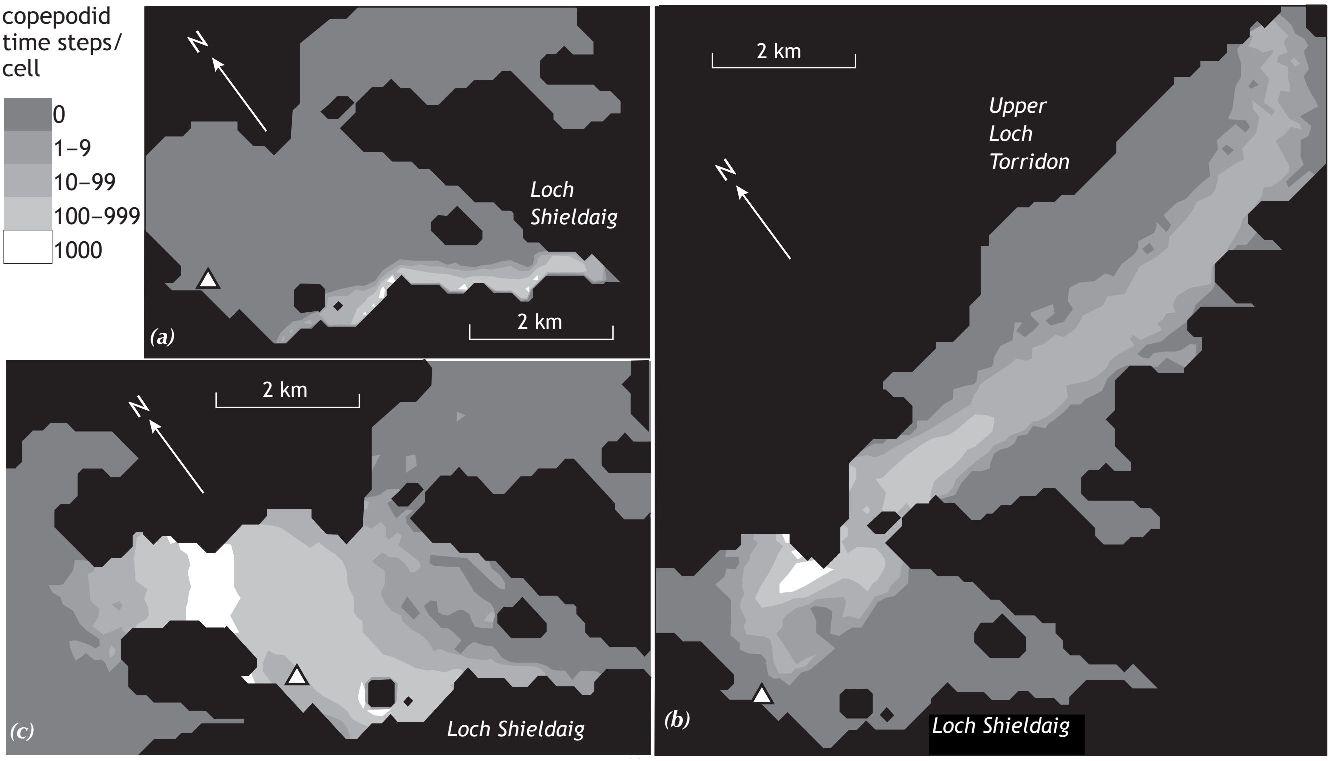
Figure 7 shows the results of selected model runs. Here, lice particles have been released from a location in Loch Shieldaig (indicated by the triangle), and their transport has been tracked for 15 days (since copepodids may only be viable i.e. infective, for this length of time after hatching). The plots show relative infection risk for fish resident in different model boxes over a model run, assuming that risk is proportional to concentration of infective particles multiplied by the time over which infection could occur. The three plots show dispersion of larvae resulting from a north-westerly wind, a south-westerly wind, and a real observed wind time-series (cf. Figure 6). Most notably, under a north-westerly wind, the larvae hug the south-west coast of Loch Shieldaig and are transported to the head of the loch, where they aggregate (Figure 7(a)). Aggregation under purely physical forcing is possible in the model simulations because the larvae are assumed to be positively buoyant and therefore remain on the water surface, even when water is being downwelled, as may occur at the head of the loch. Dead lice sink, and therefore the lice must be viable when they form such concentrations.

Under conditions of south-westerly wind, the larvae are transported into the upper basin of Loch Torridon, and some are carried almost to the head of the loch, some 16 km away (Figure 7(b)). These results demonstrate that, under suitable conditions, viable lice larvae can be transported many kilometres from the source. Whether densities of lice at these distances are sufficient to pose a serious infection risk to wild fish populations is unclear. This simulation also demonstrates that transfer of lice larvae between sea loch basins is entirely possible, and that neighbouring salmon farms are capable of infecting each other. In the case of real wind forcing, the lice larvae are dispersed throughout Loch Shieldaig (Figure 7(c)). This would seem to raise the possibility that sea trout smolts migrating to sea during this two-week period would encounter infective lice, though not necessarily in the high densities that might result from persistent north-westerly winds.

The clear dependence of lice transport on wind-driven surface currents in these simulations may

The lice transport model demonstrates that lice may disperse over significant distances, and that neighbouring salmon farms may re-infect one another

Figure 7 *Results from the lice transport model in which particles were released from Site 1 in Loch Shieldaig. Concentrations of copepodids only are shown (i.e. not nauplii). The particles were subject to **(a)** north-westerly, **(b)** south-westerly and **(c)** (bottom left) observed wind forcing. The output is in units of particle time steps per grid square, for example 10 particle time steps could mean either 10 copepodids enter a grid square for 1 time step, or 1 copepodid is present for 10 time steps (or some intermediate combination).*



explain some of the anomalies of the dataset from the mouth of the River Shieldaig. Occasionally, when egg-bearing female lice are abundant on the local salmon, lice do not appear at the shoreline; conversely, lice have appeared at the shoreline in significant numbers when lice burdens on the farm were relatively low. This could indicate that the shoreline lice population is distinct from the farm population, or it could be a sign that the shoreline population densities are controlled by the prevailing wind conditions at the time. The modelling results to date suggest that lice numbers at the head of the loch (indeed, throughout the loch) at any one time are strongly dependent on wind conditions, and that these result in sporadic peaks in the population at any given location. Certainly, the model results suggest that a link between farm lice and shoreline lice populations cannot be discounted. Work continues to refine and improve the models, incorporating physical characteristics such as the impact of freshwater inputs, and the effects of different assumptions about turbulence on dispersal, as well as biological characteristics of sea lice larvae, such as spawning, vertical migration, and viability under different temperature and salinity regimes. Data to inform these developments are also being gathered.

What does the future hold?

In recent years, salmon farmers in Scotland have been able to use some newly licensed treatment agents that seem to be more efficacious against all stages of sea lice than the medicines that were previously available. It is hoped that strategic use of these new products will assist salmon farmers in controlling the lice burdens on their farms, reducing production costs and, in the process, reducing the parasite risk for wild salmon and sea trout populations from Scottish rivers.

Throughout Scotland, the battle against sea lice infestations on salmon farms is also being taken forward through the establishment of Area Management Groups (AMGs) and Area Management Agreements (AMAs). These voluntary concordats between salmon farmers and representatives of the wild fish interests in localised stretches of water (e.g. individual sea lochs) facilitate information exchange on lice burdens and promote coordinated sea lice treatments by farmers. Past research, which has been corroborated by the present study, shows that farms in shared water can quickly re-infect each other with lice if they do not all treat at the same time. Strategic treatments, using the newly available medicines, might finally bring the sea lice problem on salmon farms under control.

Sampling for lice in Loch Shieldaig and Loch Torridon continues. During 2005, the salmon farms in Loch Torridon are in the second year of their production cycle, when previous evidence would point to heavy lice infestations. The local AMA has led to a reduction of the lice burden, both on the farmed salmon and on the indigenous salmonids. At present, the lice levels in Loch Shieldaig and Loch Torridon are at the lowest levels in any second year of production since sampling commenced. The monitoring being conducted by Fisheries Research Services (FRS) will help to establish the success or failure of this strategy in the future.

In terms of the survival of sea trout and salmon populations, it is clear that parasitism is just one of many threats that salmonid fish face when they migrate to sea. Increasing predator numbers, warming coastal and oceanic waters, marine pollution, commercial fishing and food shortages are just some of obstacles that these fish must survive and overcome in order to return to their native rivers. Tackling the sea lice problem may improve survival chances a little, but the threat to wild fish goes far beyond our inshore waters.

Acknowledgements

Much of the shoreline sampling at Loch Shieldaig was performed and managed by Maggie McKibben, who has since moved on to other things. She and Michael Penston were ably assisted in the field by Jason Milton and Colin Blyth. The sampling during 1999 was carried out by Sally Northcott, Andy Walker and Alastair Thorne. Rob Fryer helped with the statistical analysis of the data.

Further information/Further reading

Atlantic Salmon Federation: http://www.asf.ca/Nasco/nasco2001/index.html;

Atlantic Salmon Trust: http:/www.atlanticsalmontrust.org/

Butler, J.R.A. (2002) Wild salmonids and sea louse infestations on the west coast of Scotland: sources of infection and implications for the management of marine salmon farms. *Pest Management Science*, **58,** 595–608.

Costelloe, M., J. Costelloe, N. Coghlan, G. O'Donohoe and B. O'Connor (1998) Distribution of the larval stages of *Lepeophtheirus salmonis* in three bays on the West Coast of Ireland. *ICES Journal of Marine Science,* **55,**181–7.

Johnson, S.C., J.W. Treasurer, S. Bravo, K. Nagasawa and Z. Kabata (2004) A review of the impact of parasitic copepods on marine aquaculture. *Zoological Studies*, **43**, 229–43.

Krkosek, M., M.A. Lewis and J.P. Volpe (2005) Transmission dynamics of parasitic sea lice from farm to wild salmon. *Proceedings of the Royal Society B*, **272**, 689–96.

McKibben, M.A. and D.W. Hay (2004) Distributions of planktonic sea lice larvae *Lepeophtheirus salmonis* in the inter-tidal zone in Loch Torridon, Western Scotland in relation to salmon farm production cycles. *Aquaculture Research*, **35**, 742–50.

Murray, A.G. and P.A. Gillibrand (in press) Modelling salmon lice dispersal in Loch Torridon, Scotland. Submitted to *Marine Pollution Bulletin*.

Pike, A.W and S.L. Wadsworth (1999) Sea lice on salmonids: their biology and control. *Advances in Parasitology*, **44**, 234–37.

Penston, M.J., M. McKibben, D.W. Hay and P.A. Gillibrand (2004) Observations on open-water densities of sea lice larvae in Loch Shieldaig, Western Scotland. *Aquaculture Research*, **35**, 793–805.

Revie, C.W., G. Gettinby, J.W. Treasurer, G.H. Rae, and Clark, N. (2002) Temporal, environmental and management factors influencing the epidemiological patterns of sea lice (*Lepeophtheirus salmonis*) infestations on farmed Atlantic salmon (*Salmo salar*) in Scotland. *Pest Management Science* **58**, 576–84.

Philip Gillibrand is a physical oceanographer and modeller working at the Scottish Association for Marine Science (SAMS)* in Oban, Scotland. His research on physical processes in coastal waters includes modelling mechanisms of mixing and exchange in fjords, the dispersal of larvae and contaminants, and the link between fjord basin water properties and changing climate.

Email: Philip.Gillibrand@sams.ac.uk

*Scottish Association for Marine Science, Dunstaffnage Marine Laboratory, Oban, Argyll, PA37 1QA.

David Hay is a fishery biologist working at the Fisheries Research Services Freshwater (FRS) Laboratory in Pitlochry, Scotland. He has worked with salmon and sea trout, and is currently involved in a project on the west coast of Scotland studying the marine survival of sea trout, with the eventual aim of restoring the sea trout population in the River Shieldaig.

Michael Penston is a plankton biologist at the Fisheries Research Services Marine Laboratory in Aberdeen, Scotland. His main interest is exploring distributions and dynamics of sea lice larvae in the coastal environment.

Alexander Murray is an epidemiological modeller at the Fisheries Research Services Marine Laboratory in Aberdeen, Scotland. His interests in modelling the spread of fish diseases and parasites include the dispersal processes of pathogens in the marine environment.

Book reviews

The Oceans and Climate (second edition) by Grant Bigg (2003). Cambridge University Press, 273pp. £27.95 (flexicover ISBN 0-521-01634-7) (hard cover no longer available).

In the second edition of *Oceans and Climate*, Grant Bigg has thoroughly revised and updated the successful first edition. Both accessible and comprehensive, *Oceans and Climate* manages to capture the complexity of our climate system, without overwhelming the reader in technical detail. Starting with very broad breakdown of the climate system into five components (Atmosphere, Oceans, Cryosphere, Biosphere, and Geosphere), the introductory chapter goes on to emphasize the key notions of feedback mechanisms and multiple time-scales. This introduction lays the foundations for chapters on discipline-based ocean/atmosphere interaction processes (physical, chemical and biological), which are brought together in a chapter of 'case studies' of large-scale air–sea interaction phenomena. The jigsaw of natural climate variability, stretching back to Palaeozoic time, is then pieced together with increasing detail through the Quaternary and Holocene, and through the instrumental records of the late twentieth century. Only at this point are discussions regarding signals of natural and anthropogenic climate change raised, and this final chapter is probably the one most readers will return to for reference.

Whilst the first edition filled a previously unoccupied niche for introductory undergraduate texts on climate systems, the quality of figure reproduction left much to be desired. This second edition is most welcome, and, with a few exceptions, the figures have been greatly improved. There remain some minor errors in the Glossary, e.g. definitions of chlorophyll and primary production. Overall, though, the text continues to be a uniquely accessible general climate system text and I would recommended it to all environmental science undergraduates and interested lay persons alike. It provides the reader with an affordable introduction to a vast array of topics, brought together under the banner of oceans and climate. New sections on recent developments in our understanding of abrupt changes in climate bring the text up to date. The book is authoritative and yet paints a balanced view of the complexity of the climate system, drawing from a huge range of source material. Careful selection of 'further reading' material is given on a chapter by chapter basis.

The book's main weakness lies in its bold attempt to cover such a wide and diverse topic at an introductory level. Often one is left finding the given explanation incomplete – for example in the explanation of the Coriolis force only a hint is given of the vital element of the Earth's oblate spheriod shape. On the other hand, some lack of detail is not necessarily a bad thing, given the well chosen lists of further reading. More critically, the book can seem a little lost at times, lacking a coherent thread running throughout: a collection of interesting facts and ideas, not tightly woven together. That said, it is a textbook, and should be praised for its balanced and clear content if not for its literary style.

We have used Grant Bigg's book (first and second editions) for four years as the standard text in a 24-lecture undergraduate module on 'Oceans and Climate' (this is a Third Year module in the four-year Marine Science BSc. programme delivered by SAMS). There is still no other book like it, and I will continue to recommend it as a core text.

Mark Inall
Lecturer in Marine Physics
Scottish Association for Marine Science

Continued overleaf

Note for enthusiasts of the history of oceanography

The next issue of *Ocean Challenge* will include reviews of the proceedings of two conferences concerning this topic: *A Century of Discovery: Antarctic Exploration and the Southern Ocean (see p.13)* and *Ocean Sciences Bridging the Millennia: a spectrum of historical accounts (Proceedings of the Sixth International Congress on the History of Oceanography) (see p.7).*

Changing Sea Levels by David Pugh (2004) Cambridge University Press, 265pp., £70 (hard cover, ISBN 0-521-82532-6) and £30 (flexicover, 0-521-53218-3).

I was a little surprised when I was asked to review this book a few months ago, as I am certainly no expert on tides and sea-levels. However, this is not a book aimed at experts, but rather at those wishing to learn about the subject, a status with which I was somewhat more comfortable. Having worked in oceanography for 13 years now, it would be lamentable if I had not picked up at least the rudiments of the subject, and I consider myself at least knowledgeable enough to avoid the embarrassment of being caught out by the tide while working for an establishment that was once known as 'The Liverpool Tidal Institute'.

The fine detail of the subject is a large and varied field for which David Pugh provides a nicely balanced overview, and in reading the book I was pleased to see clear explanations of the inevitable scientific terminology that is routinely thrown around in the literature and at conferences, some of which I knew, and some of which I thought I knew. For those readers unfamiliar with the work of David Pugh, I should add that he has also published the more professionally oriented 1987 book *Tides, Surges and Mean Sea-Level: A handbook for engineers and scientists* (now out of print and very hard to find second-hand) and is an author on over 150 scientific articles related to the subject.

The book begins gently with an introduction to the history of tidal recording and the various ways of recording the level of the sea, a task which in the short term can be considered as the measurement of tides, but which in the longer term can be used to determine mean sea-levels. The measurement methods described range from old fashioned float tide gauges through to the latest techniques using satellite altimetry.

The basic physics of the tides are clearly explained, including a worked example detailing the answer to the ever popular interview question: why are there two tides per day? The balance of conceptual explanations to mathematical content has been pitched just right for undergraduate level. The mathematics included in this book have been kept to the minimum necessary to support the conceptual descriptions and numerous diagrams, with several more detailed technical appendices at the end of the book and others available for download from the Cambridge University Press website, along with electronic copies of a number of the figures for use as teaching aids.

Tidal analysis and prediction are covered in some detail, with reference to both the analysis of point measurements from instruments such as tide gauges, and the analysis of spatially variable data such as those generated by satellite observations.

The topical subjects of sea-level changes due to the weather and other extreme events such as tsunamis are also covered, with discussion of a number of examples of low lying coastal areas subject to inundation by hurricanes and tsunamis around the world. Since this was written prior to the Sumatra tsunami of December 2004 the examples are from earlier events that will no doubt be almost forgotten in light of that more recent disaster. In addition, the table of historical storm surge events puts into context the severity of the recent Hurricane Katrina that hit Mississippi in August 2005, which had an estimated storm surge of between 7 and 10 m, ranking it amongst the worst on record.

Rising mean sea-levels are discussed with reference to some of the longest tide gauge records held by the Permanent Service for Mean Sea Level. These include several records that appear at first sight to show falling mean sea-levels, which are explained by the fact that in those locations the land is uplifting faster than mean sea-level is rising. This in turn emphasizes the importance of measuring and accounting for vertical movements of the land on which the datums rest, when determining absolute sea levels.

The question of where the 'extra' volume of water is coming from makes fascinating reading, with assessments of the contributions to mean sea-level rise from the thermal expansion of the oceans and the possible effects of melting ice sheets; surprisingly (to me), the amount of water held in reservoirs around the world accounts for a significant volume of the water removed from the ocean budget.

The section on flood risks demonstrates the importance of long time-series of high quality measurements for assessing the probabilities of extreme events. The methods for calculating the probabilities of such events from tidal records are described, and the difference between the design-life of a structure and the return period of a flood event provide a stark reminder of the pitfalls of misunderstanding the use of such probability statistics. The impact of even modest sea-level rise on the return period of flood events is shown to be a significant issue for low-lying coastal areas in economic terms, while the ecological impacts include loss of wetlands and the inability of the slow growth rate of coral reefs to keep up with possible future sea-level rise.

The final chapter of the book focusses on the influence of the tide on a variety of physical and biological situations, from tidal inlets to the timing of fish spawnings and hatchings. There is also an interesting discussion on the changes in tidal amplitudes and phases through recent geological history, and the effect that the gradually widening Earth–Moon separation may have had on the tides over the past few million years.

I have used a great many textbooks in my career, both as a student and professionally. The readability of those textbooks varied widely, from those that almost made me lose the will to live, to those that fired my imagination with the elegance of the natural world. David Pugh's book on sea levels is a well written, wide-ranging and up-to-date book that I found interesting to read, raised the odd eyebrow and made me think. I can give it no better recommendation than that.

Paul S. Bell
Proudman Oceanographic Laboratory
Liverpool

Advance warning for photographers ...

The subject for entries for the President's Photographic Prize,
to be judged at the Challenger Conference in Oban,
in September 2006,
will be
'Flotsam and jetsam'