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Obituary: Eve Caroline Southward (née Judges) 1930–2023

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Abstract

Eve Caroline Southward (1930-2023) was a multi-talented scientist, motivated by her curiosity and love of nature. Since she was never paid as a scientist, Eve was an amateur, in the best sense of the word. She was highly proficient at transmission electron microscopy and made lasting contributions to polychaete taxonomy, morphology and ecology. Eve was internationally respected, especially for her studies on the Siboglinidae, mouthless and gutless tubeworms (formerly called Pogonophora) that are found worldwide in the deep-sea. She described how the siboglinids obtained nutrition from symbiotic, sulphur-oxidising bacteria and described similar symbiotic relationships in several bivalve species. Eve wrote over 140 scientific publications and described 56 new benthic species, 47 being mouthless and gutless 'pogonophores'. Eve assisted her husband Alan Southward in starting broad-scale intertidal surveys around the British Isles and Northwest Europe. These surveys formed the foundation for the time-series, later continued by others, that allowed assessments of the influence of climatic fluctuations, using intertidal rocky shore biota as indicators. Eve contributed, with Alan, to what became a 50-year study describing the long-term effects on intertidal communities of the oil pollution and excessive dispersant use resulting from the Torrey Canyon oil spill in 1967. Eve also cowrote the Linnaean Society Synopsis on Echinoderms of the British Isles and helped complete unpublished work by Alan Southward and others on barnacle taxonomy.

The early years

Eve was born in Bloomsbury, London. Her father, Arthur Valentine Judges, was a historian who worked at the London School of Economics and, later, as Professor of the History of Education at King's College, London. He married Kathryn Mitchell and the couple had two daughters. When Eve was 3 years old, she moved with her younger sister Rachael and her parents to Kew Green, near the River Thames. The sisters frequented Kew Gardens, feeding the ducks and fish in the pond and exploring some of the exotic vegetation. After 5 years at Kew, the family later moved north of the Thames to a house alongside the river in Chiswick, London. There the girls were able to go swimming from the steps in the front of the house at high tide.

The girls were educated at the Froebel Demonstration School in Kensington, London. The school was evacuated in 1939 when the war broke out, first to the outskirts of Oxford and then to Dennison House in Little Gaddesden, Hertfordshire, that became a boarding school (Priestman, 1940). The house had a large garden and was close to Ashridge Park, a woodland and wildlife area. The Judges sisters remembered playing and climbing trees in the large garden and exploring the woodland and ponds in the park. They were encouraged to go on nature expeditions and remembered netting invertebrates and taking them back to the School to study their behaviour in a tank.

In 1943, Eve moved home to the riverside in Chiswick, London. She attended St. Paul's School for Girls in Hammersmith until 1949. During the holidays the sisters sailed a dinghy in club races between the bridges and around the island in the middle of the river, dodging the commercial traffic. The two sisters continued their 'nature expeditions' by mudlarking in the Thames at low water. This was a potentially hazardous pursuit at a time when a lot of raw sewage was discharged into the Thames. This exposure may have led to immunity to many diseases and might help to explain their longevity. Such risks paled into insignificance with V1 'doodle-bug' rockets landing in the area, which Eve recounted to SJH. Although her sister remembers nothing of value being found on these excursions, they did find a lot of old bones as well as white 'balloons' (condoms) that were sometimes occupied by crabs, *Carcinus maenas* (Linnaeus, 1758) and ragworms, *Hediste diversicolor* (O.F. Müller, 1776). Digging through the mud proved to be early training for Eve's later career (Figure 1B).

At school, Eve studied Botany, Zoology and Chemistry for her Higher School Certificate. When she considered further studies at university, she thought about a degree in horticulture or agriculture, following her botanical interests. A family friend, who was a professor at the University of Liverpool, suggested that Eve might consider studying Zoology there, with a



Figure 1. Eve Southward and her most-studied frenulate. (A) Eve in her garden in 2017 (photograph by Tom Chester). (B) Eve sorting through a dredge haul for frenulates on Sarsia c. 1958. (C) Siboglinum fiordicum Webb, removed from its tube (B and C photographs by Alan Southward).

view to taking the Honours year Marine Biology course under the guidance of JH Orton, who had left the Plymouth Laboratory of the Marine Biological Association before the war to become Professor of Zoology in Liverpool and head of the Marine Biological Station in Port Erin on the Isle of Man. In July 1949, Eve, knowing little about the subject, read the recently published book, 'The Sea Shore' (Yonge, 1949). She thought that the subject sounded interesting, applied to Liverpool and was accepted.

During her degree she attended phycological and zoological field courses at the university's Port Erin Marine Biological Station on the Isle of Man. As the only student in her year taking the marine biology option, Eve was offered the Herdman Studentship to carry out research at Port Erin. At that time, in the 1950s, consecutive students were given different groups of the marine fauna to study, in the shallow waters around the island and in the Irish Sea. These studies helped to compile a revised faunal list for the area that would be expanded to include waters further offshore to the south and southwest of the Island. Her supervisor, Norman S. Jones, suggested that Eve should investigate the polychaetes, with respect to their distribution and ecology. Eve examined samples from the intertidal zone and also undertook dredging offshore, on RV William Herdman, between October 1952 and May 1954. During this period she added 84 species to the 191 already known polychaetes in the local species list, including two species not previously described elsewhere. One of her early discoveries was of the presence, for the first time in the Irish Sea, of adults of Phoronia mulleri Selys-Longchamps, 1903, in the minor lophorate worm-like phyla Phoronida, on sandy muds at 70 m depth (Judges, 1953). This 'horseshoe worm' lives in a tube about 1 mm diameter and illustrated Eve's ability to spot small 'worms' in mud samples, a skill well-utilized in her later career. Eve's sampling of the intertidal and offshore deposits, concentrating on polychaete species, made a major contribution to

the section on the distribution of annelids, in the 2nd edition of the Marine Fauna of the Isle of Man (Bruce *et al.*, 1963).

Eve met her husband Alan Southward whilst on the Isle of Man, where he had completed his PhD on intertidal ecology in 1951 and stayed on for post-doctoral work. An early joint effort was a description of the biota in the seawater tanks at Port Erin (Judges and Southward, 1952). In 1953, Alan moved to the Marine Biological Association of the UK (MBA) in Plymouth, on a DSIR Post-doctoral Fellowship, to continue ecological studies on the geographic distribution of rocky-shore species. Shortly after finishing her sampling, in May 1954, Eve followed Alan to Plymouth and they married in July 1954. She completed writing her thesis in Plymouth, being awarded a Ph.D. for 'Studies on the Polychaeta of the Isle of Man' in May 1955 (Southward, 1955). Eve published five scientific papers based on this. After a brief spell as a schoolteacher, Eve became an unpaid visiting scientist at the Citadel Hill Laboratory of the MBA for the rest of her career. She was still scientifically active as a Lankester Research Fellow until shortly before her final illness in November 2022.

Eve became indispensable to Alan, who had become completely deaf and lost his sense of balance after contracting meningitis at the age of 15 (Dando, 2008). Alan started surveys of the distribution of intertidal organisms on shores all around the British Isles whilst on the Isle of Man. He was interested in factors affecting changes in distributions of species and travelled around the coast on a motorbicycle, using visual cues to keep his balance. Eve joined him on many of these trips and was essential help with communication when Alan was unable to understand by lip-reading. From this time onwards, the two Southwards helped each other out on their respective projects. They collaborated on many joint activities at sea, on the shore and in the laboratory as well as much editorial input to Advances in Marine Biology.

Early research on annelids at Plymouth

The MBA acquired the new, purpose-built, 39 m research vessel, Sarsia, in November 1953. Sarsia was equipped with 3000 m of dredge wire, and Alan Southward made use of this facility to obtain samples from along the continental slope to the SW of Plymouth, as far south as Santander. Eve joined Alan on these deep-sea dredging cruises and they both tried to identify all the benthic organisms collected along the Biscay slope. In 1957 they found, for the first time in the Atlantic, species of the enigmatic tube-forming pogonophoran worms, in sediment at 1250 m depth, west of Little Sole Bank. These hair-like 'worms' were difficult to find, since the specimens lived in tubes only 0.12-0.5 mm wide and resembled the fibres of the twine in the dredge nets. Eve's observational skills were required to find them in the dredge samples (Figure 1B). The strange tubeworms captured Eve's curiosity, since they lacked a mouth, a gut and an anus. The leading expert on this group of animals was Academician Artemii Ivanov of the University of Leningrad, who confirmed Eve's identification. Over the next 25 years, Eve recorded approximately 20 species of pogonophora from samples collected in the Bay of Biscay, although not all have been described. She also described, in the Biscay samples, four new species of other polychaetes and three new species of copepods that lived in polychaete tubes (Table 1).

Since most of the literature on the morphology and taxonomy of pogonophores was in Russian, Eve had to learn the language in order to describe the taxonomy of the new species. In June 1961, under a Royal Society Exchange Programme, she visited Artemii Ivanov in Leningrad and witnessed the award of his Lenin prize, in the Mariinsky Palace, for his work on Pogonophora. Eve and her husband drove, in a car towing a caravan, via Denmark, Sweden and Finland. They spent 6 weeks on the trip, visiting marine laboratories in Denmark, Sweden and Finland, as well as Russia. Artemii had a reciprocal visit to the MBA in 1963 and a life-long collaboration was established.

Eve discussed the pogonophores with David Carlisle, who was studying chitin distribution in crustacean cuticles at the MBA. David also became fascinated by these tubeworms and also learnt Russian to read the literature about them. He was a polymath and a linguist and translated the whole of Ivanov's 1960 book (Ivanov, 1960), with large additions by Ivanov to the original text (Ivanov, 1963). Eve made an essential contribution to the translation by forming new words in English for Russian names for anatomical features of the pogonophores that did not directly translate. She also described one new species Siboglinum lacteum Southward, 1963, for the volume.

Ivanov and many other zoologists believed that pogonophores were deuterostomes. Brunet and Carlisle (1958) examined the Siboglinum tubes, which Eve and Ivanov had collected, for chitin. They found that the bulk of the tube did consist of chitin, implying that they were protostomes, as confirmed by subsequent genetic analysis. A later cladistic analysis (Rouse, 2001) placed all pogonophores in a single family, the Siboglinidae, sub-divided into three clades, the vestimentifera, the monilifera (Sclerolinum spp.) and the frenulata (the other small pogonophores including Siboglinum). Subsequently, a fourth clade was added, Osedax, the 'snot-worms' living on bones.

The problem of frenulate nutrition and research in Norway

Siboglinids on the Biscay Slope seldom occurred in densities above 200 m⁻² and weather conditions frequently disrupted sampling. In Norway, Hans Brattström, director of the Bergen University Marine Biological Station at Espegrend, reported finding Siboglinum ekmani Jägersten, 1956 in the nearby Hardanger fjord in 1959. This made Espegrend the only Biological Station, at the time, where studies could be made on living pogonophores. Michael Webb, from the University of Durban, obtained a Norwegian Research Fellowship to study pogonophores at Espegrend during 1963. He described a new species, Siboglinum

Table 1. Species named by Eve Southward

Siboglinid tubeworms

Alaysia spiralis Southward, 1991

Arcovestia ivanovi Southward & Galkin, 1997

Crassibrachia brasiliensis Southward 1968

Crassibrachia sandersi Southward, 1968

Diplobrachia capillaris (Southward,1959)

Diplobrachia floridensis Southward, 1971 Diplobrachia similis Southward & Brattegard, 1968

Heptabrachia talboti Southward,1961

Lamellibrachia columna Southward, 1991

Lamellisabella coronata Southward, 1969

Lamellisabella denticulata Southward 1978

Lamellisabella pallida Southward, 1975

Oligobrachia gracilis Southward, 1978

Oligobrachia hawaiiensis Southward,1980

Oligobrachia ivanovi Southward, 1959

Paraescarpia echinospica Southward, Schulze & Tunnicliffe, 2002

Polybrachia celebensis (Southward, 1961)

Polybrachia eastwardae Southward & Brattegard, 1968

Polybrachia lepida Southward & Brattegard, 1968

Sclerolinum magdalenae Southward, 1972

Sclerolinum major Southward, 1972

Sclerolinum minor Southward, 1972 Sclerolinum sibogae Southward, 1961

Siboalinoides caribbeanus Southward, 1971

Siboglinum angustum Southward & Brattegard, 1968

Siboglinum atlanticum Southward & Southward, 1958

Siboglinum bayeri Southward, 1971

Siboglinum candidum Southward & Brattegard, 1968

Siboglinum debile Southward, 1961

Siboglinum fulgens Southward & Brattegard, 1968

Siboglinid tubeworms

Siboglinum gosnoldae Southward & Brattegard, 1968

Siboglinum holmei Southward, 1963

Siboglinum inerme Southward & Southward, 1958

Siboglinum lacteum Southward, 1963

Siboglinum longicollum Southward & Brattegard, 1968

Siboglinum macrobrachium Southward, 1961 Siboglinum nanum Southward, 1972

Siboglinum ordinatum Southward, 1980

Siboglinum oregoni Southward, 1972

Siboglinum parvulum Southward, 1972

Siboglinum pholidotum Southward & Brattegard, 1968

Siboglinum polystichum Southward, 1975

Siboglinum timorense Southward, 1961

Siphonobrachia lauensis Southward, 1991

Unibrachium columbianum Southward, 1972 Unibrachium tenuifrenum Southward, 1975

Other polychaetes

Aricidea minuta Southward, 1956

Filogranula stellata (Southward, 1963)

Hyalinoecia robusta Southward, 1977 Laeospira sarsiae (Southward, 1963)

Phisidia aurea Southward, 1956

Serpula planorbis (Southward, 1963)

Copepods

Rhabdopus salmacinae Southward, 1964 Serpulidicola omphalopomae Southward,

Serpulidicola placosteai Southward, 1964

fiordicum in Raunefjorden (Webb, 1963) and found sites for *S. eckmani* and *S. fiordicum* much closer to the Station, as well as a new species, *Sclerolinum brattströmi* Webb 1964, in Hardangerfjorden. Both Brattström and Webb corresponded with Eve Southward, informing her of their new discoveries and Torgeir Bakke showed that *S. fiordicum* could be maintained for over a year in the facilities at the Station.

Alan Southward organized a cruise on RV Sarsia in 1973 to the Bergen fjords to dredge for Siboglinum and to trial a modified deep-sea camera. Eve and David George, from the Natural History Museum, London, accompanied him. On arrival, they found that they were limited to sampling in deep water and had to be accompanied by a pilot for the duration. Since a cabin was needed for the pilot, David George moved ashore to the Biological Station and worked with local divers to study S. fiordicum at 30 m depth in Fanafjorden. He made the first in-situ observations on frenulates (George, 1977) and obtained specimens for Eve.

From the mid-1970s and in the 1980s, Eve, either alone, or together with Alan and other MBA scientists, made frequent visits to the Marine Biological Station at Espegrend to study frenulates that lived in the shallower water more accessible sites. *Siboglinum fiordicum* (Figure 1C) was found to occur in high densities at only 30 m depth, in sheltered conditions in the mud of Ypsesund and became the 'laboratory rat' of frenulate research.

The question of how the mouthless frenulate tubeworms obtained their nutrition proved difficult to solve. Most frenulates, unlike the *Siboglinum* genus, had multiple tentacles that projected from the tube. Ivanov (1955) was convinced that the tentacles trapped and collected food particles that were then externally digested. Eve Southward was unconvinced. She had carefully observed living specimens and had not seen food particles on the tentacles. Eve developed histochemical techniques to examine the location of any digestive enzymes in living specimens of siboglinids. In addition, sections of different parts of the animal did not show, under the electron microscope, the presence of secretory cells similar to those producing digestive enzymes in other invertebrates. Protease activity could not be demonstrated in living animals or in extracts of tissues (Southward and Southward, 1966).

An alternative suggestion was that frenulates took up dissolved organic compounds from the interstitial water. Alan and Eve collaborated in measuring the uptake rates of amino acids, carbohydrates and fatty acids by several frenulates, using radioisotope-labelled substrates. Measurements were made both on animals in their tubes and on animals removed from their tubes. In all studies, the animals accumulated amino acids and sugars against a concentration gradient. However, given the most favourable assumptions, the uptake rates were insufficient to support the energy demands in adult tubeworms for both respiration and growth. Exceptions were their larvae and possibly the smallest species studied, S. eckmani. In addition, none of the measurements were made with the frenulates in sediment, where they would have to compete with heterotrophic and mixotrophic microbes for the dissolved organic compounds in interstitial water. Only recently has it been shown that frenulate tubes have a microbiota associated with the outside of the tubes, within the tube matrix, on the inside of the tubes and on the animal epidermis (Rincón-Tomás et al., 2020).

The solution to the nutritional problem took a step forward with the discovery of the giant vestimentiferan tubeworms (up to 1.5 m long and 38 mm diameter) around hydrothermal vents on the Galapagos Rift. These animals were too large to subsist on dissolved organic compounds in the surrounding water and were shown to contain CO₂-fixing endosymbiotic sulphuroxidizing bacteria in a specialized tissue, the trophosome (Cavanaugh *et al.*, 1981). Colleen Cavanaugh visited Plymouth to discuss these findings with Eve and suggested that the smaller

frenulates might also contain endosymbionts. Eve re-examined her TEM sections of species of *Siboglinum*, *Diplobrachia*, *Oligobrachia* and *Sclerolinum* and found numerous bacterial cells in specialized cells, bacteriocytes, in the post-annular region, where the gut would normally be found (Southward, 1982).

Eve and the MBA team extracted the small pogonophores from their tubes, a skill Eve had mastered and taught others. The animals were separated into pre-annular and post-annular regions before the tissues were ground up and the bacterial fraction concentrated. In the absence of modern DNA techniques, the bacteria were then lysed and tested for the activity of enzymes that would be present in sulphur-oxidising chemosynthetic bacteria. The bacterial fraction was shown to contain the CO₂-fixing enzyme ribulosebisphosphate carboxylase, the same enzyme used by chloroplasts, and also enzymes involved in sulphur oxidation. In addition, stable isotope studies showed that the animals were far more depleted in ¹³C than other polychaetes in the sediment and than the surrounding organic matter. Differences between Siboglinum species in their isotope ratios suggested that the species were benefiting to a greater or lesser extent from carbon fixed by the symbiotic bacteria (Southward et al., 1981).

The Norway visits were normally in winter, when bottom and surface water temperatures were similar. They provided abundant specimens for study. Eggs and larvae were available for Eve's embryological investigations and adults could be kept alive long term in the aquarium. It was soon shown that the symbiotic, sulphur-oxidising bacteria were almost exclusively present in the post-annular tissues of the pogonophores (Southward, 1982).

A remaining problem was that concentrations of dissolved sulphur species in the sediment around the animals were frequently $< 0.1 \, \mu \text{M}$, insufficient to provide the energy demand of the animals at measured uptake rates. There was, however, an abundant supply of insoluble iron sulphides over the tube penetration depth of *S. fiordicum*. Eve noted that there was a paler sediment layer adjacent to the frenulate tubes, suggesting diffusion of oxygen from the animal through the tube wall that might result in microbial activity and chemical oxidation in the surrounding sediment. Subsequent studies, pumping seawater through a narrow, microporous, tube buried in sediment showed that both soluble sulphide and thiosulphate were formed under these conditions and diffused into the tube. This provided a mechanism by which the small frenulates could 'mine' the insoluble sulphides to provide an energy source for their symbionts.

The Ypsesund site in Norway also contained three species of bivalves with unusually fleshy gills: *Thyasira flexuosa* (Montagu 1803), *Myrtea spinifera* (Montagu 1803) and *Lucinoma borealis* (Linnaeus 1767). Eve found that all these species had symbiotic bacteria associated with the gills and that the bacterial cells contained elemental sulphur. Thus, the dark Ypsesund mud, supplied with seaweed, phytoplankton fallout and possible fish-farm waste, supported a chemosynthesis-based ecosystem (Dando *et al.*, 1986).

Subsequent studies were made in southern Norway on another thyasirid species, *Thyasira sarsi* (R.A. Philippi, 1845), using large box core samples from Oslo Fjord that were placed in the mesocosm facility at the Norsk Institutt for Vannforskning, Solbergstrand. These revealed another method of 'mining' sulphides to provide an energy source for the sulphur-oxidising symbionts. The deep-burrowing bivalves constructed a permeable inhalant tube with their extensile foot that excreted mucus to stick sand grains together. A current of water was drawn down from the surface and some oxygen diffused through the tube resulting in partial oxidation and solubilization of the iron sulphides. Calculations showed that the sulphide oxidation rate of the *Thyasira* population was approximately equal to the rate of sulphide production in the sediment.

In recognition of her work on siboglinids in 1993, Eve Southward was awarded an honorary doctorate from Kiel University for 'her important contributions to the dissemination of the biology, nutritional physiology and embryology of the pogonophores, especially in recognition of her pioneering work on the systematics of this group of animals'. A list of the siboglinid species described by Eve is presented in Table 1.

Studies on chemosynthesis at other European sites

The research on Ypsesund in Norway had revealed lucinid and thyasirid bivalves with symbiotic sulphur-oxidising bacteria. Eve examined the same and related species from other sites, including muddy bottoms in Plymouth Sound, the borders of *Zostera* beds in the Yealm and Salcombe Estuaries, Portland Harbour, Loch Etive and drill cutting piles in the North Sea. In all these diverse habitats, the bivalves were found to have sulphur-oxidising bacteria associated with their gills.

While collecting frenulates in deep water in the Bay of Biscay, Eve also collected some small thyasirids with fleshy gills, some of which she found had two different kinds of bacteria on their gills. Another small bivalve, *Syssitomya pourtalesium* Oliver 2012, a member of the Montacutidae, she found attached near the anus of a sea urchin *Pourtalesia sp.* The gills were fleshy and covered with bacteria held between microvilli (Oliver *et al.*, 2013).

Eve also studied two shallow-water sites with hydrothermal vents, the hot brine seeps at Milos in Greece and underwater caves with hot springs at Capo Palinuro in Italy. At Milos, Eve studied the behaviour and nutrition of the gastropod *Tritia neritea* (Linnaeus, 1758) that were found to be concentrated on top of the bacterial mats overlying the seeps. At the Italian caves, where thick mats of sulphur-oxidising bacteria covered the walls (Mattison *et al.*, 1998), Eve helped to study the role of these mats in the food web and the ecosystem.

Food web studies were also investigated by Eve during three cruises to vent sites on the mid-Atlantic Ridge. She studied the nutrition of bivalves and Alvinocarid shrimps, helping to show how some species were partly dependent on a planktonic input.

The Canadian period

In 1984, Maureen de Burgh, a post-doctoral student in Verena Tunnicliffe's laboratory at the University of Victoria, British Columbia, wrote to Eve. She requested Eve's siboglinid reprints and informed her of the recent discovery of vestimentifera at hydrothermal vents on the Juan de Fuca Ridge the previous year (Tunnicliffe, 1983). Eve responded with details of her work on symbionts in the allied frenulates. The correspondence continued and more animals from the NE Pacific vents were retrieved. Both the Southwards were excited by these new discoveries and, in 1987, the University of Victoria offered a Landsdowne Visiting Fellowship to Eve and Alan to sponsor a short residency at the university if they gave some lectures. Thus began a very long collaboration that was marked by the great interest that both Alan and Eve took in the graduate students. Over the years, Eve published with three University of Victoria students, Michael Black, Kathryn Coates and Anja Schulze. That first summer, Eve observed that the tiny juvenile vestimentiferans had a functional gut. This model of symbiont acquisition from the habitat through feeding (Southward, 1988) was highly influential. The paper has nearly 200 citations and has provided impetus for the study of symbiont-host interactions.

In 1988, the Southwards returned to Victoria in the summer to 'house-sit' for Verena Tunnicliffe and to work on specimens in her laboratory. The Southwards thought about spending more time on Vancouver Island. They bought a house within walking

distance of the University campus in 1989 where they delighted in the abundance of wildflowers that grew in the back yard. While in Canada, Eve re-described and studied the development and distribution of a frenulate, *Polybrachia canadensis* (Ivanov, 1962), as well as joining Alan on frequent trips to the seashore to collect barnacles and examine possible habitats for chemosynthetic bivalves.

Alan and Eve returned to Victoria in 1990 to participate in two overlapping offshore cruises, one focussed on a seamount and the other on hydrothermal vents. The Southwards helped direct the scientific loading and boarded the CSS Parizeau in late July. The programme conducted sampling surveys of Cobb Seamount, locating enhanced productivity over the summit. However, some personnel were also involved in the mission with DSV Alvin and the RV Atlantis II, chartered by the Canadian government to map hot vents in the Canadian EEZ. Eve vividly remembered her dive on Alvin and her first live viewing of hydrothermal vents. She found the most terrifying part of the experience to be the mid-ocean transfer by inflatable between Parizeau and Atlantis II. Nonetheless, she greatly impressed her shipmates with the alacrity with which she scaled the ladder up the side of Parizeau. With her came specimens that featured in several later publications including one from Jim Blake, who named a large vent polychaete (Lindaspio southwardorum Blake & Maciolek, 1992) after both the Southwards.

Rich Lutz (Rutgers University) invited Eve on two cruises with *Atlantis/Alvin*: one in 1991 and a second in 1994. She was able to sample a broad selection of vent animals and, with Verena's laboratory, to explore the surprising variability in the tubeworms. That work was a contested topic for a while: one species, or many? However, with the advent of molecular methods and the incredibly detailed anatomical work by Eve, she was able to lead a paper that combined the described and putative species under a single name in 1995. Later came several more studies on this and other vent tubeworms that added to Eve's broad knowledge of the group. Eve, with colleagues, published several reviews of the biology of frenulates and vestimentiferans.

Eve's powers of observation made a lasting impact at the University of Victoria. She taught many how to see through careful drawings – not photographs – that made you look at exactly how the bristles on a worm were inserted or how the plates on the top of a tubeworm were stacked. Her extensive notes were a lesson in tracking specimens and the evolution of how you think about a novel species. She would put in long hours because she loved it – the students enjoyed her quiet presence, happy conversation and ever-present cookies.

Intertidal surveys and oil pollution

Eve assisted Alan in early broad-scale intertidal studies around the British Isles and Ireland in the 1950s, at first on a motorbike and then using a Bedford van with a bed in the back and eventually a caravan. She became interested in rock pool Echinoderms that led to a subsequent echinoderm-recording project and to Eve producing the Linnean Society Synopsis of Echinoderms of the British Isles (Southward and Campbell, 2006). Eve also accompanied Alan on surveys that formed part of the on-going, 35-year timeseries, on fluctuations in the distribution of warm-water and coldwater barnacles around South-west England, plus surveys further afield in Europe.

These surveys were repeated during spring and autumn each year from the 1950s to 1980s, when Alan was made to take early retirement on re-organization of the NERC-funded marine laboratories in Plymouth. Eve was an essential part in all these surveys, often taking large numbers of general photographs of the shore and organisms along the way (e.g. Southward and

Southward, 1978). Fieldwork on exposed rocky shores often involves having someone keeping an eye out for rogue waves especially when close up to the rock counting barnacles. In Alan's case, as he was deaf, Eve would stand nearby and touch him on the shoulder to either brace and get wet or retreat. These annual surveys, carried out for over a decade at multiple sites in Cornwall, provided a superb baseline to judge the impacts of the Torrey Canyon oil-spill and the excessive amounts of first generation dispersants applied (Corner et al., 1968) to clean-up the shores. Many of the western Cornish sampling stations visited each year were badly affected by the Torrey Canyon oil-spill of 1967. Alan and Eve charted recovery at these sites, as well as continuing surveillance at unaffected shores. They showed recovery was much slower on dispersant-treated shores (e.g. Porthleven, Trevone) than a shore that was untreated (Godrevy) because of concerns about impacts on seals (Southward and Southward, 1978).

In the run-up to 50th anniversary of the oil-spill, funding was secured by SJH to chart timescales of recovery and subsequent natural fluctuations from the International Tanker Owners Pollution Federation. Eve did much of the work to find and collate data and photographs, assisted in relocating sites and in the publications that resulted, as well as articles for the general public (Hawkins *et al.*, 2017).

In June 1978, the Southwards visited Brittany to see the effects of the 18th March 1978 Amoco Cadiz oil spill at intertidal stations they had previously surveyed in 1974. They noted that some recolonization of affected shores had already started, in contrast to the lack of recovery of Cornish shores at the same period after the 1967 Torrey Canyon spill. The Southwards wrote a 12-page report on their findings and noted that the damage to marine organisms was much less than might have been expected, due to the French policy of oil removal rather than oil dispersal using detergents.

The annual surveys also prompted a joint interest in the warmwater crab *Clibanarius erythropus* (Latreille, 1818), which was first confirmed in the Mounts Bay, Cornwall, at the end of a warm period in 1960 (Carlisle and Tregenza, 1960). When it started to cool again, the population began to decline, exacerbated by the Torrey Canyon oil-spill in 1967. Eventually the crab disappeared in the 1980s both in Cornwall and at Wembury, in Devon, towards the end of the colder spell (Southward and Southward, 1988). When conditions warmed again from the late 1980s, *Clibanarius* did not re-appear at Marazion or Wembury, the Southward's long-term monitoring sites, despite checks by Eve, Alan and others. In 2016, amateur naturalists in Cornwall alerted that it had been found. The species is now increasing in abundance and spreading in SW England (Hawkins *et al.*, 2017).

Barnacle taxonomy

In March and April 1978, Eve joined Alan and Bill Newman of Scripps Institution of Oceanography (SIO) on the Tropical East Pacific Expedition of RV Alpha Helix from Panama City north to SIO. Eve also assisted Alan in shore-based collections subsequently. The aim was to study the biogeography and ecology of barnacles along this section of the west coast of the Americas, especially species in the Chthamalus 'panamensis' complex. Eve helped to collect specimens from different tidal levels and different degrees of exposure, making copious field notes. The Southwards returned living and frozen specimens to Plymouth, where Paul Dando was able to separate the species by electrophoresis while leaving the sampled specimens intact. The identified specimens were put on one side for later morphological examination. Unfortunately, Alan Southward died before this work could be completed. Eve subsequently persuaded Benny Chan (Biodiversity Research Center, Academia Sinica, Taiwan) to

Table 2. Species named after Eve Southward or after both Eve and Alan Southward

Nematode
Astomonema southwardorum Austen, Warwick & Ryan, 1993
Siboglinid tubeworms
Diplobrachia southwardae Ivanov, 1963
Escarpia southwardae Andersen et al., 2004
Siboglinum southwardae Gureeva, 1981
Other polychaetes
Lindaspio southwardorum Blake & Maciolek, 1992
Bivalves
Thyasira southwardae Oliver & Holmes, 2006
Abyssogena southwardae Krylova, Sahling & Janssen, 2010
Holothurian
Labidoplax southwardorum Gage, 1985
Barnacle
Chthamalus southwardorum Pitombo & Burton, 2007

complete the morphological analysis of the specimens. Eve's recollections and notes on the collections were critical in solving the puzzle of the number of *Chthamalus* species and their ecological distributions along this coast (Chan *et al.*, 2016). Eve also contributed to a publication on zooplankton, led by colleagues from the Continuous Plankton Recorder with a chapter on cirripede and facetotectan larvae, based in part on work by Alan and strongly rooted in her own fine eye for detail (Southward, 2017). She also co-authored another on echinoderm larvae (Conway *et al.*, 2017).

Final remarks

Eve was multi-talented, motivated by her curiosity of the natural world, not just of marine worms but also of plants and insects. She grew camellias from seeds and identified which species of bee visited which flower. Eve was intrepid, whether riding on the back of a motorcycle around Ireland in her twenties or diving in the Alvin in her late sixties. The COVID-19 lockdowns suddenly cut her off from the outside world and interrupted her desire to finish a variety of strands of incomplete work. Until then, she came to the MBA laboratory most days rain or shine. Eve especially enjoyed interacting with younger colleagues and Masters students studying at the MBA - many of whom she employed, with her own money, to help her digitize photographic and paper records. Even during COVID she kept active and was still publishing right up to her sudden illness. In her 90th year, she produced a review of the history of the JMBA (Dando and Southward, 2020) for the 100th volume. She will be much missed, for her scientific contributions and her superb gardening, photography, culinary ability and being a perfect hostess. The lasting testimony to Eve is the nine benthic species named after either herself or after herself and her husband jointly (Table 2).

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