such as just why it is primarily the females that are territorial in these species. It is clearly time for more work on the vocal behaviour of tropical species.

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Agricultural versus ethological oceanography

What is the difference between biological oceanography and marine biology? Sometimes it is not easy to find a straight answer; perhaps marine biology is more coastal and is practised in marine laboratories, whereas biological oceanography is centered offshore and is practised from oceanographic vessels. But are these two approaches addressing such different questions?

The annual meeting of the American Society of Limnology and Oceanography (ASLO) (Santa Fe, New Mexico, USA, February 1997) set the stage for some of these questions in a series of sessions on plankton biology. The dichotomy between the oceanographic and the biological approach, though, was apparent even from the overlapped scheduling of sessions by the program committee. Classical zooplankton sessions, which were mainly centered on crustaceans, were scheduled at the same time as some of the less-conventional sessions on gelatinous zooplankton, as if the two main types of zooplankton somehow belong to two different worlds. What attracted our attention was a timely recognition of William and Peggy Hamner of the University of California at Los Angeles (USA), whose life work received tribute during the session entitled '*In-situ* Oceanography', chaired by Larry Madin (Woods Hole Oceanographic Institution, MA, USA).

The Hamners have always inspired (and continue to inspire) biological oceanographers to 'dive in head first', reiterating the title of Madin's talk. In the 1960s, Bill Hamner was the first to circumvent the use of plankton nets for the collection of gelatinous zooplankton, and the first to just get into the water (the blue water, far from the coast) and actually look around through a diver's mask in order to study gelatinous animals. Thus, biological oceanography became offshore-based marine biology. The main topic of the ensuing *in situ* studies has been the biology of gelatinous zooplankton, because its representatives are big and fragile and easily visualized by a diver, but usually underestimated by traditional sampling with plankton nets (which primarily yield crustaceans).

Two other sessions were dedicated to the gelatinous zooplankton, where these topics were further developed. It was Madin who, introducing the impact of the Hamners, recalled the difference between what Bill Hamner has called 'agricultural' oceanography, centered on biogeochemical cycles and black boxes, and 'ethological' oceanography, based on the observation of zooplankters in their natural environment, envisaging them as living beings and not as biomasses or energy containers. This approach has been pushed further by the use of submersibles, from which a few fortunate ethological oceanographers have been able to observe deep sea life, in the water column as well as on the sea floor.

One participant, Steven Haddock (University of California at Santa Barbara, USA), has used blue water diving at night to quantify spontaneous bioluminescence in near-surface waters, revealing unpredicted high levels of light production under natural conditions. A presentation by Erik Thuesen and James Childress (University of California at Santa Barbara) underlined the problems encountered by oceanographers who attempt to include both gelatinous and crustacean zooplankton in their studies. They compared the kinds of planktonic organisms caught by three different commonly-used modern plankton net systems and offered convincing evidence that the state-of-the-art MOC systems (used by nearly all biological oceanographers to enumerate zooplankton on major global oceanographic expeditions) collect only a small fraction of the gelatinous organisms present, whereas their modified (and non-standard) tucker trawl system collects jellies quite effectively, but in the process markedly undersamples copepods.

What came out of the ASLO presentations, although many 'classical' zooplankton students did not realize it because they were listening to zooplankton talks in a different room, is that such studies that include gelatinous and crustacean zooplankton reveal a still-undervalued importance for gelatinous organisms. Both Russ Hopcroft *et al.* (University of Guelph, Ontario, Canada) and Don Deibel *et al.* (Memorial University of Newfoundland, Canada) gave further evidence that appendicularians (planktonic tunicates) can have grazing effects on phytoplankton that are comparable to the grazing effects of the more commonly-counted copepods.

Other gelatinous organisms are, in fact, the 'lions' of plankton, being specialized predators that can strongly influence the production of the seas. Would you study the ecology of the Serengeti by studying only gnus and zebras, neglecting predators such as lions, leopards and hyenas? This is largely what has happened in plankton ecology. Jennifer Purcell (Center for Environmental and Estuarine Studies of the University of Maryland, USA) and

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Francesc Pagès (Istitut de Ciències del Mar, Barcelona, Spain) stressed the impact of gelatinous predators, in Chesapeake Bay and in the Mediterranean, but these authors and others have already demonstrated the importance of gelatinous zooplankton in various Pacific, Atlantic and Antarctic ecosystems.

Alice Alldredge (University of California at Santa Barbara) stressed the importance of visual observation for the study of 'marine snow', showing how particulate organic matter is not only a chemical entity, but also a microcosm on which many organisms find a proper settling place. Bruce Robison (Monterey Bay Aquarium Research Institute, CA, USA) sparked a lively debate among students of gelatinous zooplankton as to whether the jelly web should be considered an important side-branch of the marine food web (his suggestion) or whether it is inseparable from the rest (as argued from the floor).

Once observed in the field, many gelatinous organisms can be collected with care and transported to the lab for further observation. Ctenophores, for instance, are so delicate that sometimes there are no preserved specimens available since they are broken during handling or preservation. In spite of their fragility, though, *in situ* observations have revealed that these animals can be vicious in their feeding habits. Richard Harbison (Woods Hole Oceanographic Institution) showed an amazing video of the behavior of *Dryodora glandiformis*, a ctenophore described over 150 years ago and rarely seen since. His team has collected it at both poles and documented its unusual feeding biology. The animal has a big pre-oral chamber and is able to engulf entire appendicularian houses. The mucous-filter houses of appendicularians are not such good food, but the animal that occupies the house is a nutritious meal. In the chamber, the ctenophore induces the appendicularian to leave its home and, once out, the poor tunicate is rapidly engulfed by the mouth of the predator. In the meantime, its empty house is spat out from the pre-oral chamber. This is an example of a very specialized stucture and a very specialized behavior, leading to an apparently monospecific diet.

The ASLO meeting had much more to offer, but these sessions on gelatinous zooplankton and ethological oceanography dramatized many valuable concepts that cannot be emphasized enough. In spite of the growing interest in modeling processes in the ocean, it continues to be timely to go back to the organisms and to 'look' at them. There are still many surprises, not only for the production of scenic documentaries but also for understanding how the ocean works. The words of baseball great, Yogi Berra, evoked by physical oceanographer Tom Powell in the Hamner tribute, say it well: 'You can observe a lot just by watching'.

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Behaviour and speciation

Speciation has long been regarded as important in the generation of significant evolutionary change. This is because speciation events are thought to be necessary for conserving adaptive change by genetically isolating locally adapted demes[1]. The potential role of phenotypic modification in evolution has also been repeatedly discussed since Lamarck and Darwin. Until recently, however, its evolutionary importance has been neglected by biologists, largely owing to Weismann's influential arguments about the germ–soma separation early in development. There is now increasing recognition that individual phenotypic modifications (e.g. behaviour) influence subsequent genetic evolution by partially determining demographic and selective factors acting at higher levels of biological organization[2]. For such reasons, the choice of 'Behaviour and Speciation' for the theme of the 1996 Winter Meeting of the Association for the Study of Animal Behaviour, attracted both specialists in the field and interested bystanders (like myself) to the traditional annual outing at London Zoo, hosted by The Zoological Society of London. The meeting was held on the 5th and 6th of December, 1996, and was organized by Roger Butlin (University of Leeds, UK).

Sexual selection and speciation

Sexual selection and mate choice are prevalent themes in the current literature on the role of behaviour in the speciation process[3]. It is perhaps no coincidence, then, that the meeting opened with a talk by Kenneth Kaneshiro (University of Hawaii, Honolulu, USA). He presented a broad outline of his ideas about how selection for less-choosy females in founder populations can facilitate the speciation process by leading to destabilization and reorganization of coadapted genetic systems and thus the potential generation of novel recombinants. These ideas were then clearly illustrated with examples from the 'explosively adaptively radiated' Hawaiian Drosophilidae that have been the focus of interest for researchers in Hawaii for many years.

Along similar lines, Jin Yoshimura (Shizuoka University, Hamamatsu, Japan) presented some interesting new theoretical work (co-authored with William Starmer, Syracuse University, NY, USA) tackling the asymmetric mating preference problem[4]. This work, illustrated by comparative studies on mainland USA and on Hawaiian *Drosophila* species complexes, predicts that new (derived) species on islands (geographically isolated areas) should be less choosy than sympatric ancestral species, and vice versa on continents. This is because, during speciation in isolated areas, character release of mating preference is promoted owing to the lack of closely related species (almost all available males are conspecifics). If secondary contact between the new species and its ancestor occurs because of a repeated invasion by the latter (to the island), coexistence will be achieved as a consequence of the stricter mate discrimination by the ancestral females. Alternatively, backward invasion of the (continental) ancestral range by the new species will favour stronger character displacement (or reinforcement) and thus coexistence will only be achieved if its females become much choosier than their ancestral counterparts. This work thus provides a neat explanation for the apparently contradictory findings from island versus continental species complexes in the literature[5–7].

To establish that strong sexual selection by female choice is important in driving speciation, it is not enough just to be able to show that it is possible in theory[3]. Two talks, looking at signal–receiver evolutionary dynamics in insects, provided independent lines of evidence in support of such importance. In the first, Michael Ritchie (co-authored with Jenny Gleason; University of St Andrews, Fife, UK) presented evidence that, in the six *Drosophila* species examined, courtship song seems to have evolved much more rapidly than

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