The cetacean world as seen by physical and biological oceanographers

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Abstract

In order to understand the role of cetaceans in the marine ecosystem, it is first necessary to specify what is the role of the physics and the biology (at the nutrients and phytoplankton levels) in that ecosystem. We thus present the water masses circulation in the Mediterranean Sea, which is quite well described now in the surface layer of Atlantic origin at least, and its consequences on the biology.

It is also necessary to consider the interactions (i.e. the competition!) between the cetaceans and other high predators (notably fisheries), which requires a correct understanding of what are each competitor's abilities. We take this opportunity to raise some questions to the animals' behaviour specialists, as it seems that the role of some physical phenomena is misunderstood, at least from our readings that are far from to be exhaustive! Moreover, it is also necessary to point out some aspects of their hydrodynamical and trophic environment that cetaceans (and fishermen too!) are unable (according to us) to be aware of, in order to correctly understand how they can perceive this environment and possibly take advantage of it in a deliberate way, i.e. either to migrate (on a seasonal basin-wide scale) or look for food locally (at meso or even smaller scale). Based on what we have been able to read, we might be far from such a correct understanding.

To conclude, we point out the lack of adequate data sets in the Mediterranean, and suggest some directions for new data collection strategy.

In an annex, we raise questions, aiming at improving our own understanding of the cetacean world. We are thus asking all potential readers of this paper, as we asked the participants in the workshop, to let us know any reference that they consider is providing actual proofs about migrations (especially but not only) of cetaceans … and of any other animal as well! In other words, we are neither looking for conceptual models or theories nor for things classified as “well known” and/or “already demonstrated”; we are looking for significant data sets, so that, being first convinced by the facts exposed, we can try to put forward hypotheses –in so far that the physical and biological environment is concerned.

1. Introduction

Documenting the possible competition for fishery resources between cetaceans and human beings, or answering the question "To which extent can physical and biological features constrain cetacean feeding?" (specified in the preparation document to this workshop) is beyond the competencies of the general physical and biological oceanographers we are. However, since the dynamical and biological fields are at the base of any study of the food web in oceanography, the major aim of our contribution is to present the up-to-date knowledge (section 2) to help efficient cetaceans-related programmes to be elaborated in the Mediterranean Sea.

Writing this text and reading as many papers as possible, we were faced with many questions that can be condensed into one: do cetologists really know what they think they know about how cetaceans can perceive their dynamical and biological environment?

To be more explicit, our disciplines (physics and biology) are the sole in oceanography to benefit from autonomous sensors, either deployed in situ or embarked on satellites. This allows the collection of time series and a correct estimation of the space and time scales of the food web first levels, hence showing how complex is the "cetacean world" (and that of human fisheries as well!). Can cetaceans estimate this complexity as fishermen do (or could do with the available technology)? To which extent do they undergo or take advantage of their environment? Can this complexity constitute, for one and/or the other predator, a random parameter, possibly making difficult any significant estimation of the cetaceans' efficiency vs. that of the human fisheries? These questions are some of those that we face, and expand in an annex, because they are not the main topics of the workshop and answers are not likely to come right away. Therefore, we focus in section 3 on the case of the Mediterranean cetaceans, and suggest, in conclusion, a few directions for new sampling strategies.

2. The functioning of the Mediterranean Sea

Although the actual functioning of the sea is relatively complex, it can be thought as mainly resulting from a fundamental mechanism, i.e. the water deficit and its associated dense water formation process (section 2.1), as well as from two major phenomena driving the circulation, i.e. the Coriolis effect and the mesoscale activity (section 2.2).

2.1. The dense water formation process

The Mediterranean is a semi-enclosed sea that is characterised by an excess of evaporation over precipitation and river runoff in both the western and the eastern basins. The tendency for a difference in level between the Mediterranean and the Atlantic Ocean leads Atlantic Water (AW) encountered at the surface west of Gibraltar to flow into the sea at a rate of ~1 Sverdrup (1 Sv = 10^6 m^3/s, i.e. ~1000 times a major Mediterranean river flow). Typical values for AW at Gibraltar are T ~15-16 °C, S ~36-37 and σ ~26-27 (densities of 1.026-1.027). While progressing within the sea, the incoming AW forms a 100-200-m thick surface layer that is continuously modified, mainly due to interactions with the atmosphere and to mixing with resident waters (i.e. older AW remained at the surface and intermediate waters as defined below). All along its course, AW is warmed (up to 20-25 °C in summer in the mixed layer a few 10s m thick) or cooled (down to ~13°C, or locally less, in winter) but, overall, it becomes saltier (up to 38-39), hence denser (up to 28-29). In fall, AW has thus been pre-conditioned (densified) but it is still at the surface; the euphotic zone is mainly nutrient-depleted, and a thin chlorophyll maximum is encountered at 80-120 m. In winter, cold and dry air masses entrained by relatively brief episodes of strong northerly winds induce marked evaporation of AW (increase of salinity and loss of latent heat) and direct cooling (loss of sensible heat) that dramatically increase its density and make it sink.

Sinking occurs in specific zones located in the northern parts of both the western and the eastern basins according to two different processes. One process occurs on the continental shelves and results from the fact that waters there are markedly cooled because the relatively shallow bathymetry does not represent a large reservoir of heat, i.e. of buoyancy. However, shelf waters are relatively fresh in general (due to river runoff), so that they cannot get a density allowing them to sink deeper than a few 100s m. Such waters represent relatively small amounts, and are not directly important for pelagic species since the nutrients they possibly transport at depth cannot be exploited directly (but for remineralisation). The other process occurs offshore in some subbasins, such as the Liguro-Provençal (we use the term subbasin -or omit it- to design all the parts of the western and eastern basins that are usually -and illogically- equally defined as seas, basins or passages). Fundamentally, densified AW sinking there mixes, sometimes over the whole depth (2000-3000 m), with denser water(s) lying underneath and thus forms new specific intermediate or deep Mediterranean Waters (MWs, T~13-14°C, S~38-39, $\sigma > 29$). Because the denser waters are nutrient-enriched after some stay at depth (remineralisation), mixing on the vertical brings nutrients into the euphotic layer and allows phytoplancton growing as soon as the amount of light and the stratification (i.e. stability) are sufficient (spring blooms). The zones of dense water formation are characterised all year long by a reduced stratification and a doming structure (see section 2.2) that has nothing to do with an upwelling process. Moreover, the major process there on a yearly scale is a downwelling (of dense water). Note that the overall formation rate of the MWs is ~90% of the AW inflow at Gibraltar (10% being evaporated), among which ~3/4 (resp. ~1/4) is formed in the eastern (resp. western) basin.

The Mediterranean Sea is thus a machine that transforms AW into MWs. Dense water formation being a dynamical process that is essentially seasonal, the offshore zones of sinking are characterised by a marked biological signal at seasonal scale. Note that although dense water is formed in winter, the phytoplancton must, for a while, remain in the euphotic layer (i.e. surface waters must have re-stratified) and receive enough light, both conditions occurring in early spring only. This is evidenced in the Liguro-Provençal by the monthly composites of satellite ocean colour (chlorophyll integrated over a few 10s m) images (not well reproduced here in grey tones, but available in colour on http://www.me.sai.jrc.it) in figure 1 (see also Bosc et al., 2004). Although deep mixing occurs over a relatively wide area, the distribution of the phytoplankton bloom is by no means homogeneous spatially, as seen on figure 2, due to mesoscale phenomena (see also Morel and André, 1991, and Levy et al., 1999). Note that this zone is the one where cetaceans in the western basin are generally thought to be concentrated (e.g. Dubroca et al., this issue). Everywhere else, the dynamical processes themselves do not display such a dramatic seasonality, so that biology there is modulated on a seasonal scale mainly by light availability and stratification. For instance, in the Alboran, although the upwelling associated with the AW inflow along the Spanish coasts is quite permanent (nutrients are always available in the euphotic layer), the most intense primary production occurs in early spring too. It must be emphasised that, on a yearly average, primary production in the Alboran is higher[1] than in the Liguro-Provençal (Bosc et al., 2004).

2.2. The circulation

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[1] High values permanently associated with the major rivers outflows on these images are partly due to suspended mater, while those around the Kerkennah islands (Tunisia) are due to the few-metre depths there (the signal comes from the bottom).

Although the circulation of the various waters from/to the basins openings to/from the zones of sinking is still debated, only the authors' analysis is presented to provide a coherent overview. Moreover, we focus on the AW circulation that is of major concern for cetaceans.

To describe (intuitively!) the overall circulation of AW in the sea, let us consider the monthly composite[2] infrared image of January 1998 (fig. 3) that is representative of all winter months for what concerns the temperature values. Temperatures range from ~18°C along the coast in the eastern basin to 15-16 °C west of Gibraltar, ~13°C in the dense water formation zones of the Liguro-Provençal and ~10°C or less for the rivers outflows in the Adriatic and for the whole Black Sea. This image is also representative of all months and years for what concerns most of the overall AW circulation features, since most of them do not vary seasonally in a significant way.

Overall, and due to the Coriolis effect, all waters that are forced to circulate at basin scale tend to follow, in the counter clockwise sense, the isobaths at their own level. Therefore, the flow of AW tends to form almost permanent basin-wide "gyres" a few 10s km wide along the upper continental slope. This simple diagram is complicated by the fact that the flow of AW in the south of the basins is unstable in some specific zones (there, we identify the flow with the Algerian Current and the Libyo-Egyptian Current), generating mesoscale features that are mainly "eddies". These eddies reach diameters of 100-200 km, sometimes up to ~250 km, they propagate at up to a few km/day and some have lifetimes up to ~3 years at least. They sometimes extend down to the bottom (several 1000s m), hence following the deeper isobaths and finally separating from their parent current (where the direction of these deeper isobaths diverges from that of the upper continental slope). Together with wind-induced eddies having similar characteristics (such as Ierapetra and Pelops) they entrain AW and MWs towards the central part of the basins.

The schematic diagram in fig. 4 is from Millot and Taupier-Letage (2004). It summarises the diagrams proposed by Millot (1999) for the western basin and by Hamad et al. (2004) for the eastern one. The permanent currents that flow alongslope and are relatively stable (in the northern parts of the basin mainly) represent the clearest portions of the basin-wide gyres. They are a few 10s km wide, transport ~1 Sv each, and are a few 100s m thick, the maximum velocity in their core being of ~1 knot. These currents skirt north of the zones of dense water formation, thus leading to the doming structure previously mentioned. These zones are relatively quiet in summer and turbulent in winter (down to the bottom, horizontal scale of a few 10s km, velocities of a few 10s cm/s). Their biological impact has been mentioned in section 2.1. Transports within the largest mesoscale eddies in the southern part of the basins can be all year long of several Sv, furthermore when they extend down to the bottom, with maximum velocities still reaching ~1 knot. Such eddies are relatively intense in the zones specified by ΣA_E, ΣL_W and ΣL_E where they tend to accumulate and to induce a marked biological variability. First, the similarity between the thermal (dynamical) and visible (biological) signatures of such eddies (figure 5) shows that, at mesoscale, the dynamics drives the biological response (at least at the phytoplankton level). Second, similar images show that such eddies induce a significant biological response at scales up to seasonal and even interannual (see also Taupier-Letage et al., 2003).

2.3. Inertial currents

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[2] A monthly composite image has the advantage of giving an overview of the surface temperature in the whole sea with the same colour table and without any cloud. It has the disadvantage of giving a blurred vision of moving mesoscale features.

When the seasonal stratification (mixed layer and associated thermocline) develops, the wind temporal variability (mainly) creates oscillatory currents of a few 10s cm/s at the Coriolis period, i.e. ~17h30' at 43°N and ~20 h at 36°N. These currents are sometimes associated with vertical oscillations of a few 10s m at the thermocline level that propagate from the coast. They induce few-km loops that are superimposed on any other current, and hence increase the difficulty of interpreting a current measurement (i.e. what is it composed of?). Of course, the inertial currents drive the trajectory of any drifting object or animal swimming or not (i.e. plankton and nekton). This is demonstrated by the trajectories of drifting buoys (see fig. 13 of Taupier-Letage and Millot, 1986), and by those of whales for instance. The trajectory of a whale tagged with an ARGOS emitter and located at the maximum frequency, i.e. several times per day, describes loops at the Coriolis period (Mouillot and Viale, 2001) that, although actual, are not perceived by the animal. When positions are not acquired with a frequency allowing the filtering out of these oscillations (i.e. at once or twice a day only), they induce noise (i.e. an incomprehensible signal) in the data set and generally lead inexperienced authors to assume that the strange resulting pattern results from erroneous positions (i.e. they reject more positions than we do).

3. Discussion

There are indubitable facts about displacements of animals at seasonal and ocean/basin (100s-1000s km) scales, i.e. migrations. However, although reasons for migrations might be generally well accepted, how do animals navigate to accomplish their migrations? In case animals have sensors that we are unable to imagine and/or reproduce, can we assume that they use these sensors to navigate rationally (i.e. not randomly) to find food at mesoscale (10s-100s km) in the open sea/ocean? Are the data sets already collected about these displacements correctly analysed, or at least could they be analysed in a different way? In addition, considering the difficulty to collect adequate data sets about the links between the animals behaviour and their physical environment, are the available data sets sufficient to consider that definite proofs have been provided? In many cases, we have had another reading/another interpretation of the data sets than that proposed by specialists in the field, who state that some facts are "well known" and "already demonstrated". Indeed, the more one collects data (i.e. the more one knows!) about populations, the more one doubts about some alleged migratory patterns, up to abandon completely some formerly "well known already demonstrated" facts. This is the case for instance of the alleged eels migration between the Sargasso Sea and the European waters, including the Mediterranean. In the same way, some recent papers (e.g. Myers et al., 1998) do not take for granted that the salmon backward migrations aim quasi-exclusively at returning to their native river (success). Salmon tagging data sets actually show an impressively wide dispersion of salmon along the coasts (both upstream -with respect to the alongslope oceanic circulation- and mainly downstream the native river mouth), which cannot be interpreted solely as “failure”.

Part of the misunderstanding might also be due to the “anthropomorphic” formulation of the observations. This is the case for instance when papers say that an animal is “*taking advantage of the current*” to accomplish its migration. In the open sea, without any visual help from the bottom or the coastline, the animal has no way to detect and “*know the current*”[3]. Therefore, we object to that formulation which implies that there is a strategy –implying a puzzling corresponding know-how!-,

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[3] In the same way, a person walking in a train in the night without any visual clue does not experience more difficulties in walking “upstream” than “downstream”. Provided the train maintains a constant speed, it is even impossible for that person to tell in which direction the train is heading; and that person perceives a deceleration in one direction exactly as an acceleration in the other direction!

when we only observe that the animal is drifting in the current, just as a coconut would do. To provide examples about how a given data set can be analysed in quasi-opposed ways, let us consider two papers dealing with loggerhead and green sea turtles shown, from a set of ARGOS positions, to move westward, respectively in the central South Atlantic (Luschi et al., 1998) and in the central North Pacific (Polovina et al., 2000). Routes followed by several turtles equipped at Ascension Island that are similar and "*show an impressive coincidence with the current direction*" are interpreted by the authors as deliberate "*migrations taking benefit of the current and remaining downstream from the island*" towards a common target that is said to be the shortest course for reaching the Brazilian coast. Noting that turtles have "speeds" of the order of the speed of the current (when expressed in similar units!), we rather consider that the turtles drift at least for most of their displacement, with the current (passively, as that they cannot “feel” it), and finally reach the Brazilian coast ... just because this is the main path of the current! Why not then build a drifting buoy having the density of a turtle, release it together with turtles and compare the various trajectories? In addition, why not try to specify from where the turtles found at Ascension are coming, and/or why not equip turtles in Brazil to evidence backwards migrations toward Ascension, a much difficult "target", if any? In the second example, turtles are said to swim against the current (but how can they feel it?), modifying their route according to the current intensity (could it rather be that the variations observed are due to the combination of the variations of the current intensity plus those of the swimming activity of the turtle? i.e. the turtle would be more or less entrained by the current), and to concentrate wilfully close to temperature fronts. Why not assume that, in the same way as their forage, turtles are entrained by converging processes towards these fronts and that they will tend to remain there either passively (as any drifting material or plankton), or actively because their forage is concentrated there?

There is an understatement problem when stating that the animals are located where the food is the most abundant, or that a given animal is preferentially found close to thermal or ocean colour fronts, or any other environmental feature (be this interpretation the result of plain statistics or actual observations). Indeed, as for the case mentioned above, this implies that there is an active strategy to find the adequate feature: how can animals proceed, not having any information about the spatial distribution, such as the one provided by satellites? Determining gradients is not an easy task (see the annex), and to establish that there is more strategy than luck in the location of an animal in its preferred environment will require numerous tracking with a very high temporal and spatial interval.

In a general way, significant improvement will come from tracking at high temporal resolution for whichever displacements where the sight is invoked, as it will provide information on potential differences in trajectories or behaviour between day and night, and between clear and cloudy days as well, provided the cloud cover can be monitored finely enough. In the same way as for the potential foraging strategy, this will require many analyses of individual tracks, simultaneously with that of the environmental parameters. Although there are some definitive improvements such as the CTDs carried by e.g. sea lions, we think that there is still a long way to go.

Therefore, we would like to take the opportunity of this publication to ask, not only to the participants in the workshop but also to all future readers of this paper, the questions that we still ask to ourselves (see annex). To be answered, any question needs a theory supported by significant data sets that have to be analysed consistently. Whatever the theory (already published/accepted or new), one must rely on the available data sets (whatever they are) since new data sets require special efforts (out of our reach) to be collected. No doubt that technological improvement in animal tracking, genetics and biochemistry will greatly help. As for us, we point out some questions, and suggest some sampling strategies for collecting convincing data sets, trying to settle some issues about the cetaceans in the Mediterranean.

Let's take the example of the fin whale distribution in the Mediterranean. Specialists agree that fin whales aggregate offshore during summer in the northwestern Mediterranean (e.g. Nortobartolo di Sciara et al., 2003; Littaye et al., 2003, Dubroca et al., this issue). There is probably no doubt about that fact, would it only be simply because they tend to remain in an adequate environment, as would do potential (additional) newcomers (potentially attracted by the calls of their kin). But do we have the data sets adequate to establish that fin whales do migrate in winter? And where? As nearly all efforts to look for them have been carried out in this part of the basin and in summer only, a complete and reliable picture of their distribution at the basin and yearly scales is still lacking[4]. In addition, satellite imagery shows that the Liguro-Provençal is not the most productive place (in terms of primary production, see fig. 2 and Bosc et al., 2004) of the Mediterranean. Because the Alboran is the most productive place and the most regular (due to a quasi-permanent upwelling), how comes that whales do not concentrate there, if they were able to "guess" or use a strategy to find richer zones? It is indeed hard to conceive that animals can know/guess where better trophic conditions are, furthermore when considering the tremendous spatial and temporal variability at mesoscale evidenced on satellite images. We rather imagine a simple lucky-unlucky search for forage. So here is the alternative scenario that we imagine when analysing the whales' trajectories presented by Dubroca et al. during the workshop. Whales are looking erratically for food, and thus remain preferably in the richer zone. Some did not find enough food and decided to move away. Two did not find richer zones and, being afraid of being on a more severe diet, decided to move back. The third one was either more lucky in his looking for food, or less afraid by not finding much more food nearby, so that it decided to continue … and luckily found convenient conditions west of Gibraltar.

As a final illustration of the lack of adequate data sets about the cetaceans in the Mediterranean, it must be outlined that a few species have been only observed in the Mediterranean … once stranded.

4. Conclusion

We have raised some diverse and specific questions (see also the annex) in order to trigger exchanges of ideas with the whole community –or so we hope. We summarize here the main points which we feel need be tackled to make significant steps in understanding the role of the cetaceans in the marine ecosystem, and suggest new strategies to acquire data sets appropriate to settle some basic issues regarding the cetaceans in the Mediterranean.

It is clear that the migrations of cetaceans in the ocean are driven by feeding and breeding needs, and are mainly directed poleward-equatorward. Such migrations can be triggered by environmental parameters (water temperature optimum vs. food availability), and the navigation based just on the sun observation and/or on the direct perception of the temperature (additional hints not excluded).

We think that the populations of cetaceans in the Mediterranean result from the facts –and feeling- that the place is relatively convenient for both feeding (sufficiently rich) and breeding (sufficiently warm). And then it is not clear to us that any population would like/have to migrate out the Mediterranean, as it has been suggested years ago ... and maybe still believed!

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[4] Facing the same uncertainties about the dolphins (*Tursiops truncatus*) distribution during wintertime, acoustic surveys of carried by F.Dhermain (GECEM) showed that, most probably, there was no seasonal change in the population density.

Many hypotheses about the cetacean's ecology s.l. that have been issued from pooled data sets and statistical approaches cannot be considered as sufficiently tested and definitely validated. Now that there is a way to get satellite images of SST and of chlorophyll distributions in near real time, we start having the opportunity to test these hypotheses significantly. We can be helped on one side by numerical simulations, which allow predicting primary production and hence prey abundance, and on the other side by satellite localisations, such as the ones shown by Dubroca et al. during the workshop.

However, these helps require non-negligible financial and logistic efforts, so that we could start by continuing to locate animals using the visual technique for which there is already a significant experience. An objective sampling strategy using this technique is i) to look for cetaceans everywhere, i.e. in places predicted as favourable as well as in the other ones, and over a period as long as possible (a full year at least) and then ii) to confront these observations with the satellite contemporaneous observations. Even if such a strategy seems over-ambitious, we see two feasible steps.

The first step is related to the issue of the fin whale distribution during winter and their alleged capacity of migrating rationally to find most convenient places for feeding. In the western basin for instance, the phytoplankton bloom occurs earlier in the south (it begins in November – December, e.g. the January and February images on fig. 1), and is especially strong within Algerian eddies (fig. 5, Taupier-Letage et al., 2003). Meanwhile, the north is relatively poor (the bloom begins offshore in March –April). According to the hypothesis that whales in the western basin migrate to find more convenient places that they should be aware of -or be capable of- finding, they might be more numerous in the south during winter. Given the appropriate tracking of eddies that can be done, a fast and efficient cruise could be designed to estimate the abundance of fin whales in such eddies and compare it between late fall - early winter and late winter - early spring.

The second step could be to conduct a more objective experiment and make regular observations on a regular route during a sufficiently long period. In this regard, the project we are elaborating under the auspices of CIESM to install a thermosalinometer and a fluorometer (plus a meteorological station) on a Trans-Mediterranean ferry could be an excellent platform for a cetacean observational program. Indeed, weekly routes from Marseilles to Algiers and from Marseilles to Tunis are scheduled, and arrangements could be discussed with the ferry company to host observers.

Finally, arrangements should be thought with the navies to get the information from their acoustic records relevant to cetaceans. In addition, an attempt should be made to get autonomous, objective and regular monitoring, as we are used to do to study dynamical phenomena and their consequences on the biology. Why not set hydrophones, fitted with adequate filtering and recording software and devices, on top of dedicated mooring lines or “moorings of opportunity”? The recorded time series might allow identifying and counting several species of cetacean, and would provide months to years long observations, whatever the meteorological conditions. It would be especially efficient in relatively small areas such as Gibraltar, allowing monitoring the passages between the Mediterranean and the Atlantic Ocean, and tell in the end whether they are migrations or not. It would also be efficient in places where moorings are continuously maintained and regularly operated, such as in the Ligurian, or in places where operations are scheduled for a limited period, such as in the Egyptian in the forthcoming years.

Annexes

We list here some of the questions we are facing about migrations processes and mechanisms. These are just "naïve" questions, raised by the fact that we probably have an apprehension of the physical environment different from that of the other participants in the workshop, and surely by the fact that, mostly unaware of the “incredible abilities” of the animals, we always tend to look first for the simpler explanation. The goal of this annex, and of our contribution to the workshop as well, would be reached if an open discussion would rise.

Let us address first the migration in the atmosphere, which is probably easier since animals (we mainly consider birds) have a perceptible fixed referential, and after that the migration and other displacements of other animals in the ocean, which is maybe more extensively documented

1. Migration in the atmosphere

As far as we know, birds’ migrations are essentially (if not only) seasonal and north-south, more exactly poleward-equatorward (we are not aware of migrations going east-west or concerning both hemispheres). Migrations can extend over one full hemisphere, and it is well accepted that food availability (generally higher closer to the pole) and nursery requirements (generally more convenient closer to the equator) drive them. Whatever, which kind of sensor is requested to migrate poleward-equatorward?

Before involving sophisticated sensors based on geomagnetism or astronomy, why not consider that it is very intuitive for any leaving creature (including plants … and cetaceans!) to associate the temperature with the sun, since their sun-exposed side is always warmer than the other? Is it difficult to imagine that animals, said to navigate with respect to the magnetic pole and/or stars, can more easily infer that the closer to the sun, i.e. the more equatorward, the warmer, i.e. the most convenient place for breeding? Is it difficult to assume that, the sun describing an arc in the sky everywhere on the earth, any animal will consider that the higher the sun the warmer the sun-exposed side of its body? Why not imagine that, looking for warmer conditions, a “stupid” animal will move more eastwards in the morning and more westwards in the evening, while an “intelligent” one will interpolate the course of the sun and move directly towards the equator so that, in any case, the average course will be in the adequate direction, i.e. equatorward? Why not imagine a reverse poleward route, to find more convenient places for feeding, guided in the same way with the sun behind? Hence, could it be that, to migrate poleward-equatorward without any terrestrial/astronomical referential, no sophisticated sensors, except the natural visual (the eyes) and thermo-sensitives (the skin) ones, be requested?

Whatever, although the sun might be the only waypoint for a pelagic cetacean or fish, those birds that are living not far from the coastal zone have a clear vision of the “terrestrial referential”. Therefore, they can remain close to the land and even follow some specific features of it, either for going their way or just for remaining not too far from resting-feeding places. Because most of the major continents (America, Europe and Africa) have, fortuitously, a north-south extension, why not consider that migratory birds easily make a link between the coastline direction and the overall north-south one to migrate over large distances more safely, although not efficiently?

Could such a link between the large-scale coastline direction and the overall north-south one be made more or less intelligently by more or less “evolved” birds? In other words, could it be that places where these directions are markedly different, such as an east-west coastline in the northernmost part of the Mediterranean Sea, be adequate for testing this hypothesis? Whatever, our personal experience is that, in both fall and spring (that we take for the migration periods for birds), all “big” birds such as ducks, herons and storks fly following the coastline, what we consider an intelligent route. At the same time, “small” birds such as passerines, swallows and martinets fly roughly southward or northward, what we consider a more risky (if not “stupid”) route. For instance, the direct-risky-north-south route across the western basin (e.g. from France to Africa) is roughly equivalent to the safer one over Spain or Italy or, at most, only ~1/3 shorter. When in the open sea in both seasons, we never see big birds and often see small ones. Since these small birds are able to follow a ship sailing against winds as large as ~50 knots, let us consider that this is their cruising speed. They are thus able to cross the sea in its largest part (~400 nautical miles) in ~8 hours with calm winds, which is nothing else than a single “heavy day”, or even in ~4 hours with favourable 50 knots winds, which appears to be an efficient and somehow “pleasant trip”. However, if they unluckily have to face wind speeds ≥ 50 knots, they would have to fly for days. For sure, they will die before crossing the sea, as demonstrated by the numerous birds that “strand” on our ships and die, not being able to rest or eat and drink what we give them. If “intelligent”, why don’t all these small birds look for the 12-km wide strait of Gibraltar …a quarter of an hour (a stone’s throw) or wait for better meteorological conditions?

Now, after having navigated at “large scale”, i.e. north-south possibly just based on the sun and/or the coastlines (an oceanographer's observation!), some birds (e.g. storks) are known to return to their nest far inside the mainland. If not involving memory, this would require a navigation accuracy that humans are unable to achieve, even with a compass and a speedometer, with a sextant and astronomical tables, or with an ARGOS beacon, a satellite and a computer (humans need a GPS at least)! At this phase of their migration, these birds need to navigate as accurately as homing pigeons that, obviously, are able to find their house from several 100s km away within few hours only. "How do homing pigeons navigate?" is a question that even their owners/trainers have been unable to answer properly up to these very last days ... simply because adequate data sets were not available yet! Indeed, it has just been proposed by Tim Guilford (Oxford University) from a large set of GPS trackings (as reported in "Nature Science Update", February 10, 2004) that “modern” homing pigeons follow characteristic land features such as … roads and mainly highways, preferring following them and turning at cross-roads instead of flying straight back home! Hence, could it be that birds such as e.g. storks just use their vision and memory (of rivers, plains, mountains in "ancient" times) to achieve their migration?

2 Migration in the ocean

After having considered birds, let us first consider the fish said to migrate across an ocean back and forth such as e.g. salmon (back to their own river after a several-100s-km trip in the open ocean), eel (to and from the Sargasso Sea) and tuna fish (various trips worldwide). Not having enough time for a deep investigation of all the published papers, we have focused on those (the most recent ones) dealing with salmon that are the most numerous papers since i) several sensors and mechanisms have been invoked for salmon, ii) it can be captured for tagging and recaptured in rivers, and iii) it has been grown in farms and hence studied for a while. In addition, the “alleged" migration of eel is more difficult to document since it involves a larval stage, and it seems less and less believed (for Mediterranean eel, catches in the Strait of Gibraltar are would be tremendous!); tuna fish seemingly has not been tagged a lot, probably because easily wounded or preferably kept after catch.

Let us specify that these so-called "migrations" are not directed north-south, so that the sun does not has to be involved to look for “explanations” (if necessary!), although "data support the hypothesis that chum salmon utilize orientation clues associated with the sun during open sea migration" according to Friedland et al. (2001). Let us also specify that such fish, when pelagic and contrary to birds, do not have any terrestrial referential that they can see. Hence, and although e.g. "processes underlying open-ocean migrations by salmon have been debated for years but little evidence exists regarding the sensory mechanisms and clues used in these migrations" (Dittman and Quinn, 1996), "knowledge of the migrations and geographic distribution of post-smolts of Atlantic salmon in oceanic waters is sparse" (Holm et al., 2000), and "there is still no definite answer to migration of salmon" according to L. Hansen (pers. com. late 2003), how could such fish navigate accurately towards a waypoint?

Could the presence of magnetite, found in salmons and in other fish as well, and generally considered as not fortuitous, be fortuitous indeed, or dedicated to another use? Whatever, using the magnetic field just gives a direction with respect to the magnetic poles… that have markedly migrated themselves (the northern pole has already been in the southern Pacific). Could it be that fishes have corrected, year after year or century after century, their own "compass variation" (magnetic vs. geographic North)? In addition, lines of the magnetic field being not straight, do we have to assume that fishes modify their course mile after mile? And what about the use of such a sensor when close to the magnetic pole? Whatever, and although "Such a magnetic field detection system could aid in salmon navigation...", which applies to any navigator (!), "...no conclusive field experiments have been conducted on this subject" according to Hansen and Quinn (1988).

Could fish use astronomical navigation as invoked for birds? This hypothesis seems no longer accepted in general, maybe just because the stars and planets are continuously moving and have a relatively small dimension while the fish vision might not be adequate.

Using olfactory sense (e.g. Hasler and Scholz, 1983) just allows smelling a particle that comes into your nose. Assuming one is able to memorise the "odour of his/her birth place", and if, by an extraordinary chance, a particle from that place enters your nose when several 100s km away, how could this help in telling where (even in which direction) is your birthing place? Similarly, sharks are attracted by the smell of blood only if blood particles come into their nose, obviously. Considering that such particles emitted by an injured animal drifting with the current or by any animal without any current will not diffuse a lot around the animal and that, more generally, diffusion will only occur downstream from a fixed source, such a source cannot be smelled from even a few metres upstream. Why not consider then that sharks can efficiently use (i.e. as a predator) their olfactory sense for blood only if they can perceive the current, i.e. if they see the bottom, in order to swim upstream? (in any case, it would be more efficient for them to listen and use acoustic (directional) waves).

Dead reckoning, i.e. integrating speed and heading, allows accurate navigation … provided the speed is measured in a fixed referential (not with respect to the water, which is the sole speed easily measured). Since humans without any sophisticated instrumentation cannot do this, how could animals proceed?

Whatever the clues invoked for salmon to return to their native river, many papers present results about tagging either in a river or in the open ocean (e.g. Hansen et al., 1993; Hvidsten et al., 1994; Friedland et al., 1998; Jonsson et al., 2003). Why are all these papers unable to convince us that salmon retrieve their native river? Why not consider that only some salmons from a given river will re-enter that river (obviously!) while most of them will re-enter rivers located mainly downstream (with respect to the overall oceanic circulation)? Why not consider that salmons tagged in the open ocean will not enter the river in a preferential place, but rather enter the closest one or the one they will randomly reach? This is, by the way, the mechanism invoked for population spreading, which is a successful trait. So that, assuming that the successful migration for a salmon is to return to its native river would mean that some (many?) have to "mistake" to ensure the future of their population. This is not a straightforward and very satisfying hypothesis.

3 The specific case of the (migrating) cetaceans

In the framework of this monograph, let us focus now on mammals, first on their migrations and second on their displacements at smaller scale. Dynamics evidently drives the primary (at least) production. For instance, in the western tropical zones of the Atlantic and the Pacific, the trade winds and the Coriolis effect both combine to upwell nutrient-rich deep waters into the euphotic layer, hence triggering productive food webs that, although permanent, encounter seasonal latitudinal displacements. Dynamics also drives the primary production and the whole food web at higher latitudes, more or less mixing the surface of the ocean and seasonally bringing nutrients into the euphotic layer. Unfortunately for fishermen, the high latitudes zones, which are richer than the low latitudes ones, are also characterised by more severe meteorological conditions. This prevents them from fishing there all year long and leads them to “migrate” equatorward for somehow “breeding”!

Simultaneously, the other mammals that are cetaceans are reported to migrate seasonally, at least in some coastal zones of the World Ocean, most probably triggered by environmental factors. Could these migrations be driven, at least partly, by the environmental conditions becoming too harsh, e.g. the water temperature becoming too low, or the surface too icy for breathing normally? Alternatively, is it widely accepted that cetacean, as other animals (maybe having a specific internal temperature), have to migrate between feeding and breeding grounds. It can be considered that cetaceans migrate towards the equator for breeding in relatively poor but warmer waters and towards the poles for feeding (as shown by Mate et al., 1998, at least during a part of what is expected to be a poleward route; in fact, many other bearings have now been observed according to Mate, pers. com.), remaining there as long as environmental conditions are convenient and as long as they do not have to breed (Mate et al., 2000). Now, some populations that used to migrate have been observed to settle definitely (at least for some years) in places where environmental conditions allow feeding and breeding in the same environment (usually in places where the winter is no longer to harsh). Could this be a hint on the triggering mechanism and the hierarchy of the (numerous?) process that enter into the migratory pattern? What if the climatological conditions become too severe again? Are there any observations of migrations that resumed after a several-year interruption? Because most of the tropical/migrations zones have large space (100s-1000s km) and time (seasonal) scales, could they allow genetic or inborn / ancestral knowledge to motivate efficient migrations? To answer these basic questions, it might be easier to first answer more simple ones.

Is there any scientific evidence of migrations other than north-south (poleward-equatorward) in the open ocean or back and forth along a roughly north-south coastline (as documented, although without any solid conclusion, by Mate et al., 2000)? To be explained, do these migrations have to take into account physical processes and features not directly related to breeding (in warmer waters located equatorwards) and feeding (in richer waters located polewards)? In other words, are there migrations between a warmer-poorer place systematically polewards and a cooler-richer place systematically equatorwards?

In any case, we can make some additional remarks and ask some additional questions. Could it be considered that the actual migrations of cetacean and fisheries (fishermen migrate according to fish -and formerly cetacean!- migrations, or at least according to what they think that fish migrations are) are motivated by the same reasons (i.e. feeding vs. giving birth or simply living for fishermen!)? Could it be that the north-south orientation of these coastal zones is fortuitously convenient for some navigation simply based on the sun direction, in particular for the cetaceans? Would such migrations be the same with poleward trade winds and coasts with induced upwellings oriented east west (if possible!)? Are there cetaceans migrating towards such upwellings located along east-west oriented coasts, such as off northern Spain? What about the migrations before the continents started drifting?

When trying to understand the role of cetaceans -and that of human activity as well- in the marine ecosystem, sea-going oceanographers (who are not specialists of cetaceans!) first try to consider themselves as cetaceans or fishermen equipped with the most sophisticated sensors they have or that they could imagine. They realise that, although they can measure locally with the utmost accuracy any kind of state parameter (for instance the temperature or any kind of concentration of chlorophyll or whatever), they cannot measure it remotely (at any distance, even a few metres away). In case they want to find a place with a different value of that parameter (for instance to find warmer or more productive waters) they can sail / swim either towards a "known better place" or look for such a place. In the second case, they can sail / swim randomly, and maybe fail, or they can proceed with some strategy and try to estimate some specific gradient. To do so, they have to swim in a given direction (to be estimated and memorised) for a given distance (several 100s m to filter out the small-scale turbulence, i.e. a distance larger than the cetacean dimension). Then, they have to estimate the change in the parameter they track and decide to continue in the same direction or swim in another one. Finally, they have to summarise all the observations and specify the gradient. Is such a strategic attitude possible / realistic? Alternatively, is the search for a place with better conditions more erratic and random?

For sure, cetaceans and fishermen have more or less efficient hydrophones, so that they can passively listen to the noise emitted nearby. Similarly, they have more or less efficient sonars, so that they are able to echolocate suspended particles (zooplankton mainly) or fish shoals. However, is the dimension of the sphere that they can prospect in such a manner relatively large (i.e. as large as 10 000s to 100 000s m)? Are these sensors able to provide significant information for migrations (over 10 000s to100 000s m) or are they only efficient at a more local (100s to1000s m) level? In addition, is the fact that cetacean songs can be heard over relatively long distances (whatever they are) indicative about the eventual message that could be in these songs (i.e. "Come here, the food is abundant!")?

Another parameter of interest for both cetaceans and fishermen is the current. Fishermen may have some instruments allowing them to know the current while sailing on their ship; however, this requires such a high level technology, especially in deep and open waters, that they do not get accurate measurements of the current. For a physical oceanographer in the open sea (away from any terrestrial referential), it is necessary to have a DGPS and a current profiler (ADCP), or what are called XCP probes. Without such instruments, human beings are unable to feel any current, whatever its intensity and direction. Then how could cetacean or fish "feel" the current, and possibly use / avoid favourable / adverse ones? What are the tools and means cetacean (or a fisherman without any instrument, or fish) could have to "use the current"?

Finally, a major feature conditioning the attitude of naive classical oceanographers is that, being faced with accurate, detailed and numerous data sets collected either remotely or in situ, they have now realised that the "cetacean world" is extremely complex. Do both the cetaceans and fishermen actually feel an environment changing so rapidly in both time and space at all scales? Are they able to efficiently use their actual (i.e. not subjective) senses? In other words, has the natural variability to be considered as significantly felt by cetacean and fishermen or more or less as a random parameter? In this latter case, does this lead to a white noise (no consequence on a yearly scale for instance) or could this condition the success / failure of one predator with respect to the other during a given year? Consequently, can competitions between such predators and constrains imposed by the environment be estimated in a significant way?

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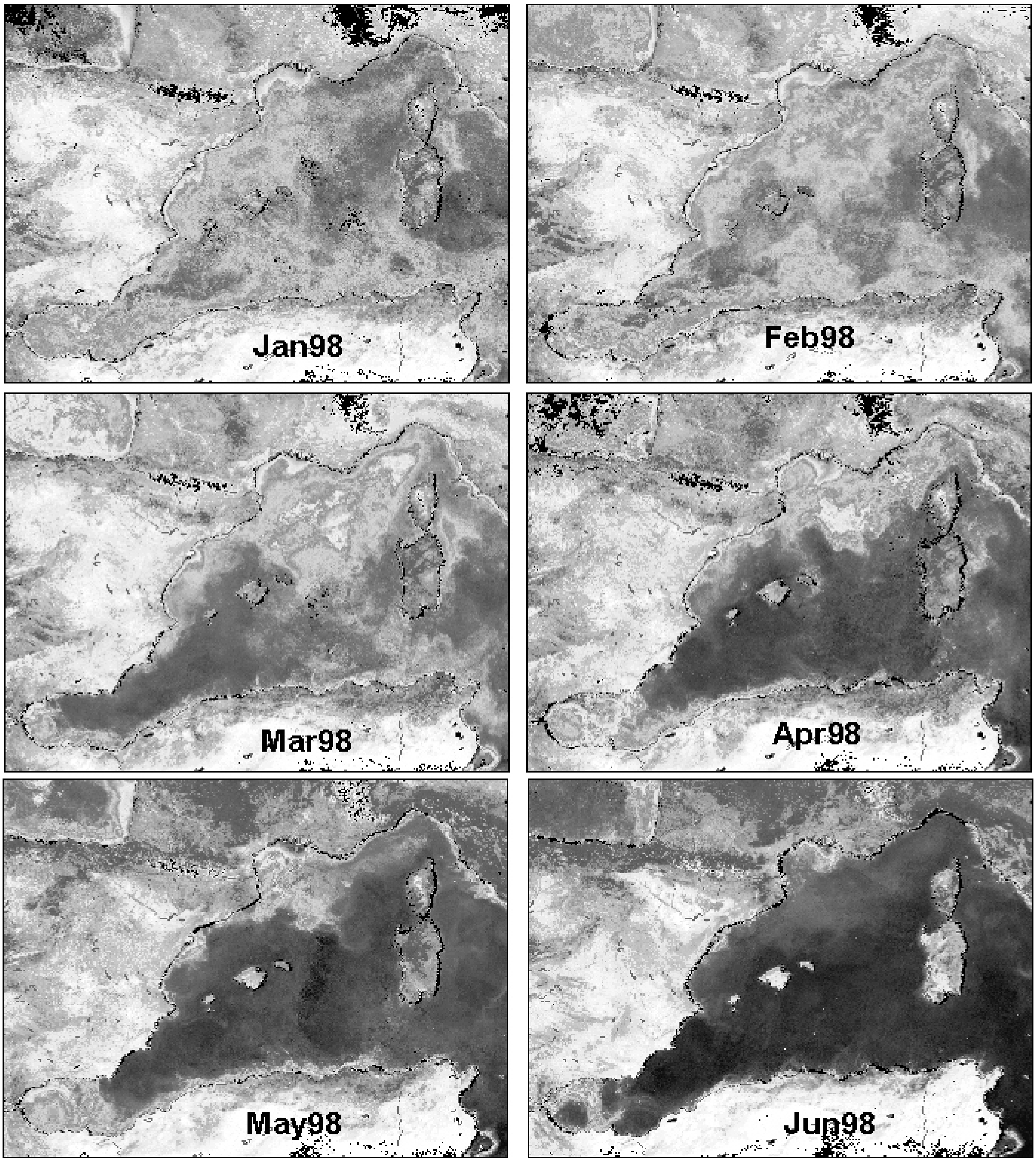

Figure 1 : Monthly composites of the chlorophyll concentration distribution from January to June 1998 (SeaWiFS images processed by the JRC).

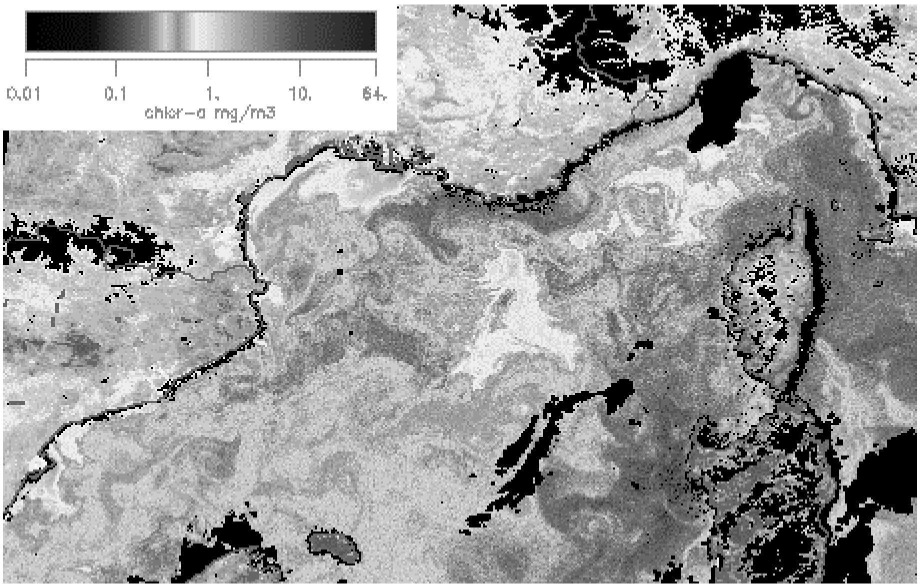

Figure 2: Chlorophyll concentration distribution on 26 February1998 (SeaWiFS images processed by the JRC).

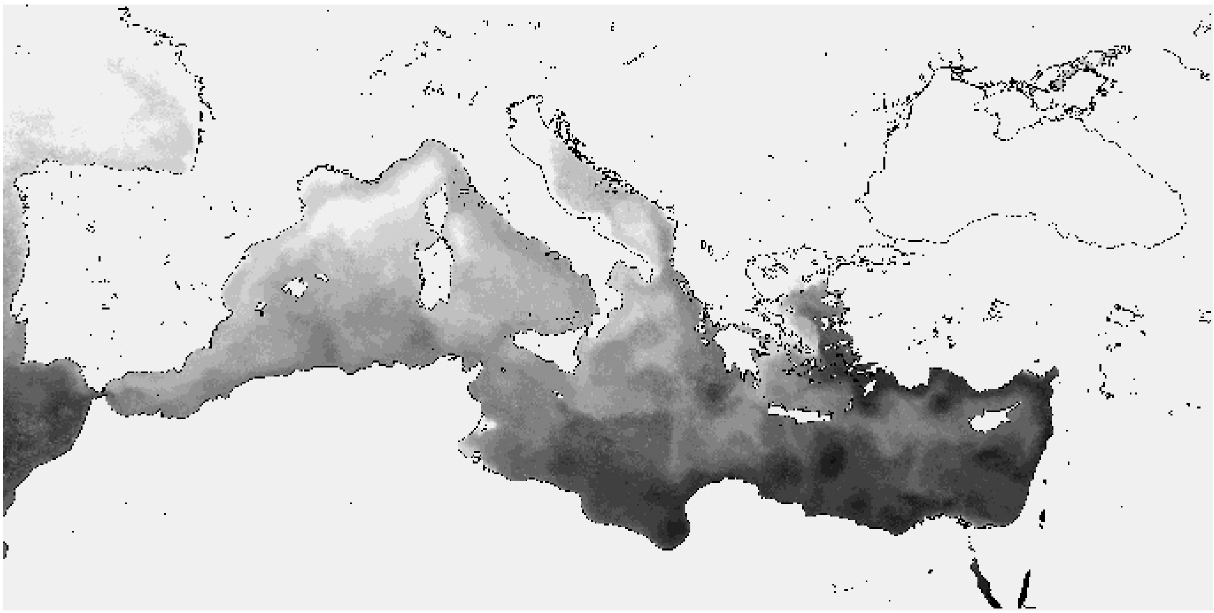

Figure 3: Distribution of the sea surface temperature (SST), monthly composite of January 1998 (NOAA/AVHRR image processed by the DLR). The temperature increases from light to dark grey.

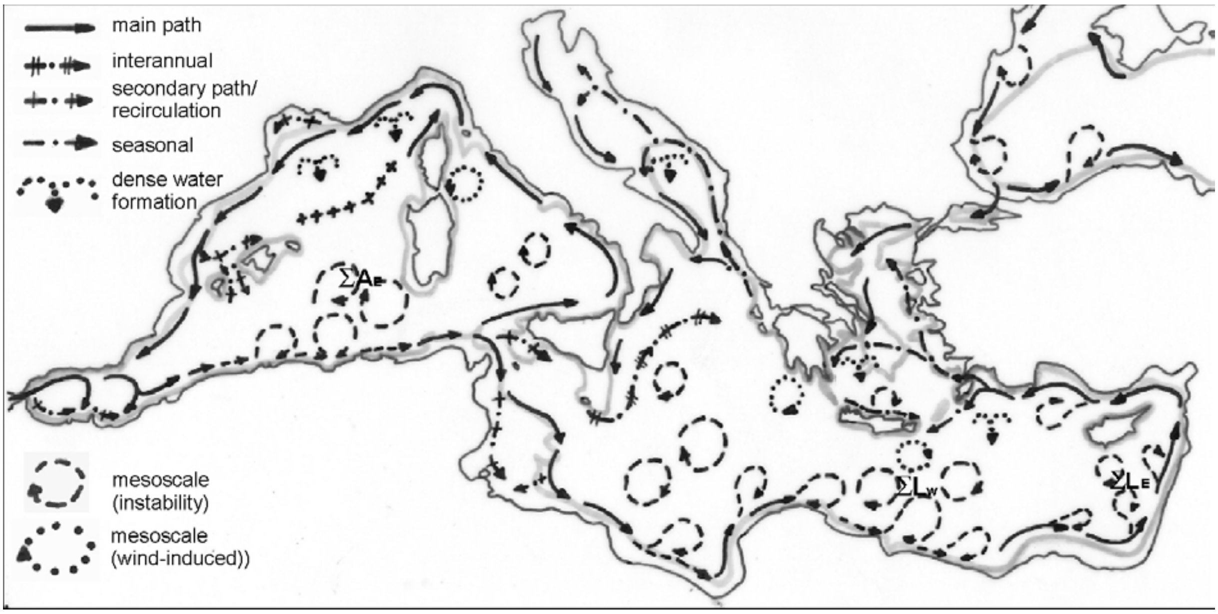

Figure 4: The surface circulation (of AW, mainly along the 200-m isobath) in the Mediterranean (from Millot and Taupier-Letage, 2004).

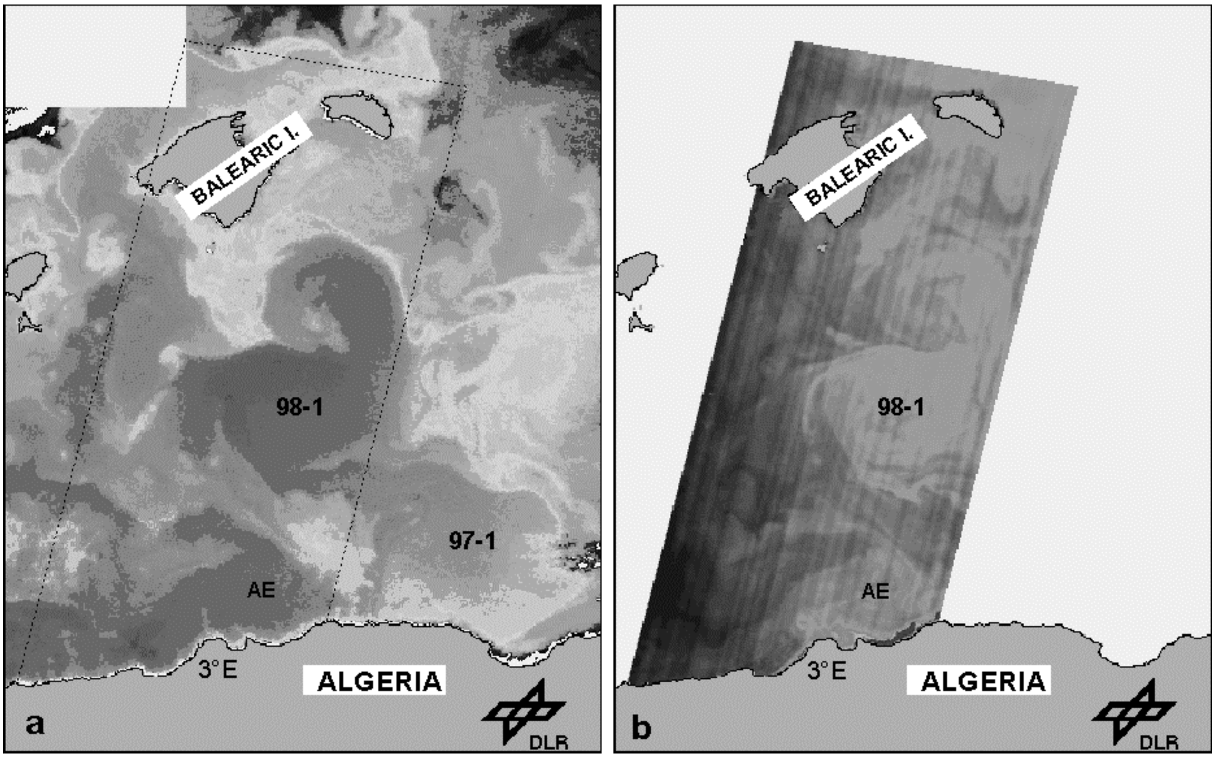

Figure 5: SST image (left; temperature increases from light to dark grey) and chlorophyll concentrations (right; concentration increases from dark to light grey). The eddies are identified as in Puillat et al., 2003.