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The Problem of Open-sea Navigation: The Migration of the Green Turtle to Ascension Island

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Green turtles, *Chelonia mydas,* make lengthy, regular migrations from Brazil to their nesting grounds on Ascension Island, 1400 miles away. The navigational systems used by *Chelonia* are unknown; but recent measurements of visual acuity in green turtles suggest that they cannot use stars for guidance. In this paper, we evaluate the possibility that orientation is based, in part, on the detection of some chemical substance originating at Ascension Island.

Calculations based on the turbulences and structure of the oceanic currents in the South Atlantic Ocean show that the concentration of any substance emanating from the island would be only 100- to 1000-fold lower in the Brazilian coastal region than in the upstream waters in the immediate vicinity of the island. In order to use this chemical trail as a cue in navigation, the turtles would have to be able to follow the gradient of increasing concentration to the center of the stream and then travel against the current in an easterly direction.

The potential problems of sensory receptor habituation, of the determination of polarity in a shallow chemical gradient, of the detection of compass direction or the direction of current flow, and of the maintenance of a straight course in the open sea, are discussed. The potential advantage of having the hatchlings imprinted by the taste or odor of the waters near their birthplace, in terms of reducing the amount of genetic information needed for successful orientation, is also considered.

1. Introduction

The refractory problem of animal navigation seems most clearly epitomized in the capacity of some migrants to travel long distances in the open sea, as indicated by scheduled assembling on small oceanic islands. No animal has ever been tracked in such island-finding travel, and the lack of information as to the routes they take is a major obstacle to animal navigation theory.

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There is, thus, no theory that convincingly explains the process by which animals are guided in or over the open sea. Three different classes of guidance systems suggest themselves as possibilities: (1) piloting by detecting features of the planet so far hidden from us; (2) navigating by dead reckoning, through the use of some sort of inertial system; and (3) navigating by means of a compass sense combined with a bi-coordinate position determining capacity.

Some years ago a tagging study showed that the green turtle, *Chelonia mydas*, makes regular nesting migrations to Ascension Island in the South Atlantic between the bulges of Africa and Brazil (Fig. 1). Of 556 nesting

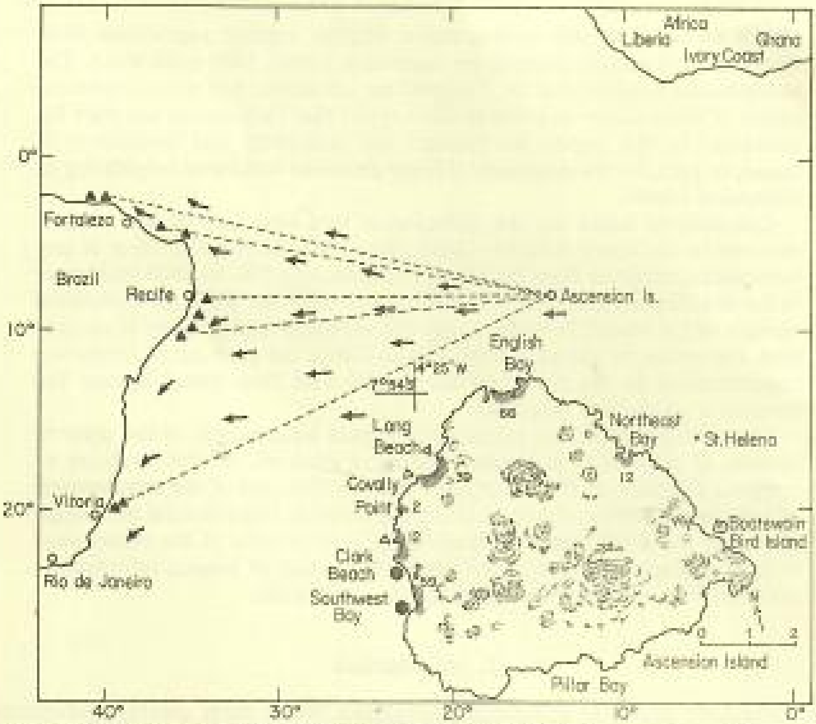

FIG. 1. Results of a tagging project at Ascension Island. Shaded crescents on the Ascension shore mark the five separate nesting beaches on the island, where green turtles were tagged. Solid triangles indicate the localities on South American mainland where tagged turtles were recovered. Hollow triangles indicate points to which tagged turtles returned to nest after a 3-year interval. Solid hexagons represent places to which turtles returned after 4 years, presumably for a second time, after two round trips to Brazil. All but one of the turtles recovered at Ascension had gone back to the original tagging site to nest again. The one that failed to home precisely came out on a closely adjacent beach that had recently been formed by storm waves. Arrows represent surface current trends.

females tagged on Ascension Island over a seven-year period, ten have been captured and reported by fishermen, all in the coastal waters of Brazil. Five tagged turtles have been observed when they returned to nest at Ascension after intervals of more than one year; none has been reported nesting elsewhere. There is no source of food (turtle grass) for adult green turtles at Ascension, nor is there any green turtle rookery of significance on the Brazilian coast adjacent to the feeding grounds. The best rationalization of these data would appear to be that the turtles, sustained by extensive fat deposits, travel directly from Brazil to Ascension Island to nest, over a distance of 1400 miles (Carr, 1967).

When these tagging studies were initiated the best explanation of the guided travel of the best-known migrants, the birds, seemed to be that it is done by determining both direction and position from celestial bodies. The German students von Frisch (1950) and Kramer (1950) simultaneously demonstrated the existence of sun-compass guidance—the former in the honey bee, the latter in the starling. Others found biological clocks and an innate compass sense to be widespread among animals, both vertebrate and invertebrate (*Cold Spr. Harb. Symp. Quant. Biol.*, 1960). When the work of Sauer & Sauer (1955) suggested that birds are able to determine position and to set appropriate new courses after displacement, by reference to features of the night sky, celestial navigation began to seem the least objectionable theory to account for long-range animal navigation in general.

In the case of the Ascension migration of *C. mydas*, major defects in this theory can now be seen. One, which applies specifically to the Brazil–Ascension travel, is the inability of the green turtle eye to see stars from above the surface of the water (Ehrenfeld & Koch, 1967).† Another, as pointed out by Hoffmann (1964), is that all experiments with biological clocks carried out so far suggest that the clocks are reset by any shift in the external cycle of day and night. If this is really the case, bi-coordinate navigation by the sun seems automatically ruled out. Besides a resettable clock to be used in direction finding, sun navigation would require an additional timer to be used in position finding, and this would have to be rigidly resistant to any such shift. Adler (1963) gives additional objections to a sun-navigation hypothesis, based on the probable limitations of angle-measuring capabilities of visual systems. Another weakness in a celestial navigation theory as an explanation of island-finding is the difficulty of visualizing the initial evolutionary stages of the process by which a reproductive colony is established on a tiny island remote from the feeding grounds (Carr, 1967).

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† It might be argued that the stars could be viewed from under water, however this is clearly impossible in the constantly rough waters through which the turtles must travel.

Nevertheless, finding an island, more clearly than any other navigation exercise, would appear to demand some process of bi-coordinate position finding, by which the migrant "knows" the position of the island and goes to it by keeping track of his own position and making continuous corrections of his course. A way the natural selection of such a habit might be supposed to have occurred is that it evolved when the island was either (1) much larger, or (2) much closer to the mainland. Even today, however, with the theory of continental drift gaining strength from new geo-magnetic and radiometric age data (Hobart University, 1963; Hurley *et al.*, 1967), a combined celestial navigation and continental drift hypothesis builds theory upon theory in what seems to be an unacceptable way.

The problem is to see how the Ascension migration could have been an effective route to survival in its earliest stages. It appears necessary to derive the colony from descendants of occasional gravid waifs that arrive on the island from elsewhere. Being hereditarily migratory animals, the offspring of the waifs might be expected to have the capacity to be imprinted in a brief period of time with the receptivity to certain guidesigns that could take them back to their natal shore, when they in turn reached maturity. But if the place where the waifs strand is a tiny island in the open sea, it would seem impossible for the racial imprinting and guidance equipment to be, from the start, so prodigiously accurate as to make the return a successful venture, if only celestial position-finding systems were involved. It would also have to compete with the seemingly far more promising evolutionary aberrancy of nesting on the Brazilian mainland beaches adjacent to the feeding grounds.

Despite the probable lowered predation on most island nesting beaches, colonizing Ascension thus seems a prohibitively unpromising new adaptation if celestial bi-coordinate navigation, alone, is the guidance system. Since inertial guidance is also difficult to imagine for such a lengthy journey,† we return to the first category listed and seek some less complicated mechanism that might continuously reorient a traveller through direct sensory response.

The simplest way to travel is to pilot by landmarks—to see, smell, taste, or hear signals from the "goal" or from fixed stations along the right way to it. Since seeing and hearing over the distances involved are most unlikely, we have re-examined the possibility that smell or taste might provide the clues for navigation. While navigation by such mechanisms presents serious problems, including receptor habituation and the detection of gradient

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† According to Barlow (1964), there is no positive experimental evidence to indicate that inertial guidance is ever used by animals to maintain direction for distances greater than a few meters.

polarity, they are not necessarily insurmountable. If physiologically possible, the use of an odor or taste trail seems reasonable as an evolutionary innovation.

The main purpose of this paper is to show that a chemical trail more than a thousand miles long can probably exist in the ocean, and that this might be used in combination with other environmental features in a process of island-finding navigation. One obvious objection to a chemical-perception theory is that it applies solely to aquatic migrants and leaves unexplained the island-finding feats of the sooty tern and other birds. Nevertheless, in spite of our reluctance to set aside the idea of a general theory of island-finding navigation, chemical perception as a source of pilot signals for Ascension-bound sea turtles must be evaluated.

2. Oceanographic Features of the South Equatorial Current

Although the route of travel of the Ascension migrants is unknown, logic would seem heavily to favor a direct, upsteam course from Brazil out to the island (Carr & Hirth, 1962). The following description of this area is pieced together from the literature of oceanography. Many of the observations made below can be found in the oceanographic classic by Sverdrup *et al.* (1942) or in the treatise of Hill (1962, 1963, 1965). Detailed information on the South Atlantic equatorial current appears in Defant (1961). References to the original literature can be found in these works. In each case we will here cite the most easily accessible reference.

The surface current moving from Ascension Island toward Brazil is one of the most constant in the world, throughout summer and winter progressing at a rate of 24 nautical miles in 24 hours. It is more than 1000 miles wide. The current is produced by three primary forces: (1) the constant trade winds that blow towards the northwest at a velocity some twelve times faster than that of the surface ocean current (Hill, 1962, p. 145); (2) the hydrodynamic pressure gradient to the northeast (Defant, 1961, p. 425); and (3) the Coriolis force running toward the southwest. It is a surface warm water current and extends down to the thermocline discontinuity, which near the coast of Africa, is at a depth of 30 m or less. This reaches a maximum depth of 70 to 90 m near the coast of Brazil and then rises nearer the surface. Figure 2 shows thermocline depth taken from temperature depth data (Fuglister, 1960) in a transect across the Atlantic at the latitude of Ascension Island. It is within this shallow layer that essentially all of the water in the current is carried. Its thickness is much less than that of surface currents in temperate parts of the oceans.

Above the thermocline there is vertical mixing due to wave action. The half-times are of the order of several days (Defant, 1961, p. 104). This means that substances in the water above the thermocline are transported as a whole from east to west, even though the velocity decreases with increasing depth and even changes direction within this layer.[†]

The temperature of the water above the thermocline is constant, independent of depth, and shows no detectable diurnal variation. The thermocline layer has a strong negative temperature gradient and contains a region in which salinity is higher than that either above or below. This high salinity region occurs throughout almost the entire length of the path that the turtles are presumed to follow. The existence of the salinity maximum shows that the forces of mixing are virtually reduced to the levels of molecular diffusion in the thermocline layer, because this tongue-like protrusion of higher salinity persists for thousands of miles from the source of the higher salinity waters to the south. Below this, the salinity decreases, although the density continues to increase, and the temperature continues to fall until an oxygen-poor, carbon dioxide-rich region is reached. This marks the lower margin of the true troposphere. In this part of the ocean this margin is not deeper than 350 m. Besides its distinctive character with respect to oxygen, carbon dioxide, temperature, density and salinity, the waters below the thermocline are known to differ from those above in pH and in concentrations of phosphates (Sverdrup *et al.*, 1942, p. 210; McGill, 1964, p. 127) and silica compounds.

[†] Measurements of the details of the velocities within the surface layer are not available for this region at the pertinent time of year; but theory, and measurement in other places, would suggest the following velocity structure: at the surface the current should be more than 45° to the west of the north-northwest direction that the wind blows. For an infinitely deep homogeneous ocean the surface current would be precisely at 45° to the wind. This deviation from the 45° of the Ekman spiral arises because the thickness of the stirred layer is much less than the Ekman frictional depth associated with the wind strength and the latitude. Since turbulent mixing does not occur at the thermocline, the eddy viscosity here decreases by nearly a factor of 10^4. Thus, the component of velocity perpendicular to the direction of the wind is almost constant down to very near the thermocline and then abruptly decreases to that of the much more slowly moving thermocline waters. The component in the direction of the wind stress at the surface is weaker than the perpendicular component and decreases progressively with depth. Near the thermocline it is very small and even reverses direction. This is much different from the prediction of the Ekman spiral for a homogeneous ocean, where, at certain depths, the velocity in the direction opposed to the wind would be sufficient to precisely cancel all net velocity of the entire current in the windward direction. The important implication for the present purposes is that the mean current flows in some direction between 90° to the west of the direction to which the wind blows and the direction toward which the current at the upper surface flows. From the westerly direction of the latter, as shown in published charts of ocean currents, it follows that the mean current from Ascension Island flows to the south of the Brazil prominence. The geostrophic component of the current also produces a mean flow going somewhat south of west. To predict the exact direction and velocity of the mean flow, a precise knowledge of the velocity structure is needed.

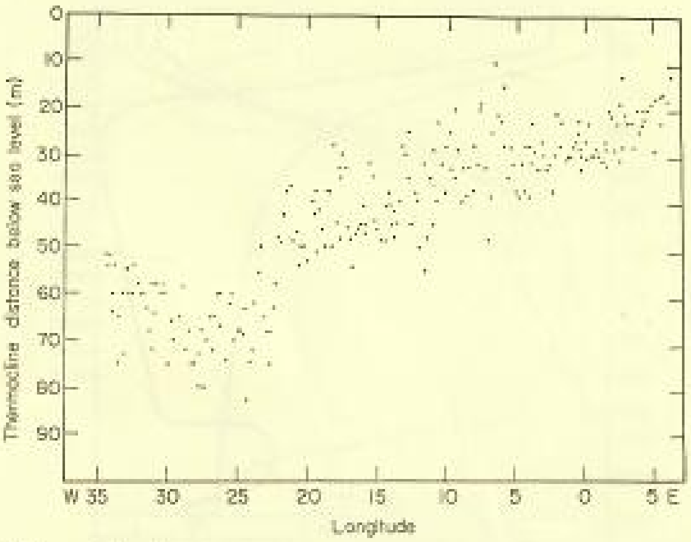

FIG. 2. Thermocline depth at the latitude of Ascension Island. The distance below sea level at which the temperature drops perceptibly is plotted. These data are derived from temperature versus depth graphs prepared from measurements made during I.G.Y. 1957–58 and reported in Fuglister (1960). Because of internal waves of amplitude of 10 to 20 m, the depth of the thermocline appears to fluctuate. The major component of these waves has a 12·3 hr period; these waves have little effect at the surface. For example, the average tide at Ascension Island is only 0·5 m. The longitude of Ascension Island is 14°W, that of the east coast of Brazil 36°W.

All of these variables can be understood in terms of the sources of the water and of the biological load. In Fig. 3, we have indicated how the variables change with increasing depth. This is a composite of various data taken from the literature. Some of the values are extrapolated, but probably approximate conditions that obtain during most of the migration.

3. Diffusion of a Chemical from Ascension Island

Previously, the idea that the Ascension migrants might be guided to the island by some chemical substance arising from the goal was considered unlikely because of the supposed tremendous dilution of such a substance in the vast volume of the ocean waters. This presupposition is certainly incorrect. There is almost no mixing with the enormous body of stratospheric water because the thermocline discontinuity acts as a barrier to all downward migration of materials. Diffusion with or against current causes no dilution effect if the substance is continuously being emitted from Ascension Island. Diffusion then proceeds only in *one* dimension instead of three; this circumstance tremendously decreases the dissipation of chemical substances in the

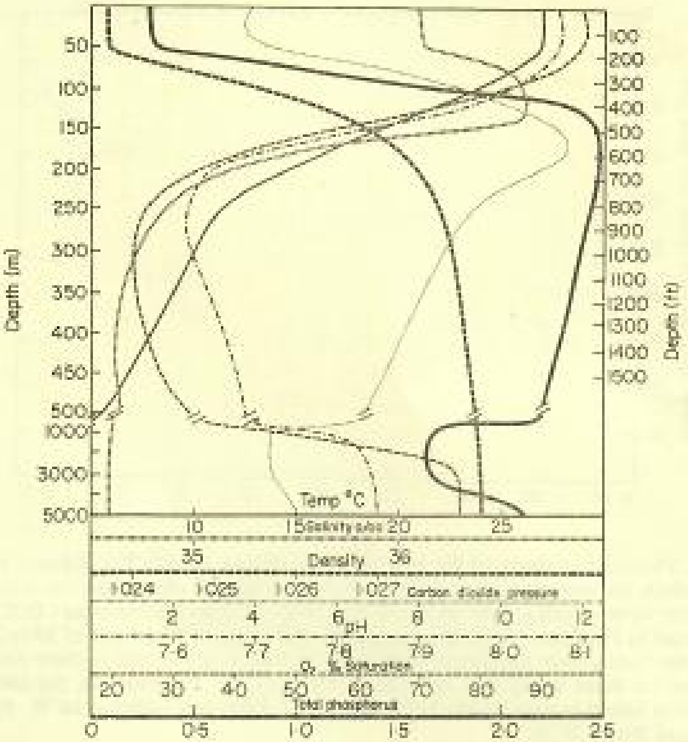

FIG. 3. Changes of chemical properties of the ocean with depth. This is a composite graph adjusted for a thermocline depth of 50 m and the boundary of the troposphere and stratosphere at about 250 m. These are, then, typical values for most of the path over which the turtles are assumed to migrate.

current. Even the effects of mixing in the horizontal direction at right angles to the current are surprisingly small. The argument proceeds as follows.

Mathematically, Ascension Island can be considered as a fixed point in a perfectly homogeneous flux of ocean water of shallow depth and constant velocity. If the island continuously emits some chemical species, or specific combination of chemical species, into the flowing water, at short distances downstream this would appear as a thin line of substance-containing waters resulting from the continuing flow of the ocean around the island. It then would tend to diffuse to the north and to the south as the current carries it to the west. Because of the relatively rapid vertical mixing within this layer, the chemicals are, and remain, uniformly mixed above the thermocline. For the present, we neglect the fact that as Brazil is approached the layer increases in depth by a factor of less than two, and can treat the concentration as a diffusion problem in a plane. Thus, the time available for diffusion and convection in the north–south direction is directly proportional to the distance travelled by the current in the east–west direction from Ascension Island, assuming, for the present approximation, that the velocity of the current is substantially constant. Thus, all that is necessary to write out is the diffusion equation for a point source of one dimension, y = (north–south), and then translate the time variable to the distance in the x = (east–west) direction. Until recently, mixing in the oceans has been assumed to follow the laws of the same form as for molecular diffusion or for conduction of heat. Even though this view has been superseded, we start with the Fick diffusion model because the mathematics will be familiar to more of our readers and because, even for this unfavorable case for our argument, chemical perception still would appear to be feasible as an aid to navigation. The well-known solution of the diffusion equation from a point source in one dimension (see for example, Crank, 1956) is:

$$C = \frac{M}{\sqrt{(4\pi Dt)}}\, e^{-y^2/4Dt}. \tag{1}$$

Its similarity to the Gaussian distribution is evident, differing only in that $\sqrt{2Dt}$ replaces the standard deviation. C is the concentration of the material at any point (y, t); D is its effective diffusion constant; t is the time permitted for diffusion, and y is the north–south distance from the stream line containing Ascension Island, at which the concentration, C, is to be measured. M has the units of amount per area and is then the total amount of material present in a plane perpendicular to the direction of the current.

To modify the equation for our present purpose we substitute u, the constant velocity of the current, for x/t. We also substitute I/uh for M. I is the total amount of specific chemical material poured into the ocean per unit time, and h is the depth to the thermocline. With these substitutions we obtain:

$$C = \frac{I}{h\sqrt{4\pi Dxu}}\, e^{-y^2u/4Dx}. \tag{2}$$

Calculations based on this formula are given in Fig. 4 for an idealized Atlantic ocean, using reasonable estimates of the parameters u, h, and D, and with I arbitrarily assumed to be one mole per second. Note, however, that the per cent change in C with the distance west of Ascension Island and with the distance to the north and to the south of the stream will be independent of the completely unknown value of I.

Even though equation (1) is based upon analogy to the diffusion theory that was derived to apply to molecules under the action of Brownian move-

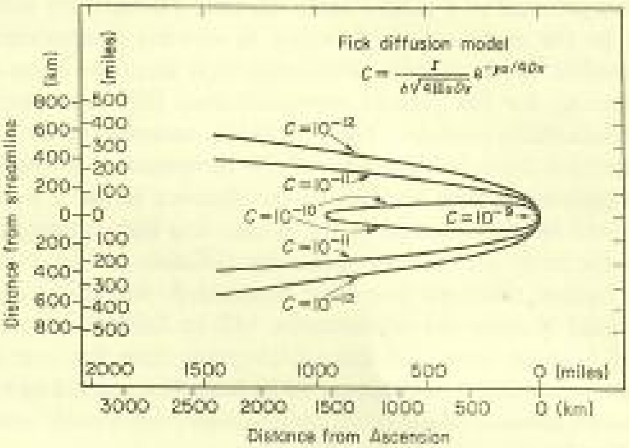

FIG. 4. The steady-state concentration based on the Fick diffusion model. Isoconcentration lines are plotted on the basis of reasonable estimates of the various parameters: velocity of current, $u = 24$ nautical miles/day, depth of current, $h = 50$ m, and $D = 5 \times 10^7$ cm^2/sec. The rate of production I has been set at 1 mole/sec. The resultant concentrations are in moles/l. The ocean has been assumed infinite to avoid boundary problems. The current has been assumed to be of constant speed, direction, and depth. For this model, concentration directly on the stream line is inversely proportional to the square root of distance from Ascension Island.

ment or to the diffusion of heat through random collisions of molecules, there is precedent and justification for applying diffusion theory to mixing in the ocean where the prime effects are not those due to molecular diffusion but to the convection and turbulences caused by wind currents. We will see below that this model is probably not correct in that D is not constant, but most of the oceanographic literature is based on this assumption and data have been fitted to Fickian diffusion laws. For mixing processes in the ocean, D is many orders of magnitude larger than the molecular diffusion constant and is different for movement in the horizontal and vertical directions. The literature values for various oceanic areas would estimate D at the order of 0·1 to 320 cm^2/sec (Defant, 1961, p. 104) for diffusion in the vertical direction. The highest value listed was obtained in the surface layer of the South Atlantic equatorial current. For comparison, values for the molecular diffusion constants of a small molecular weight substance, such as tryptophan or sucrose, are approximately 10^{-6} cm^2/sec. It is estimated, and frequently stated, that the horizontal diffusion constant in the surface layers of the ocean are even several orders of magnitude larger than are the vertical diffusion constants. In fact, estimates of 4 to 8×10^7 cm^2/sec (Defant, 1955; Montgomery, 1939; Montgomery & Palmer, 1940) are given for the surface current in that part of the ocean under present discussion. The reliability of these estimates is not great, and it would certainly be worthwhile to make accurate measurements in the South Atlantic Ocean at the time of year (January and February) when turtles are migrating.

An important aspect of the problem may be formulated so that the value of the effective diffusion constant does not matter: we can ask what is the relative concentration of the material at two points directly downstream from the island. Substituting $y = 0$ in equation (2) shows that the concentration is inversely proportional to the square root of the distance from Ascension Island. Thus, for Fickian diffusion the concentration at 1000 miles exactly downstream will be one-tenth the value that it is at 10 miles. We conclude, on the basis of the above calculations, that being carried vast distances by the South Atlantic equatorial current does very little to change the concentrations of continuously emitted substances as measured on the stream line leading from their source.

Further inspection of Fig. 4 shows that the simple extension of molecular diffusion theory to the problems of mixing in the ocean, while often done, is not the most realistic model to apply when large and small scale phenomena are both involved (Bowden, 1962, p. 802; Bowden, 1965). Near the source, the diffusion normal to the current appears to be faster than the current. The reason for the discrepancy is clear; the chosen value of $D = 5 \times 10^7$ cm^2/sec takes into account all the turbulences in the ocean over a long period of time and over thousands of miles of ocean. While a large eddy will cause mixing of waters on a large scale, small particles close together will not move relative to each other, and the effects will not be apparent. Thus, large scale movements distort the stream line but do not cause small scale mixing. We should, therefore, alter the diffusion constants, depending on the distance over which the measurements are made. One should use a smaller value near the source and a larger one further away. The problem has been approached from this point of view by Joseph & Sendner (1958). They replaced D by px, where p is a constant found to be about 1 cm/sec in a variety of cases of oceanic diffusion, and x is still the distance from the source. The replacement must be made in the differential equation and not simply in the resultant equation. They showed the equation was in accord with experimental results of a variety of kinds, including both small scale dye or radioactivity tracer experiments or large scale measurements of the composition of ocean waters. They conclude that p is approximately constant at 1 cm/sec, even for widely variant oceanic conditions.

On this basis, we have extended the Joseph–Sendner model to the one-dimensional case. Then, Fick's second law becomes:

$$\frac{\partial c}{\partial t} = \frac{\partial\left(py\,\frac{\partial c}{\partial y}\right)}{\partial y} \tag{3}$$

which on integration and evaluation of the constant becomes:

$$C = \frac{M\,\mathrm{e}^{-y/pt}}{2pt}. \tag{4}$$

On similar substitution as carried out before, this becomes:

$$C = \frac{I}{2hpx}\,\mathrm{e}^{-yu/px}. \tag{5}$$

Calculations based on this formula with $p = 1$ cm/sec are shown in Fig. 5. Joseph & Sendner (1958) showed that for large scale phenomena the effective diffusion constant from this treatment $p(x)/2$ and the experimental values based on the Fick diffusion model agree.

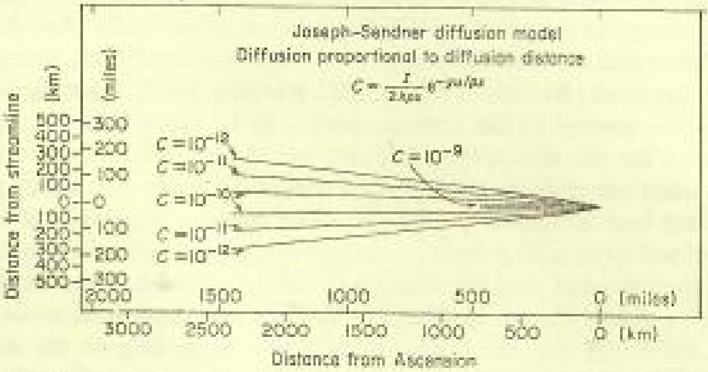

FIG. 5. The steady-state concentration based on the Joseph–Sendner diffusion model. Most of the parameters are used as in Fig. 4. The value of p is consistent with the value of D chosen in Fig. 4 at a distance of 400 km. In both figures, average values are presented. For this model, concentration directly on the stream line decreases inversely with distance.

It is clear that the Joseph–Sendner model predicts much higher concentrations and much narrower regions of high concentration near the stream line. The concentration is inversely proportional to x on the stream line where $y = 0$. Thus the gradient in the stream line is steeper in the direction of the current than for the Fick model.

To summarize the results of these calculations, we can use the values of the parameter D, crude though they are, to get the results shown in Fig. 4. The Fick model is certainly wrong in that dispersion is exaggerated near the source. The Joseph–Sendner model is a more accurate description that overcomes this and predicts a narrower distribution of substance, largely because the initial rapid dispersion is eliminated. The calculation shown in Fig. 5 is probably quite accurate. At large scale there is little difference between the two models: the chosen value for p gives the chosen value of D at 400 km for Ascension Island. While the latter model is more correct, p has never been estimated directly in this current. Either model, with any reasonable parameters, leads to the conclusion that the dilution factor is not so great as to exclude chemical perception of an Ascension specific substance in the coastal waters of Brazil.†

Certain limitations of the properties of this hypothetical Ascension emanation can be specified. It must not be either ubiquitous or chemically unstable. Yet it must not be recycled in the surface current, rather it must either be slowly destroyed or diluted with deeper water as the current approaches Antarctica. It would have to be detectable and distinguishable from other substances two months after entering the current. This would exclude many organic substances, which would be decomposed, altered, or consumed by the oceanic flora and fauna.

4. The Navigation of Chelonia

A number of migratory, marine vertebrates have already been shown to have an exceptionally high sensitivity to the presence of dissolved substances (Idler, Fagerlurd & Mayor, 1956; Creutzberg, 1959; Teichmann, 1959). The predicted 100- to 1000-fold dilution of any Ascension-specific substance that would occur in transit across the South Atlantic Ocean would still give a concentration many orders of magnitude higher than a reasonable threshold value, even if our modest guess of 1 mole/sec for the release of this substance is an overestimate. (Note that the units of concentration in Figs 4 and 5 are in molarities, and smell perception has been reported down to 10^{-20}M. For aquatic animals the lowest threshold reported is 3×10^{-18}M for eels tested with *β*-phenylethyl alcohol (Teichmann, 1959).) It seems reasonable to assume that a green turtle is able to detect the presence of a dissolved emanation at distances the order of those to be traveled in migrating to the island.

There remains the question of how the migrant is able to keep moving in the direction of the island. The problem of gradient chemoperception has received little attention. Certainly there appears little likelihood that direction

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† Other models have also been proposed. Perhaps the best model justified on theoretical grounds results from the Richardson neighborhood concentration model (Bowden, 1962, p. 802; Bowden, 1965), where distance is raised to the 4/3 power instead of the power 1. But this and yet other models that fit certain oceanographic data would not change the basic conclusion that the dilution of substances in the current is small.

could be taken from the tenuous east–west gradient between Brazil and Ascension Island. Even the sensory feat of perceiving the much steeper gradient in the north–south direction, thus enabling the turtles to keep traveling in the latitude of Ascension Island, presents serious conceptual problems even under optimal conditions, as the following considerations show.

According to the Joseph–Sendner model, at a point 1000 miles west of Ascension Island a turtle would have to travel approximately 50 miles north or south in order to experience a tenfold change in concentration. This would take several hours. This, in turn, implies that the concentration of perceived chemical species at one place would have to be remembered and compared a few hours later with the concentration at another place several miles distant. Two problems are immediately apparent: (1) how to prevent or overcome receptor fatigue and/or adaptation during the interval; and (2) how to remember the exact intensity of a stimulus for hours or days.

It is at least conceivable that the adaptation or fatigue of receptors might be avoided by a migrating green turtle that had periodic access to waters free of the chemical. Such waters could be reached by diving into the thermocline zone. This would, as Fig. 2 shows, lie at relatively shallow depths in the region between Ascension and Brazil, and would contain negligible amounts of the Ascension substance.† It also may be that fatigue does not occur with very low concentrations of substances.

But how could turtles be able to follow the north–south odor or taste gradient? There is no evidence to indicate that any animal is able to follow a gradient in which detection of polarity involves comparisons of consecutive sensory impressions separated by more than a few seconds in time. A number of vertebrate and invertebrate animals are thought to orient themselves in chemical gradients by the use of spatially separated chemoreceptors, but in all cases the gradient is sufficiently steep that significant differences in concentration can be perceived simultaneously by the separate receptors (Martin, 1965; Hemmings, 1966; Bardach, Todd & Crickmer, 1967).

A possible answer that suggests itself is that if there exists in the surface current a reference substance present in uniform concentration, then variations in the ratio of concentrations of Ascension-specific substance to reference substance might be perceived as a qualitative change in an odor or taste sensation. This could provide a more precise, albeit indirect, measure of concentration and possibly permit detection of a shallower gradient.

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† A turtle resting there would not only avoid continuous exposure to the chemicals in the current above, but might also avoid displacement by current during times of rest. Lack of detailed information on the diving habits of *Chelonia* makes such a proposal highly conjectural, but the turtles have been observed to rest overnight on the bottom while at their feeding grounds.

However, the turbulent mixing of the ocean, with the resulting interspersal of patches of high and low concentration, augments the difficulty and may require the equivalent of an averaging over time. The problem is to find and remain in the center of the stream. This problem becomes simpler as the island is approached, but at present we have no way of knowing the point at which the turtles first intersect the chemical trail. Still, at some time during the journey, after the chemical trail has been encountered, the turtles must travel obliquely to the current in the same direction long enough to detect a significant change in concentration, and then alter course accordingly. The methods by which such an orientation course might be held are discussed below.

Even if the animal can detect the change in concentration with time, there is still the problem of going upstream once the center of the stream has been found. Some means of determining the upstream direction of the current would be the most straightforward way to maintain a correct heading. However, an animal embedded in a current would have no way to perceive its motion. One place where clues to its direction might possibly occur would be at its edges, but the northern and southern edges of the South Atlantic equatorial current are hundreds of miles away from any reasonable green turtle migration route. This leaves only the upper and lower surfaces of the current to be searched for possible indications of the direction of current flow. In the former case, it seems conceivable that some effect of the prevailing winds to north–northwest might offer a directional clue, either directly or via perception of surface wave orientation. At the bottom of the stream a directionality might possibly be perceived in the shearing force of the current, in the narrow zone where it comes in contact with the relatively still waters of the thermocline and abruptly loses velocity. Neither of these possibilities can be evaluated at this time.

An alternative to sensing the current is to have and to maintain a long range heading. Mechanisms that have been considered in the literature are: (1) a magnetic field response, (2) a Coriolis force response, (3) inertial systems, and (4) a celestial compass sense. Of these four direction-holding mechanisms, only a time-compensated, sun-compass sense would appear to be a likely possibility as a component of the navigation system of the green turtle.

5. Conclusions

The purpose of this paper is to assess the possibility that chemoperception can serve in the long range navigation of *C. mydas* at sea. Navigation by this mode depends on the animal successfully solving four problems:

(1) It must be able selectively to detect emanation from the target.

(2) It must be able to detect the direction of the current, or must be provided with a time-compensated, sun-compass sense and knowledge of the approximate direction of the goal.

(3) It must be able to detect a difference in concentration at one time compared to another time hours apart.

(4) It must be capable of going far enough in a fixed direction with a cross-current component to sense a meaningful change in concentration, and alter course accordingly.

If the conditions of these and other untested assumptions are met, and if the distribution of a hypothetical chemical emanating from Ascension Island is properly predicted by models given here, it would be biologically and physically possible for *Chelonia* to make use of a chemical landmark during its Ascension Island migration. Alternative mechanisms have suggested themselves for several of the parts of our four-part theory; and the theory, itself, is incomplete because we have not specified how the turtles overcome the initial problem of orienting in the broad area off the South American coast where the equatorial current splits and meanders and is diluted by offshore water of varied scent and flavor.

The principal virtue of the theory is that there is less trouble visualizing the historical origin of the orientation pattern than in the case of other systems. The first-generation hatchlings would only have to carry away the instruction to take a certain heading when a certain, imprinted smell or taste above a threshold level is encountered. Both detection of a current-borne odor at great distances from a source, and determination of compass direction can reasonably be assumed to be within the sensory capacity of *Chelonia*.

It is known that salmon are imprinted by the scent of the waters in which they are reared (Donaldson & Allen, 1957; Hasler, 1966). If this is also true of sea turtles and, possibly, other marine migrants, then the infrequent colonization of new environments by such site-specific animals can be satisfactorily explained, because little or no genetic modification would be needed for the establishment of the navigation process appropriate for the new migration route.

Our proposed navigation mechanism is incomplete and encumbered with untested assumptions; but few advances in science have been made by shying away from outrageous hypotheses. We submit this theory because no better one is available to account for the migrations of *Chelonia*; nevertheless we are aware that there is still no entirely convincing explanation of the island-finding feat of any animal anywhere.

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