A CONSIDERATION ON AN AVAILABLE SOURCE OF ENERGY AND ITS COST FOR LOCOMOTION IN FIN WHALES WITH SPECIAL REFERENCE TO THE SEASONAL MIGRATIONS

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ABSTRACT

The energy cost for locomotion and possible distance of the migrations to and from the feeding grounds for southern fin whale were estimated being based on the amount of whale oil by girth measurements. A 18.1 meter fin whale keeps about 90 m^2 of the blubber area as substantially important for expending the preserved whale oil, and about 1.8 m^3 of oil is preserved in 2.0 cm thick of the blubber. The energy cost for locomotion by swimming in material fin whale was estimated as 0.022 Kcal$^{-1}\cdot$Kg$^{-1}\cdot$Km^{-1} by extrapolating parameters onto the known regressions of body weight-energy cost relationships in aquatic animals, and an integrated distance of migrations which is covered by following above mentioned parameters would be somewhere between 20,000 and 30,000 Km. These figures lead to a consideration that it is not unlike but generally quite possible to do have some food intake through the breeding migrations of whales since energy budget for locomotion in large rorquals seems to be scarcely well balanced in general pattern of their movements. These overall situations regarding the energy for locomotion were discussed along with the seasonal distributions of whales and also with the so-called problem of the breeding grounds.

INTRODUCTION

In the consideration on the seasonal changes of nutritive condition in California gray whale, *Eschrichtius robustus,* Rice and Wolman made a calculation on the expected amount of energy expenditure throughs wimming locomotion being based on the body weight difference due to the combustion of tissue before and after their migratory journey, and the weight loss was assumed as a function of oxidation of fat (Rice and Wolman, 1971). Being found that the overall energy budget for locomotion seems well balanced, Rice and Wolman (1971) concluded that gray whale must be able to perform migrations of such large distance as invade far deep into the Bering Sea and/or the Chukchi Sea without causing any malnutrition, and described, " there is no reason to assume that gray whale must feed while on the winter grounds ". Since gray whale is one of a well known regular migrators among large whales, the above mentioned result itself would be appropriate in the subject of controversy concerning to energy budget of migrating whales. Very

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recent aerial observations, however, revealed that gray whale clearly feed on small fishes on the way of their southbound migrations (Sund, 1975).

On the other hand, however, the baleen whales other than gray whale actually distribute with more larger numbers in the world oceans. They are balaenid and balaenopterid species of which the latter would be historically most important relating to human activities as an industorial resource. The general ecology around balaenopterid whales especially in so-called rorquals much differs from that in gray whale, that is to say, we are still in need of a verification in rorquals on this matter whether or not we will find similar conclusion to the results by Rice and Wolman. Under these circumstances I made a calculation and assessed the energy cost in relation to the swimming locomotion along with the overall energy budget through the seasonal migrations in southern fin whale, *Balaenoptera physalus*, and then extended a consideration to the seasonal distribution of whales.

NOTES ON THE SEASONAL MIGRATIONS OF WHALES

The conception that large whales are very likely to make seasonal migrations which extend over those vast oceans seems to have come in general knowledge as a result of accumulating a great deal of fragmental evidences brought on by navigators, fishermen and whalemen through many past years, but its substantial features remains still obscure even today. One of well dealt descriptions on the seasonal distributions in a north and south direction in the North Atlantic balaenopterids species was worked out by Scoresby (1820), by which our knowledge on the migrations of whales made much progress. Discussing on the evidences of whale sightings in nineteenth centuries, Scammon (1874) could describe only a possible north- and southbound migratory habits for humpback whale, *Megaptera novaeangliae*, and right whale, *Eubalaena gracialis* in northern hemisphere is unlikely to migrate crossing over the equator. There are another evidence that some blue whale, *Balaenoptera musculus* remains in the waters off California throughout the year. The seasonal migrations and the movements of whales are such variable and complicated by each whale species and place from time to time that the matter cannot be said as the comprehensively well explained subject.

Although it was not the aim in his discussion, True (1904) described that some North Atlantic humpback whale migrates down to at least 18°N latitude. Kellogg (1929) well reviewed on the migrations of six species of baleen whales based on the available evidences by that time. Although his descriptions were mainly confined to the northern species of whales, he (Kellogg, 1929) also mentioned but briefly on the migrations in southern species. By his above mentioned review the general idea concerning to the migrations of whales became much clear but still mysterious especially in recognizing the movements of whales as a large scaled and successive event performed through a life span of each whale individual, that is, the migrations of animals in broad sence. The comparative field study by Mackintosh and Wheeler (1929) on the biological and morphological characters in southern blue and fin whales of both South Georgia and Saldanha Bay made our knowledge on the migrations of whales much concrete. Shortly, it can be said that pattern of the whale migrations to the extent as have currently been recognized conception may be basically established by their work. However, movements of whales and where they may stay during winter or so-called non-feeding seasons are almost unknown even today except those traditional expressions of somewhere of " warm temperate or tropical waters."

According to Mackintosh and Wheeler (1929) connective tissue lies beneath the very surface skin of whales is the main body for depositing fatty substances, and the thickness of the blubber itself varies by season in southern species, that is, more thin layered blubber is found just after the winter and get more fat by an approach of autumn as a result of voracious feeding through the past several months in the feeding ground, whereas little feeding takes place in South African waters. With these facts along with a possible identity of whale populations which occur in both South Georgian and South African waters, it was obvious that both blue and fin whales are likely to make meridional migrations by season through which they do not feed but can continue swimming around by expending the blubber oil as the energy source for their locomotion. The general idea of the seasonal migrations of large baleen whales became clear to such somewhat fixed forms as having been recognized. At the same time the reason why they have to migrate into those " warm temperate or tropical waters " was well explained by supposing that cold feeding grounds of almost freezing point would be disadvantageous for parturition and for new born calf to keep well its body temperature. The conception seems fairly well established and there have found no additional evidences or explanations regarding this matter even in recently published articles which in part dealt seasonal distributions, feeding and breeding migrations for large whale species of the world oceans (e.g. Slijper, 1958; Jonsgård, 1966; Mackintosh, 1965, 1966; Nishiwaki, 1966; Matthews, 1968). However, Kellogg (1929) considers that there must be some fin whales throughout winter season in the South Georgian waters, and Mackintosh (1965) thinks the status of whale migrations as a possibly very loose and/or somewhat random movements in general, that is, some individuals may stay in the feeding grounds throughout a whole year while the other may not undertake those annual back and forth movements so regularly. Reviewing on the geographic ranges and seasonal distributions for large whales in the North Atlantic, Jonsgård (1966) considered that some whales may stay in the boreoarctic part of the North Atlantic, but he did not deal much about the breeding migrations by reason of less documented subjects. On the other hand, Mackintosh (1966) described two kinds of interesting and suggestive ideas on the status of migrating whales whether they are apt to concentrate or disperse in the breeding grounds. Matthews (1968) explained the seasonal migrations of whales schematically but he remained within showing a " warm temperate or tropical seas " as the destination of migrating whales. Recent description by Gaskin (Gaskin, 1972) concerning to whales migrations made a subject clear in a concrete form that the sea region where the reproduction of fin whale takes place would be found in the offshore waters within 150 miles or thereabouts.

Where are the large whales during winter or reproductive season is still mysterious subject which could be approached only by accumulating a scattered evidences on whale sighting. In the North Pacific region, for instance, a possible place for over wintering in fin and sperm whales seems to be still beyond of our scientific knowledge. Although an approximate movements of migrating whales may be recognized after the general principle as mentioned above, it seems still in need of further investigations and considerations to prove the matter more clearly. For

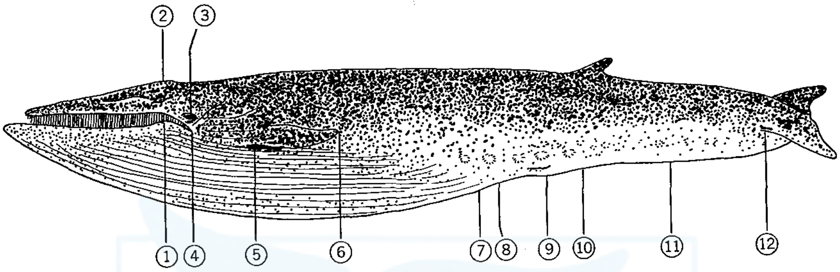

Fig. 1. Points for girth measurements. Encircled numerals correspond to those in Table 1 and Fig. 3.

TABLE 1. GIRTH MEASUREMENTS IN THE SOUTHERN FIN AND

	Ser. No.	1656†	1671††	1673	1676
	Sex	F	F	M	M
	Body length (m)	21.1	17.5	17.6	17.5
	Thickness of blubber (cm)	7.0	6.5	6.5	5.0
	Date of catch (month/day)	3/11	3/12	3/12	3/13
	Position of catch (S)	49-09	49-16	49-16	49-28
	Position of catch (E)	77-42	79-32	79-32	80-31
1	Highest point of lip	—	—	—	200
2	Center of blow hole	—	—	—	—
3	Eye	—	—	—	—
4	Angle of gape	—	—	—	860
5	Anterior base of flipper	—	810	900	850
6	Tip of flipper	—	—	—	—
7	Posterior end of ventral grooves	—	—	—	—
8	Unbilicus	780	644	674	630
9	Center of genital aperture	—	—	560	530
10	Anus	560	496	448	464
11	Center between dorsal fin and base of tail flukes	—	—	330	300
12	Base of tail flukes	286	238	208	208

* Measurement at 140 cm anterior from the base of tail flukes
** " 110 " "
*** " 150 " "
1) Measurement at 238 cm posterior from the base
2) Posterior margin
†) Pregnant: foetus of 281 cm, female
††) Not pregnant

instance, whether or not non-feeding activity during seasonal migrations explains or actually fills overall locomotion energy required for migrating into those " warm temperate or tropical seas " only by expending the blubber oil without causing malnutrition.

MATERIAL AND METHOD

During the course of 1971/72 Antarctic whaling season when I was on boad of the mother ship " Tonan Maru No. 2 " of the Nippon Suisan Co. Ltd., girth of fin and minke whales was measured at three to nine points of the carcasses (Fig. 1). True (1904) noted several girth measurements on the basis of one side or whole of carcasses, and Captain Roys gave 39 ft. of girth for 95 ft. blue whale in 1800's (Scammon, 1874). However, since very little girth measurements have been done in the ordinal program of the biological examinations on whale carcasses, I would like present here the whole row data of the girth measurements in nine fin whales (6 male and 3 female) and four male minke whales for the convenience of later use (Table 1). As shown in Table 1 both fin and minke whales were caught in the mid March of 1972. Two-meter measure was used for actual measurement by

MINKE WHALES CAUGHT IN 1971/72 ANTARCTIC SEASON

Fin					Minke			
1678††	1679	1692	1702	1705	16-1	16-2	23-1	26-2
F	M	M	M	M	M	M	M	M
19.3	17.4	20.9	17.7	18.1	8.4	8.2	?	8.4
6.5	5.5	6.0	5.5	7.0	4.6 (Avg.)	4.6 (Avg.)	4.6 (Avg.)	4.6 (Avg.)
3/13	3/13	3/14	3/14	3/14	3/16	3/16	3/16	3/16
49-28	49-28	49-46	49-46	49-46	53-58	53-58	53-58	53-58
80-31	80-31	80-03	80-03	80-03	85-16	85-16	85-16	85-16
—	—	240	180	220	—	—	—	—
—	—	—	—	770[2]	316	316	314	354
—	—	310	—	—	—	—	—	—
—	—	—	794	—	420	426	408	412
—	—	860	854	—	480	492	448	470
—	—	—	804[1]	790	—	—	—	—
—	—	—	—	—	490	500	440	452
—	—	720	640	920	450	480	426	432
596	560	626	540	600	372	376	346	356
558	480	560	470	532	296	290	262	280
380*	296**	354	300*	320***	234	216	200	216
268	186	232	192	220	100	108	108	100

sliding the scale like a looper. The air which had been filled in the ventral cavity to make the carcasses afloat was discharged when the carcasses were pulled up onto the flensing deck except no. 1673 fin whale which kept some amount of air but not fully. Each girth measurements given in Table 1 are obtained by doubling the actual figure from one side measurement. Measurements at nos. 1 and 3 points show only the upper half, that is, only a part of the skull.

Since no measurement for so-called body proportion analysis on the carcasses concerned in Table 1 was conducted, the proportion data obtained in the South Georgian fin whales by Mackintosh and Wheeler (1929) were adopted as the possibly most well representing figures to know relative position of the girth measurements (Fig. 2). Of six fin whales 18.1 meters of male individual (no. 1705 specimen in Table 1) which was most well measured was selected for the calculation of body surface area, and consequently, the volume of the blubber. By this treatment the whole body surface area was calculated section by section as given in Fig. 3. Anterior part from blow hole and tail flukes were excluded from the calculation since these two are considered unlikely to relate to the question to be discussed here. Dis-

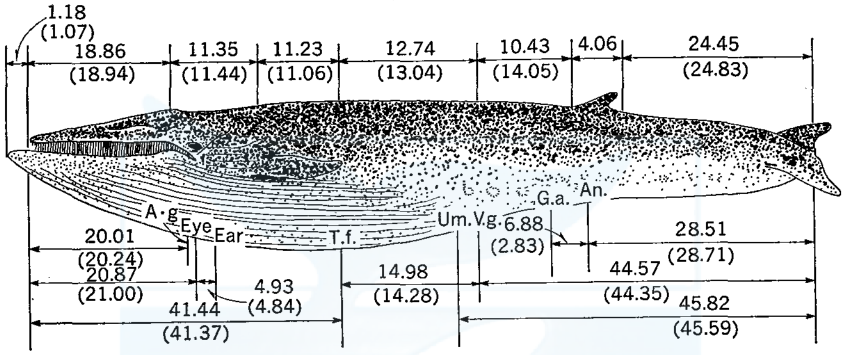

Fig. 2. Average body proportions (in percentage figures) for the southern fin whales. Figures for female are given in brackets (Calculated from the data by Mackintosh and Wheeler, 1929).

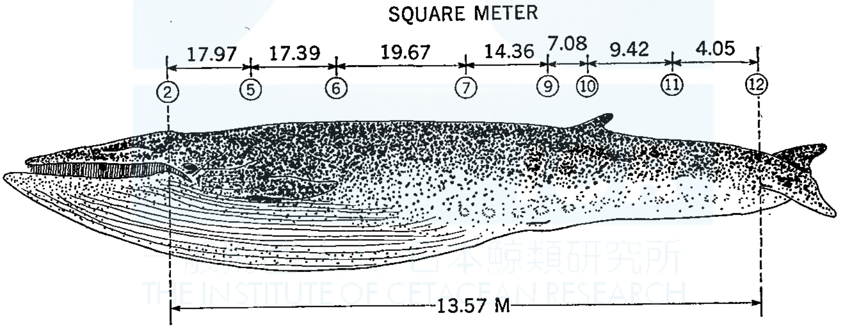

Fig. 3. Surface area of body trunk for a southern fin whale (18.1 m, male).

tance between notch of flukes and the anterior base of tail flukes was hardly determined clearly, and 4.0 percent was adopted tentatively for its proportion: then the actual body length which concerns to a consideration is 13.57 meters, and the whole body surface area corresponds to 13.57 meter body length is calculated as 89.924 square meters (ca. 90 m^2).

The thickness of the blubber with connecting tissue beneath the epidermis and dermis considerably varies with the seasons. In southern fin whales caught in the South Georgian waters averaged difference in the thickness of the blubber against body length in percentage figures was 0.37 for summer and 0.27 for winter respectively (Mackintosh and Wheeler, 1929). The material of 18.1 meter fin whale showed 7.0 cm thick blubber, that is, 0.39 percent against its body length while it was only 5.0 thickness (ca. 0.29 percent) in another material of 17.5 meter male fin whale. Comparing these figures with those obtained in South Georgian waters, the 7.0 cm thick blubber in 18.1 meter fin whale would possibly be at its upper most extremes as the function of depositing whale oil, and similarly, 5.0 cm thick blubber would be at its lower extremes. These facts suggest that the blubber oil which corresponds to 2.0 cm difference in the thickness of the blubber is likely to be consumed through the migratory journey. According to Slijper (1958) about 40.0 percent of the blubber is in general consisted of connecting tissues. So if we take this figure into considerations the total volume of whale oil preserved in the 2.0 cm thick blubber for 18.1 meter fin whale would be calculated as about 1.80 cubic meters. Assuming five months between May and September as for the duration of whale migrations, the blubber oil as the energy source for locomotion would

TABLE 2. DATA AND ASSUMED CONSTANTS CONCERNING TO THE CALCULATIONS FOR FIN WHALE LOCOMOTION*

Species	Fin whale: *Balaenoptera physalus*
Position of catch	49°46′S, 80°03′E
Date of catch	March 14, 1972
Body length	18.1 m
Sex	Male
Thickness of blubber	7.0 cm
Area of blubber concerned**	89.9 m^2
Body weight***	34.0 tons
Thickness of blubber expended	2.0 cm
Caloric value for blubber oil	9.34–9.45 Kcal/gr.
Specific gravity of blubber oil	0.92
Energy cost for locomotion	0.022 Kcal/gr./Km
Efficiency of muscle in performing external work	25%
Condition of swimming	10 knots, laminar flow
Estimated migration distance	2.1×10^4–2.3×10^4 Km

* for further detail see Schmidt-Nielsen (1970, 1972) and Kawamura (1973a, b)

** body trunk proper: anterior part from blow hole and appendages are excluded

*** after the formula by Ash (1952)

be about 0.36 $m^3 \cdot month^{-1}$, or 1.2×10^4 $ml \cdot day^{-1}$. Since generally known caloric value and specific gravity of fin whale oil is 9.34–9.45 $Kilocalories \cdot gram^{-1}$ and 0.92 respectively, the unit volume of consumable whale oil could be converted to 1.1×10^4 $gram \cdot day^{-1}$, or $10.27 \times 10^4 - 10.39 \times 10^4$ $Kilocalories \cdot day^{-1}$. The grand total of consumable energy during five month migrations in 18.1 meter fin whale would be about $1.55 \times 10^7 - 1.57 \times 10^7$ Kilocalories. Data and some constants concerning to above mentioned calculations are given in Table 2.

ENERGY COST FOR LOCOMOTION IN FIN WHALES

The energy cost for swimming locomotion in large whales is still unknown. However, it seems possible to speculate the energy cost for locomotion by the aid of known data in small toothed whales and in some another kind of aquatic animals (e.g. Schmidt-Nielsen, 1970, 1972). As I showed previously (Kawamura, 1972), the energy cost in large whales seems to be very less expensive when it is compared with the case found in another species of aquatic animals. Only four percent or thereabouts in daily feeding rate in sei whale (Kawamura, 1974) and possibly similar figures in another species of baleen whales would support very less energy expenditure for locomotion in those large whales. According to Schmidt-Nielsen (1972) the energy cost in a dolphin of 100 Kilogram body weight is about 0.1 $Kilocalories \cdot Kilogram^{-1} \cdot Kilometer^{-1}$ when it swims through laminar flow of water over the body at 10 knots in speed if we assume its conversion efficiency of muscle in performing external work would be 25.0 percent whereas 22.0 percent was assumed by Gawn (1948). In general the energy cost for locomotionin animals is closely related to the body weight of animals, and changes by following after the exponential like curve (Schmidt-Nielsen, 1970, 1972). Then the energy cost or metabolic rate such as 0_2 $ml \cdot gr^{-1} \cdot h^{-1}$ in relation to the body weight of animals can be expressed under logarithmic scale by three different regressions each of which shows difference by the kind of living media; whether the animal flys, runs, and/or swims. Since these corelations can be followed in aquatic animals and seems to be not unreasonable for extrapolating treatment, the energy cost for locomotion (= swimming) in large whales would be known reasonably by extrapolating their body weight onto known energy cost—body weight relationships.

Then the energy cost for swimming in 18.1 meter fin whale which weighs about 34 tons is estimated as 0.022 $Kilocalories \cdot Kilogram^{-1} \cdot Kilometer^{-1}$ if the same parameters are assumed as in the case of dolphins, that is, the animal swims at the speed of 10 knots under laminar flow of water over the body and 25 percent in the efficiency of muscle in performing external work. (See Schmidt-Nielsen, 1972, fig. 7) Similarly a blue whale of 100 tons of body weight would expend about 0.014 $Kilocalories \cdot Kilogram^{-1} \cdot Kilometer^{-1}$ as its energy cost for swimming. The data indicate that the large rorquals seem to expend some 1/5 to 1/7 times of energy cost than the dolphins.

The actual energy cost in 18.1 meter and 34 tons of fin whale may be 7.48×10^2 $Kilocalories \cdot Individual^{-1} \cdot Kilometer^{-1}$, and some $2.10 \times 10^4 - 2.36 \times 10^4$ times of these cost would be required for five months migration since its totaled energy corresponds to 1.55×10^7–1.57×10^7 Kilocalories. These facts indicate that the 18.1 meter fin whale can migrate for the distance of some 2.1×10^4–2.3×10^4 Kilometers by expending its blubber oil preserved in 2.0 cm thickness of the blubber. Actually, however, slightly more energy expenditure must be took into considerations since the metabolic rate as examined in human body increases for 10–20 times according to the physical conditions whether he moves vigourously or rests (Yoshikawa, 1959). Jumping, leaping or breaching (Racovitza, 1903) behaviours in large whales are often observed on high seas, and several times of these kind of violent movements which may be induced by playing, chasing, and/or escaping from the enemy would possibly be a quite daily event in the wild life. All of these are responsible for increasing the energy expenditure, since whales were assumed as migrate constantly under 10 knots of swimming speed throughout their migratory journey. In gray whale, however, Rice and Wolman (1971) have found well balanced energy budget being based on the " actively swimming animal ", and 10 knots in swimming speed would also be allowed for general considerations as a totally averaged figure in energy expenditure.

CONSIDERATION ON THE AMOUNT OF WHALE OIL AND THE ENERGY COST

The calculation as has been described in previous section was introduced by following after the several assumptions: 1) Whale oil preserved in the blubber around head and ventral grooves, and that in bones and internal tissues are not utilized as the energy source for locomotion, 2) Whale oil which corresponds to 2.0 cm thickness of the blubber which covers over main body trunk is consumed as the energy source for locomotion, 3) Energy cost for swimming locomotion in large rorquals was estimated by extrapolating the parameters into the known regression line in aquatic animals and, 4) As it was assumed in the case of dolphins, the efficiency of muscle in performing external work would be 25 percent, and the animal swims at 10 knots under laminar flow of water over the body.

Concerning to an absolute amount of whale oil itself, the whales body under alive would contain much more than that considered in this report. For instance, Omura *et al.* (1942) showed that the 18 m meter fin whale caught in the coastal waters of Japan yielded 0.73., 0.5 and 0.5 tons of whale oil from the blubber, bones and internal organs respectively. Arai *et al.* (1950), on the other hand, showed that 53 percent of the blubber around whales head contained whale oil and 65 percent was in the blubber around the back. Following to these oil rich parts the muscle around lumber to tail flukes, ventral grooves and/or abdomen contains rather rich (Feltmann *et al.* 1948) but less than 20 percent or so of whale oil. That is, the potential in preserving the whale oil as the energy source would be reduced to about 1/3 when it is compared with oil rich parts, and the amount of whale oil from an individual must be more greater than usually expected, whereas their importance as the energy source for locomotion would be less than the blubber oil, since most of whale oil preserved in bones or some other parts other than the blubber is considered to be unlike from physiological reasons to be consumed for the purpose of locomotion.

It is well known fact that whales caught in the beginnings of Antarctic whaling season show slender body trunk due to not only their thin layered blubber but also possible consumption of oil and fatty substances preserved in the whole body. Considering on this fact along with a comparison in metabolic physiology found in another animals, the whale oil preserved in the tissues other than the blubber would be consumed to some extent as the energy source for locomotion. And if we assume some physiological analogy between whales and human body (Yoshikawa, 1959), whales under some peculiar occasions or situations may consume not only their oil but also do even proteins of body tissues.

Whale bones also contain a considerable amount of whale oil, but it is presumably not consumable as the energy source for locomotion by reason of the function of bones themselves. The strength of animal bones is the function of their sectioned area and it increases only by following after a square number relations with body length whereas body weight of animals which must be suspended by the bones increases by cube number relations. Although the whales, a typically well adapted animals for aquatic environment, do not need such strength as terrestrial animals, and the bones of whales are not structured well like those animals. Then the function or physiological process which makes the strength of bones reduce much by consuming the contained whale oil may have to be kept as little as possible. Still more, the deposit of whale oil among many organs seems to occur firstly in the internal organs, fatty layer and then in the bones by this order (Omura *et al.* 1942). This fact also supports the assumption that whale oil preserved in the bones seems to be hardly consumed as the energy source for locomotion.

From these discussions it would be reasonable to consider that there are some still more amount of consumable whale oil in living animals while some are not available as the energy source for locomotion. As it was described previously the whale oil only from the blubber can make the whales swim for 20,000 km or thereabouts. Then if some additional energy source for locomotion is expected, the distance could be moved potentially without reducing any physiological functions such as a malnutrition in large rorquals would be somewhere between 20,000 Km and 30,000 Km. On the other hand, Mackintosh (1966) supposed the migrating distances covered by large rorquals must be somewhere between 1,000 and 3,000 miles. These figures, however, correspond to only about 17 to 50 degrees of latitudes, and are considered rather under estimations.

There are no ways to prove how much extent the energy cost obtained by an extrapolation for large rorquals is appropriate or not. The estimated energy cost of about 1/5 of dolphins, however, can be discussed little more in the point of metabolism of animals. The basal metabolism of animals closely relates to the body surface area. Bottlenosed dolphin, *Tursiops truncatus* which weighs 100 Kg. has 1.85 m^2 of body surface area (Ridgway, 1972). If it is assumed that the surface around its head occupies about 20 percent of the whole, the surface around body trunk would be 1.5 m^2. On the other hand, 18.1 meter fin whale has about 90 m^2 of body surface area which actually corresponds to 13.5 meter long of body trunk only, and weighs 34 tons. Comparing with these figures of both bottlenosed dolphin and fin whale, the ratio in body weight shows 340 times larger in fin whale whereas only 60 times in the ratio of body surface area. The well averaged number of respiration in dolphins and phocids is 2 to 3 $\text{respirations}\cdot\text{minute}^{-1}$ while it is 1 to 2 $\text{respiration(s)}\cdot\text{minute}^{-1}$ in fin whales (Scholander, 1940). The large whales consume comparatively little amount of oxygen than the dolphins, and are able to swim under very well controlled energy coefficient. In this respect a slight change in body length or body surface area affects well on the whole metabolism of animals by following after the Rubner's surface law. Actually, since the body surface area of fin whale would reduce to some extent while they are enroute through migrations, the energy cost for locomotion may also reduce. This may be one of the reasons why large rorquals perform seasonal migrations by less energy expenditure than the dolphins and also possibly than the figures estimated by extrapolation. It is possible, therefore, that the energy cost and body weight relationships in large whales may not expressed by a simply extended regression lines but by a slightly curved or the folded lines with different coefficient.

However, these relations which have been known in another animals are well expressed by setting up a simple regression even for between mouce and horse. Concerning to this extrapolating problem, Schmidt-Nielsen (1972) described as "Although we have no inherent right to extrapolate from the salmon to the dolphin, we can safely assume that both animals are hightly adapted and effective swimmers, and extrapolating from a 1-kilogram salmon to a 90-kilogram dolphin is not unreasonable ". Similarly it was considered that large whales also could be extrapolated onto the regression line. In concluding this section the followings may give a standards: the energy cost for swimming locomotion in average sized fin whales is 0.02 $\text{Kcal.}\cdot\text{Kg}^{-1}\cdot\text{Km}^{-1}$, and overall distance which could be moved without feeding both on breeding grounds and on the way would be somewhere between 20,000 km and 30,000 km.

MIGRATIONS OF WHALES AND ESTIMATED DISTANCE TO BE PERFORMED

Generally recognized destination for migrating rorquals is " warm temperate or tropical seas " if not exclusively. Therefore, it would be worth to discuss whether or not the distance which was estimated by the available amount of energy for locomotion and its cost for swimming in fin whales is an accessible distance along with the known evidences regarding the migrations of whales to the warmer waters.

If we assume that the whales leave the Antractic feeding grounds at 60°S and start their northbound migrations heading for the equator and again return to the start line along the same meridional pathways, the distance covered by this round trip is 13,320 km. That is, the whales are able to move or play around more for only 7,000 km or corresponding energy expenditure. Since little is known on the pattern of daily life in large whales except several but fragmental observations (e.g. Schevill and Watkins, 1966; Cousteau and Diolé, 1972), it seems still in some difficulty to estimate even an integrated distance performed by a whale in a day. It is, however, reasonable to consider that whales are unlike to swim straight but trace a quite complicated pathways which gives far more doubled distance than is considered by an actual situation, since the daily behavior of animals may possibly have not necessarily any objects from one end to the other.

Following fact is very suggestive concerning to the daily movements of whales. In the whaling ground which is one of the terminal places in whales migrations, where the whales stay for some duration within a certain range to feed by moving back and forth, it is often experienced that the whales having been spotted in the previous evening are hardly found again in the next day. In this case it is well supposed that the whales had moved for a considerable distance during the previous night. To make the matter clear it would be convenient to assume the case that those whales were sighted again after 3 hour scouting through surrounding waters at the speed of 15 knots. Then about 2 hours out of 3 hour scouting would be the component giving away from the starting point, that is, the whales moved at least for 2 hours as to give the distance between catcher boat and themselves. J.-Y. Cousteau attached a specially designed marks on the back of a fin whale to make him easy for chasing it through the night, and he observed that the whale usually continued to move at the speed of 6 to 7 knots though the whale stopped several times during the observations (Cousteau and Diolé, 1972, p. 72). Their observations give us a knowledge that the whale may considerably move around even through a night. From these facts it would be quite natural to consider that the whales are apt to move at least for several tenth miles within a night. If the whale migrates from 60°S to the equator at 10 knots in swimming speed, 15 days would give them enough time to get to their destination; the terminal sea regions of so-called " warm temperate or tropical seas " where the whales stay for the rest 4 to 5 months. There is no reason to doubt that the daily behaviour of whales differs much both in feeding and breeding grounds. The estimated distance for nocturnal movements in large whales, 30 miles per 10 hours agrees well with the swimming speed found under the natural or undisturbed conditions, and that distance would be a minimum or close to the lower extremes, since it was estimated being based upon a possible zigzag movements. The whales seem to move at least about 72 miles (=130 km) in a day, and 15,000 to 16,000 km would be the integrated distance covered during 4 month stay in the terminal sea regions.

Accordingly the grand totaled distance which is performed through 5 month round trip migrations would be at least some 28,000 to 30,000 km. As it was shown previously the 18.1 meter fin whale is able to move only for 20,000 km or thereabouts by expending its blubber oil of 2.0 cm thickness, and may have to face a shortage of locomotion energy unless the whale oil or fat of another source was consumed supplementally. These estimations suggest that even well adapted whales for aquatic environment are hardly possible to perform migratory journey to those " warm temperate or tropical seas ".

However, if the supply of whale oil from the muscle and connecting tissues in addition to that from the blubber could be considered, and/or if slightly more than 2.0 cm thick of the blubber oil was consumed, the budget of energy expenditure required for those migrations would be well balanced. Actually the large rorquals distribute all over the world oceans and most of them sternly keep 4 to 5 cm thick of the blubber even after a very long journey for 5 to 6 months. On the other hand, there are actually the whales which keep very thin blubber even in late March, the time they have to leave the feeding grounds for breeding. These very slender bodied whales seem unlike to consume their blubber oil any more as the energy source for locomotion, since it may cause some physiological difficulties to reduce their blubber oil deposit, and the statistics on the thickness of the blubber also suggest its unlikelihood. Then slender bodied whales have to change or modify their migratory pattern and fashion of life, which may somewhat different substantially from that of the majority of normally fatted whales. For instance, poorly fatted whales cannot but remain within some migratory range and/or have to migrate into some productive and organism rich coastal waters where they can feed to a certain extent. The whales may have to swim so economical basis as to reduce the energy expenditure as little as possible since the energy for locomotion in any kind of whales does not seem to have been provided sufficiently. It is well known fact in the Antarctic feeding grounds that the whales move longitudinally for rather widely ranged zone extending for two or three of six sectors, whereas they are apt to follow the cource along the continent or islands in breeding migrations, and little of them migrate into the real mid oceans. These general tendencies are well observed by whale sighting at high seas and by the recovery of whale marks (e.g. Dawbin, 1959; Ivashin, 1971; Mözer, 1971). Whales which have distributed rather randomly within the feeding grounds are apt to concentrate along their migratory pathways but it is far sparce and loosely packed gatherings like a stream and is hardly comparable to so-called school or herd of animals. Humpback whale apparently shows some gatherings as a unit of local populations enroute their breeding migration (Dawbin, 1964; 1966), but these kind of whale movements if not clear like the humpback whale may also be found in rorquals. These general tendency in whale movements or migratory habits may closely related to the productive seas or the occurrence of rich standing stocks of organisms, and most of which is found in the marginal waters along the continent or islands. A fertile zone such as an equatorial divergence regions too attracts whales even if it is found on high seas. Considering on the food and feeding of baleen whales, Nemoto (1959, p. 281) concluded that the movement of whales in the North Pacific and Bering Sea regions is closely related to the geographical characters such as the shape of the sea, and fin whale occurring in those waters can be considered as " ocean and marginal denizen ".

The energy for locomotion in rorquals migrations seems to be balanced on the whole. It is, however still desirable to minimize the energy expenditure as little as possible since an amount of whale oil preserved in a body is far less for a luxuariant consumption. Therefore, it would be better and/or appropriate for most of migrating whales to take linear like pathways both in north- and south-bound migrations.

For instance, little number of whales in the southern waters of Australia would migrate to the tropical African coast by crossing the Indian Ocean diagonally. Sperm whales evidently swim at least 600 miles within 8 days between the Antarctic and South African coast (Clarke, 1972). This fact strongly suggests that the whales on the whole, once they begin the migrations, can travel very rapidly even though they feed on squids on the way.

The migrating whales are considered to be apt to invade into the almost same or very close region of terminal seas every season. In the coastal waters off Abashiri, Hokkaido, there once was a fin whale which was easily identified by its characteristically well damaged dorsal fin, and this animal used to be spotted if not entirely in the same place at least in the beginning of season (Omura and Kawamura, 1968). Similar evidence or possibility is also documented in the Antarctic fin whale of Area II based on the recovery of whale marks (Brown, 1962, p. 14), and, these situation was expressed as " something like a migration route " (Mackintosh, 1966) which is somewhat similar to " corridors " called in the migration of birds (Orr, 1970). Since it would be hardly possible to modulate the season and place of migrations with considerable accuracy, the migration of whales as a everlasting phenomenon could be recognized only when the migrations of whales were assumed as follows; in order to perform the migration with those above mentioned kinds of accuracy, the whales may have to migrate at full or near at full speed without wasting time on the way by following well known migratory pathways along with the aid of well experienced navigation.

GENERAL CONSIDERATIONS IN CONNECTION WITH THE DISTRIBUTION OF WHALES

As it has been discussed in the previous section, the budget of energy expenditure for locomotion in large rorquals seems rather complicated, and cannot but consider the subject analogically by the aid of some assumptions, since there are so little suggestive evidences which were obtained in the field observations. For instance, it is still beyond of our knowledge where and when the perturition and mating of rorquals will actually take place in those vast " warm temperate or tropical seas ". No other evidences except those have been refered to seem to be left for the further discussion, and following discussions are a kind of conclusive view points in which the movements of whales is considered along with the general features of the distribution of whales.

In rorquals the pattern, habits and the behaviours in the way of life are quite naturally and generally recognized as a regular migrators which move between cold polar seas and warm temperate or tropical seas, and these are considered appropriate from the overall budget of their energy expenditure for locomotion, since majority of whales are likely to be well balanced in this instance. However, an amount of whale oil or fatty substances preserved in the whales body considerably varies with the physiological status or biological characters endowed with each whale species. Still more, the wild animals would presumably have to keep afford in the energetic budget to make their behaviour more fruitsfull under the wild environment whereas the budget in energy expenditure actually seems to be very tight. In this instance, it would be reasonable and natural to suppose that the whales usually must feed to a certain extent even if they are on the way of migrations. California gray whale which are supposedly well balanced in the energy expenditure can perform seasonal migration without taking any foodstuff through their round trip migrations (Rice and Wolman, 1971). Even in gray whale, however, feeding activity seems to be not unusual at least in their southbound migration close to the regions of their breeding grounds (Sund, 1975). The idea that more rorquals do not seem to feed or be under almost starved condition during their migrations (e.g. Jonsgård, 1966; Mackintosh, 1966) would be hard to believe if not exclusive. In general the metabolic rates increase high in the warmer environment than in the colder one, and this may become serious in small younger animals since they swim under relatively high energy cost for locomotion than the well aged animals. That is why large rorquals do not concentrate much in mid oceans where a monotonous but well stabilized environment prevails, but more commonly found in some coastal or offshore waters of structural complexity, that is, the region of high production or rich in standing stocks of organisms which is undoubtedly advantageous for occasional feeding. Two ways of the possible status for migrating rorquals whether they concentrate or disperse in the breeding grounds (Mackintosh, 1966) are quite suggestive on the whole. In the latter instance the evidence that many whales are spotted in offshore waters within a certain ranges in lower latitudes strongly suggests a possible feeding activity of whales as the case explained by Clarke (1962). Even planktivorous species of baleen whales apt to feed on shoaling small fishes and their larvae according to the time and place. A typically similar situation is found in the comparison for food habits between the North Pacific and the Antarctic (Nemoto, 1959; Kawamura, 1973, 1974). That is, there reason to believe that the baleen whales in breeding grounds may feed on some organisms such as the larvae of skipjacks, tunas and of many other warm water fishes. By taking these general situations along with presumed physiological conditions and feeding habits in large rorquals into consideration, it seems reasonable to believe the food intake during breeding migrations as the comments by Dr. Sergeant. (Mackintosh, 1966, pp. 143–44).

One of explanations why rorquals migrate to those " warm temperate or tropical seas " is an advantage for breeding especially for the safety of newborn calf of very thin blubber and make them easy to keep body temperature from chilly environment. Antarctic minke whale, *Balaenoptera bonaerensis*, likely to show rather irregular breeding cycle (Ohsumi, personal communication) than the other rorquals which show an approximately one-year cycle. In this instance some individuals of the Antarctic minke whale may have perturition during their stay within the colder region, and how is the case for the calving in bowhead whales, *Balaena mysticetus*, explained. In this respect the Kellogg's pointing out that " it is not the sea temperature but the food conditions that induce whale migrations " would be quite suggestive itself (Kellogg, 1929, p. 45). Kellogg's idea also make us consider that the migrations of whales is desirable to be treated by each whale species.

Results of whale sighting in the Atlantic and Indian Oceans show the year round distribution of large whales in the temperate and tropical regions (e.g. Townsend, 1933; Brown, 1957, 1958; Zenkovich, 1962). In those waters population of whales may be consisted of the several different origins: some may come from newly migrated population and the other may somewhat from endemic or locally separated population such as the fin whales in the East China Sea (Fujino, 1954; Ichihara, 1957) and sei/bryde's whales in the northern waters off North Island of New Zealand (Dawbin, 1959, p. 15). Those locally separated whales seem to stay there throughout the year, and consequently, may have to feed on regardless the seasons. Then it is quite unlikely that the only newly migrated whales do not feed on among those taking food in those local waters. In the waters off California blue whales are usually seen throughout the year (Kellogg, 1929), and they can feed on sardine and prawn in San Quentin region, lower California (Scammon, 1874).

Apart from the seasons, great number of large whales are apt to concentrate in the zones between 30° and 40° of both south and north latitudes of the Atlantic and Indian Oceans (Brown, 1957; 1958), and humpback whale, *Megaptera novaeangliae* stay in the offshore waters of lower latitudes throughout the year along the west coast of South America. In the Arctic regions of the North Atlantic some humpback whales stay throughout the winter (Kellogg, 1929). One of another instances is Pacific black right whale, *Eubalaena gracialis* which are found close to the ice-pack in the Okhotsk Sea and Bering Sea regions, and then fin whale in Queen Charlot Sound, north of Vancouver Island of approximately 50°N during February (Scammon, 1874). These facts indicate that the actual pattern of distributions in large baleen whales, if not entirely, do not always coincide with those ideas generally known as migration cycles. The " tropical seas " is considered unlikely for most whales as to be a destination being invaded after the painstaking long journey, and this make us even doubt whether or not those habits are inevitable for carrying out an appropriate life of whales. In the general fashion of the distribution of whales, however, age, sex, and physiological status of each whales would relate to their migrating movements though the details on this subject have been known little except the case in sperm whales, *Physeter catodon*, which once had caught in all over the world oceans and are known as very highly socialized animals in the mode of line among large whales (e.g. Mackintosh, 1965; Gaskin, 1970; Berzin, 1972). Then the structure of population in baleen whales which occur in " warm temperate or tropical seas " may be a subject to be known in future. The baleen whales may have to feed to a certain extent in food rich waters regardless seasons, kind and origin of whales stocks. Some blue whales are believed to feed actively in the waters south and south east of Madagascar, which are located far north from the Antarctic feeding ground proper (Gambell *et al*, 1974). The ideas of both non-feeding activity and seasonal migrations in large whales are not primarily the phenemon of two sides of a thing but independent each other, if not, the actual features in the distribution of whales would hardly be explained.

CONCLUSION

Some whales keep rather sufficient energy source to perform the migration between cold feeding ground and warm breeding ground while others are hard to accomplish their migrations unless they take food to some extent on the way. Migrating population of whales is composed of individuals which greatly vary in energy potentials. On the whole the budget of energy for locomotion does not always balance well or clearly unbalanced. Under these circumstances some whales may migrate to the tropical seas and others may have to take different pathways of less far or, have to modulate the ways of life although some of them will be fatty in another year and can migrate much distance as the standards. It would be convenient to suppose that whales feed primarily on the way of their breeding migration to get an additional energy for locomotion although the extent of feeding may actually vary with each individuals. Some whales which had not preserved much whale oil cannot but follow the ways along more productive and food rich waters, and/or have to remain within the waters of rather higher latitudes throughout their breeding migration. The migrations of whales, therefore, seem to be a stream like movements of animals as called by Mackintosh (1965), and may be performed with much flexibility from variable fashions of migratory movements. The " warm temperate or tropical seas " which have been believed as the destination of breeding migration still remains as an ambiguous conception. As it has been discussed, however, whales keep potential for making a round trip which corresponds to 120 degrees or more of latitudes, and consequently, the whales in the archipelago of Micronesia, for instance, cannot always be considered as the stray from local population but also possible to consider as the migrants from the polar regions. In this instance, mingling of the populations between northern and southern hemispheres at one of their terminal sea regions would be quite possible but considered the case to be very little. Kellogg (1929), however, suggested much the possibility of mingling in the case of blue whale populations.

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