Body Fat Condition in Northeast Atlantic Fin Whales, Balaenoptera physalus, and Its Relationship with Reproduction and Food Resource

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Age Dynamics

Body Fat Condition in Northeast Atlantic Fin Whales, *Balaenoptera physalus*, and Its Relationship with Reproduction and Food Resource

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Measurements of body girth, blubber thickness, and the lipid content of blubber, muscle, and visceral fat of Icelandic fin whales (*Balaenoptera physalus*) showed a consistent pattern of body fat condition for each sexual class in all years between 1977 and 1982, with pregnant and anoestrous females being fattest. There was a trend of increasing body fatness between 1977 and 1982 which is supported by data on oil production from the catch. Parallel to this was an apparent increase in food abundance and whale fecundity.

Les mesures qu'on a prises chez des rorquals communs (*Balaenoptera physalus*) d'Islande pour déterminer le diamètre de l'animal, l'épaisseur du panicule adipeux et sa teneur en lipides ainsi que le pourcentage de gras dans les muscles et les viscères ont montré qu'il y avait une tendance uniforme dans la teneur corporelle en gras pour chaque groupe sexuel à chaque année de 1977 à 1982, et que les femelles en gestation et en phase de repos étaient les individus les plus gras. La quantité de gras a eu tendance à augmenter entre 1977 et 1982, fait qui est appuyé par les données sur la production de l'huile tirée des prises. Parallèlement, il y a eu une augmentation sensible de la quantité de nourriture disponible et de la fécondité des baleines.

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An average catch of 242 fin whales (*Balaenoptera physalus*) has been taken annually off S.W. Iceland since 1948 (Lockyer 1981a). The season normally lasts through the summer months of June to September, when the whales are feeding locally on swarming euphausiids, notably *Meganyctiphanes norvegica*.

North Atlantic fin whales are generally believed to exhibit the same migratory and breeding habits as their Southern Hemisphere counterparts (Lockyer and Brown 1981; Lockyer 1984; Lockyer et al. 1977; Martin 1982) which have an annual migration towards polar waters in summer for feeding, and towards more subtropical and temperate waters in winter for breeding. The basic reproductive cycle is a 2-yr one comprising 11 mo of gestation (with conception and birth taking place in midwinter) followed by 7 mo of lactation so that the calf is weaned on the feeding grounds in the summer following birth. Whereas Brodie (1975, 1978) and Mitchell (1974) observed that coastal northwest Atlantic fin whales off Nova Scotia, of which some possibly originate from Newfoundland, may be locally resident and feeding for most of the year, I am considering a different fin whale stock on the eastern side of the north Atlantic for which I am assuming some seasonal behaviour.

The catch is biased by International Whaling Commission (IWC) regulations (IWC 1950, 1983) which impose a minimum size on the catch of 50 ft (15.2 m), and prohibit the take of calves and any adult accompanying a calf (i.e. a lactating female). In addition, in the Icelandic fishery, the belly is cut open at sea to cool the body, which usually results in loss of fetuses and, frequently, damage to the reproductive organs. This practice influences the measurements of girth, and the detection of pregnancy.

An increase in body fatness throughout the feeding season has been shown for Southern Hemisphere fin whales, especially pregnant females (Lockyer 1978, 1981b, 1981c). Further, the difference in fatness between pregnant and lactating females supported calculations of the energy drain during reproduction, mainly due to the costs of lactation. For Icelandic fin whales, the extra cost of reproduction above that required for maintenance would be 23–32% for adult females, depending on age, over the 2-yr cycle. On an annual basis, the extra food energy required for pregnancy and lactation (assuming 80% assimilation efficiency) would thus represent 16–23% and 29–41% of total intake, respectively. The costs of reproduction are energetically expensive and the underwriting fat reserves must be laid down during the summer feeding period. Presumably the rate of deposition and the total deposit are affected by food availability.

My objective is to demonstrate that in addition to variation in body fatness between individuals of different reproductive status (Lockyer et al. 1985), year to year variations occur, which can be linked with food resource and ultimately with fecundity.

Materials and Methods

Fin whale tissues were collected for total lipid content analysis in 1978 and 1981 during the period July–August at the coastal Icelandic whaling station, Hvalur H.F. Blubber and muscle were sampled from the posterior dorsal position (determined as most suitable for indicating body fat condition by Lockyer et al. 1985). Blubber was collected as described in Lockyer et al. (1984), with about 100 g of the attached underlying muscle. About 100 g each of visceral fat from the cardiac and intestinal regions, liver, and kidney was also sampled. All tissues, once sampled, were deep frozen and maintained at −26°C. Postmortem times ranged from approximately 13 to 26 h.

Lipid extraction was by the method of Bligh and Dyer (1959) using chloroform−methanol, as described by Lockyer et al. (1984). Muscle, visceral fat, and the visceral organ tissues were homogenised from 0.5- to 1.0-g pieces of frozen tissue cut from the innermost parts of the samples (to minimise effects of autolysis and volatile lipid loss). All lipid contents are expressed as percent lipid weight per wet weight tissue.

Anatomical measurements on length, girth, and blubber thickness were also made. Blubber thicknesses were mainly taken in situ, at the same site as the tissue samples. Body girth was determined by measuring half-girth, while the whale lay on one side on the flensing plan, from approximately the mid-length position assessed as most sensitive for detecting changes due to fattening (Lockyer et al. 1985). Two main problems existed here: some body shape distortion occurred from the whale resting on a hard surface, and occasionally, parts of the carcase protruded through flensing cuts. Both factors, especially the latter, caused the girth to be overestimated by 5−8% (Lockyer et al. 1985), and girths collected when extensive flensing cuts were present were not used for analysis. Body length from jaw tip to tail fluke notch, measured in a straight line, was also recorded for each whale.

Complementary data collected by or on behalf of the Sea Mammal Research Unit (SMRU), Cambridge, were available on blubber thickness measured from one standard position on the posterior flank of every whale caught each season from 1977 to 1982 inclusive during June−September inclusive. Factory production data on oil yield for the 1977 to 1982 seasons (years of comparable data) were kindly made available by Hvalur H.F. These data covered periods of 14−17 wk from the end of May to early October, and included total rorqual oil production for both fin and sei whales combined.

Data collected by or on behalf of SMRU on presence of a corpus luteum in the ovaries of mature females taken between June and September each season, 1976 to 1982, were available. The presence of an active corpus luteum was taken to indicate a likely pregnancy, and certain ovulation. Absence of a corpus luteum but presence of corpora albicantia was indicative of the mature anestrous condition.

Data on euphausiid abundance were supplied by the Institute of Marine Environmental Research (Natural Environment Research Council) in Plymouth, England, from the continuous plankton recorder (CPR) system, collected during 1971−82. The system operates with plankton recorders being towed by merchant ships and Ocean weather ships along standard routes at monthly intervals throughout each year. The plankton recorders are towed at a standard 10-m depth with an aperture 12.5 mm^2. Filtration operates through a slowly moving band (bolting cloth, 24 $meshes \cdot cm^{-1}$), held in place by a second band, at a rate of 100 $mm \cdot 10$ mL of tow^{-1}, when 3 m^3 of seawater is filtered off into a storage spool of formalin. The collected samples are sorted and analysed according to the data processing system described by Colebrook (1975). The CPR system has been operational for over 45 yr and represents a unique time-tested long-term record of plankton availability in the north Atlantic. Data analysed here were from samples collected in the region bounded by 59−63°N and 31−43°W in the Denmark Strait, representing part of, but an unknown proportion of, the feeding area for the Icelandic whales. Data from the months July−September were selected for analysis, these representing the relevant summer period for which a complete monthly series of samples existed for all the years. The euphausiid abundance data were pooled for the entire period 1971−82 and a mean value ±SD obtained. Each season's estimate of abundance was then represented in units of standard deviation of the mean for the 12-yr period to gauge relative seasonal abundance over this time span.

Data on stomach contents of Icelandic fin whales caught in 1977−82 inclusive, collected and examined by or on behalf of SMRU, were also available for analysis of feeding activity. Data from June to September each year were combined and analysed for proportion of empty stomachs and food type.

Results and Discussion

Anatomical Measurements

Data and analyses on body length, girth, and blubber thickness have been presented by Lockyer et al. (1985). They concluded that significant differences existed between the reproductive classes, with adult females, usually the pregnant ones, being thickest in girth and in blubber thickness, followed by sexually mature males, immature females, and, thinnest, immature males. The whales in 1981 had significantly thicker blubber than those examined in 1978. Despite significantly smaller body lengths for all sexual classes in 1981 compared with 1978, and significantly thicker girths for all sexual classes in 1981 compared with 1978, a comparison of the body length − girth regressions for each year indicated that the two slopes were significantly different, with 1981 whales thicker regardless of length. The concomitant increase in blubber thickness, however, is not sufficient to account for the massive girth increase in 1981. This latter increase may be attributable to body fat being deposited elsewhere, presumably in muscle and in and around visceral organs.

Biochemical Analyses — Lipid Content of Body Tissues

The variation in mean lipid content in blubber, muscle, liver, and visceral fats is given in Table 1. The blubber lipid content does not appear to vary significantly between reproductive classes within a season, but 1981 shows a 30% increase over 1978 ($p < 0.01$, two-way ANOVA). The muscle lipid content shows more variability between classes, although 1981 is again higher for most individual classes. The juvenile males have least lipid, followed by immature females. The mature pregnant and anestrous females have most. A two-way ANOVA (Table 1) indicates that the seasonal difference is also highly significant for muscle ($p < 0.01$), and although there is no significant difference between reproductive classes for blubber, in the muscle there is a highly significant difference between reproductive classes when adult males are excluded ($p < 0.01$). The single lactating female in each season has lowest blubber lipid content of all whales.

Neither liver nor visceral fats appear to vary between classes (Table 1). There is limited sampling in 1981 although for individual classes, the visceral fat in 1981 may be increased in lipid content over 1978.

TABLE 1. Mean ± SE lipid content (expressed as percentage of wet weight) of body tissues of Icelandic fin whales.

Sex	Sexual condition	Posterior dorsal blubber 1978	Posterior dorsal blubber 1981	Posterior dorsal muscle 1978	Posterior dorsal muscle 1981	Liver 1978	Liver 1981	Visceral fats 1978	Visceral fats 1981	Sample size 1978	Sample size 1981
M	Imature	53.2±7.9	70.6±1.5	7.8±4.3	12.4±1.6	3.2±0.7	Nil	57.5±5.7	Nil	3	5
M	Mature	52.7±11.6	72.5±2.4	15.6±6.4	11.5±1.3	3.6±0.7	Nil	50.5	62.1±8.6	4	5
F	Immature	58.5±9.1	71.0±1.2	15.8±2.8	21.2±0.7	3.5±0.4	Nil	54.2±12.7	Nil	3	6
F	Mature, anoestrous	65.5±0.3	76.8	21.6±10.1	29.3	5.2±3.0	Nil	63.8±12.2	Nil	3	1
F	Mature, pregnant	45.0±6.4	75.1±3.3	18.8±4.0	26.0±1.9	3.5±0.7	Nil	64.0±4.7	73.5	6	3
F	Mature, lactating[a]	39.4	59.0	17.6	18.5	3.3	2.8	62.8	79.3	1	1

NOTE: Two-way ANOVA. Blubber: sex ($p > 0.05$, v.r. = 1.31, df = 4/4), season ($p < 0.01$, v.r. = 29.52, df = 1/4); muscle (adult males excluded): sex ($p < 0.01$, v.r. = 81.83, df = 3/3), season ($p < 0.01$, v.r. = 71.76, df = 1/3).
[a]Excluded from analysis.

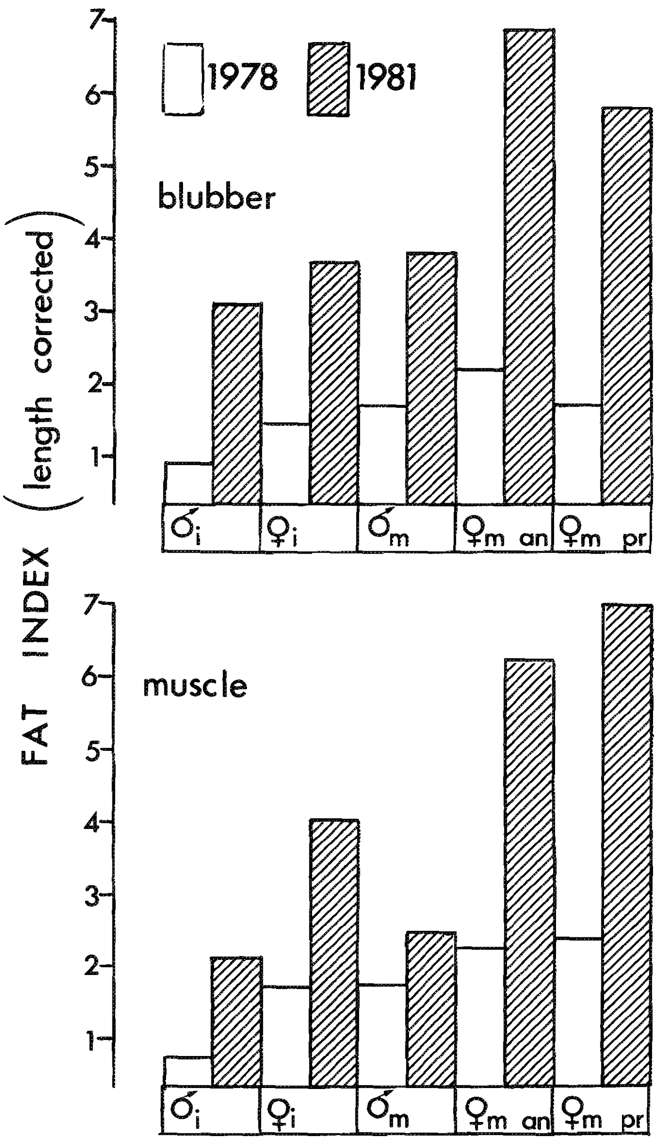

FIG. 1. Body fat condition in fin whales expressed on a relative basis for 1978 and 1981 by reproductive class. i = immature; m = mature; an = anoestrous; pr = pregnant.

Body Condition Assessed as a "Fat Index"

The anatomical and biochemical data demonstrate that all whales were significantly fatter in the 1981 season compared with the 1978 season. There is also an indication that pregnant and anoestrous females are fatter than other reproductive classes.

No actual weight data for tissues are available so that I have attempted to integrate the data on fat condition results in a measure of "fat index" defined as follows.

(1) Blubber: Mean body girth × mean blubber thickness × percentage lipid content of blubber

(2) Muscle: Mean cross-sectional area of the body inside the blubber layer × percentage lipid content of muscle.

Because of differences in body length between the classes of animals, and the length−girth correlation, the fat indices have been adjusted to a standard body length. This adjustment changes the basic results insignificantly between the seasons of 1978 and 1981 by 0.8−5.1% and does not alter the fatness pattern between reproductive classes. The length-adjusted fat indices are shown in Fig. 1.

The differences in body fat condition between 1978 and 1981 are clearly evident, and the relative fatness of mature females is very marked in 1981. In 1981, the muscle as well as blubber is notable as a fat store in females.

Some questions still remain regarding actual differences in fatness both between seasons and between individual reproductive classes. Despite sampling periods in both 1978 and 1981, individual reproductive classes may, by analogy with the Southern Hemisphere stocks (Lockyer and Brown 1981), arrive at different times during the season, so that whilst precise information is unavailable for Icelandic fin whales, one might expect the fatness of pregnant females to be exaggerated relative to other classes because of a slightly earlier arrival on the feeding grounds (Lockyer 1981b). Similarly, juveniles frequently arrive later than adults, so that again the fatness of adults might be overemphasised. Consequently it is possible that these data are slightly biased.

Independent Assessment of Fatness

An attempt to examine the fattening process both over the entire summer season and over several years was made by

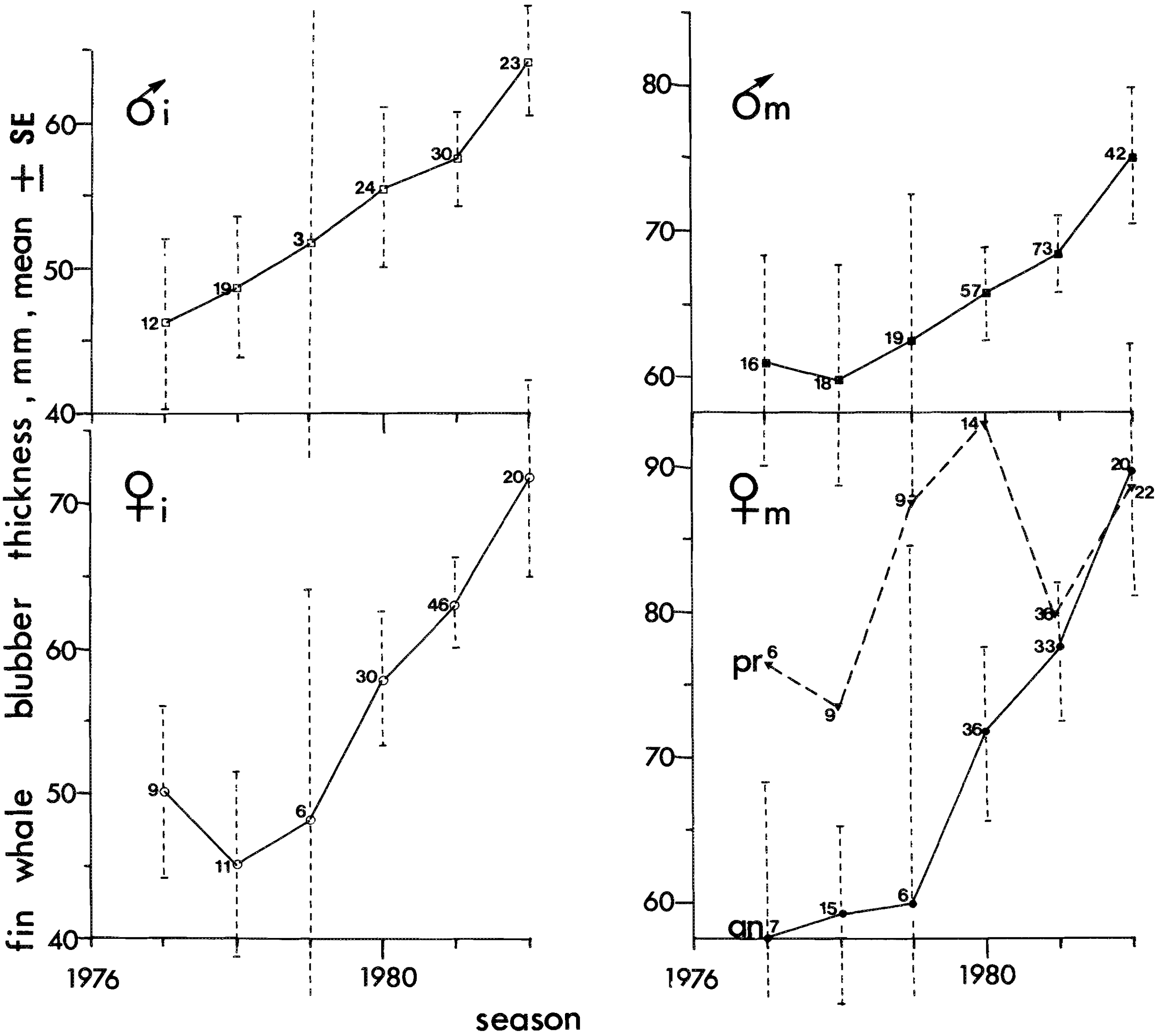

FIG. 2. Blubber thickness on the dorsal flank in fin whales during 1976–82 by reproductive class. i = immature; m = mature; an = anoestrous; pr = pregnant. Sample size is given beside each mean value.

analysing independently collected data on blubber thickness and oil production from the same Icelandic stock of fin whales during the period 1977–82 inclusive.

Figure 2 shows mean blubber thickness by reproductive class. The means (±SE) indicate an increase in fatness between 1977 and 1982, complementary to the results given for 1978 and 1981. Again, pregnant females are the fattest animals.

The whaling company oil production figures were adjusted to allow for the variable proportion of sei whales (*Balaenoptera borealis*) in the catches by assuming an equivalent of (a) two sei and (b) three sei to each fin whale, based on the old Blue Whale Unit (Mackintosh 1965). Despite variations in sex ratio and size of whales of both species, different peak catching periods, and variability in meat quality each season resulting in changes in the ratio of frozen meat to oil production, all factors complicating the utilisation of the data, there is an increasing trend with year (Fig. 3), supporting the data on body fatness. Between 1978 and 1981 inclusive, a regression coefficient of 0.567 is significant at $p < 0.05$ ($t = 4.462$, df = 2).

These data on blubber thickness and oil yield therefore indicate that there has been an overall improvement in whale body fat condition between 1978 and 1981. They also confirm differences in fatness between reproductive classes.

Food Supply

An increase in body fat should be correlated with an increase in the available food. To test this relationship, I examined the data on stomach fill and euphausiid abundance.

The percentage of empty stomachs has declined between 1978 and 1981, and conversely the percentage containing food items, regardless of quantity, has increased (Fig. 4). The difference in stomach fill between 1977 and 1982 inclusive is highly significant, using a χ^2-test ($p < 0.001$, $\chi^2 = 45.95$, df = 4). Most seasons do not provide details on food quantity in a standard way, so that more elaborate analysis of stomach fill is not meaningful. Of all stomachs examined during 1977–81 inclusive, the euphausiid *M. norvegica* comprised 93.8–100% of the diet; no association of diet component and year was

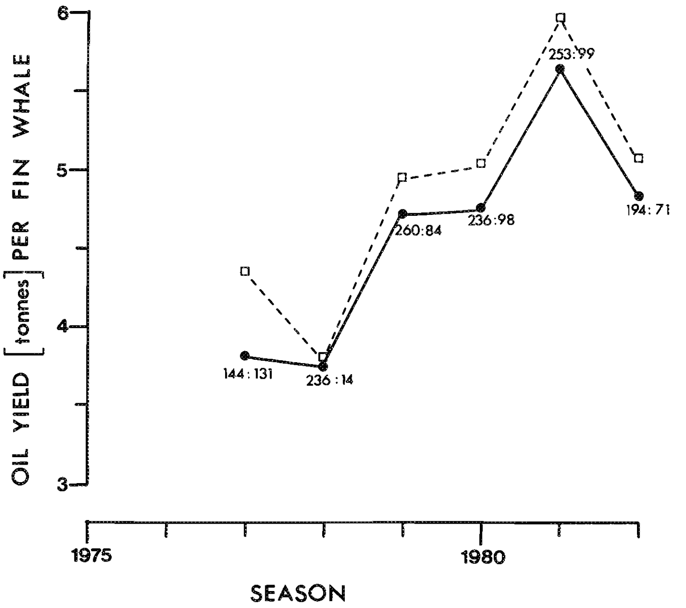

FIG. 3. Calculated oil yield per fin whale from factory oil production, 1977–82, at Hvalur H.F., Iceland. Fin whale to sei whale catch ratio: ●, 1 fin = 2 sei; □, 1 fin = 3 sei.

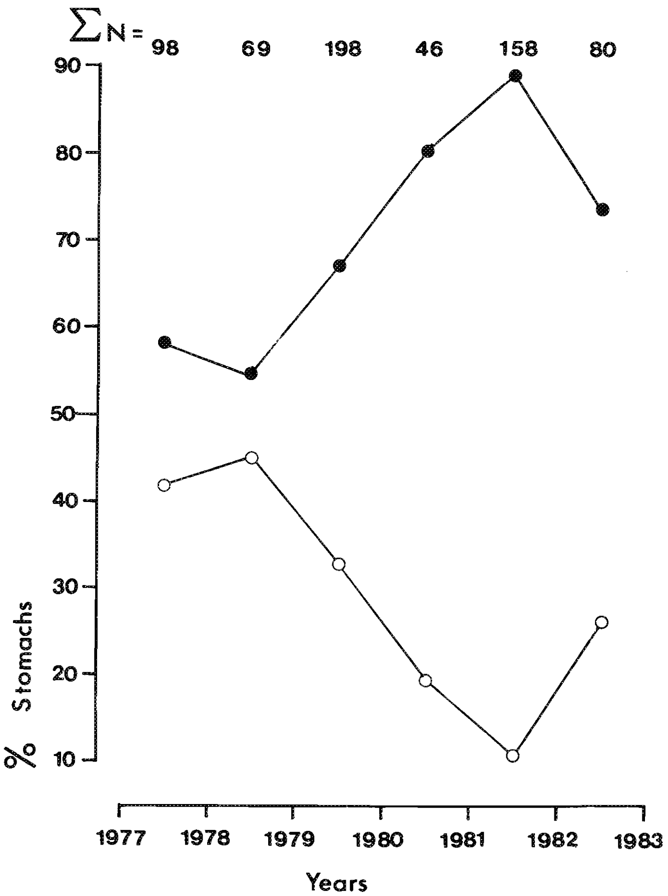

FIG. 4. Stomach fill of fin whales examined June–September inclusive during 1977–82 inclusive. ○, empty; ●, containing food.

found. Other food items included capelin (*Mallotus villosus*) and squid identifiable only from beaks or flesh. I conclude, therefore, from Fig. 4, that between 1978 and 1981, fin whales were increasingly successful in obtaining food.

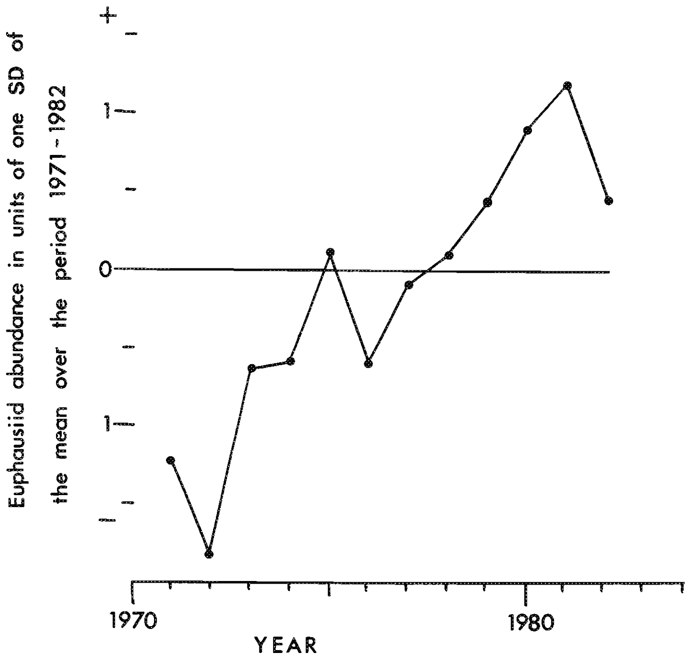

FIG. 5. Relative abundance of euphausiids in waters off S.W. Iceland during July–September in area bounded by 59–63°N and 31–43°W. Data by courtesy of IMER, Natural Environment Research Council, England.

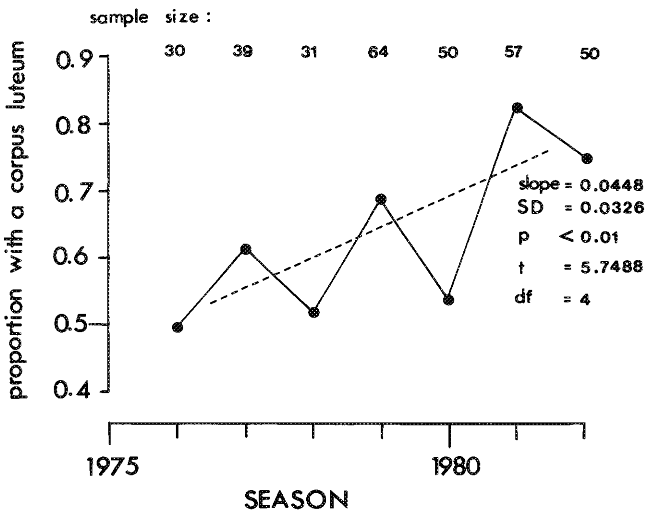

FIG. 6. Relative fecundity of female fin whales by season, 1976–82, gauged from the proportion of nonlactating females with a corpus luteum in the mature female catch.

Euphausiid abundance in the Denmark Strait (Fig. 5) appears to have been increasing between 1972 and 1981 with a crossover point from below to above average between 1975 and 1978, the upward trend between 1978 and 1981 being significant ($p < 0.01$, $t = 15.929$, df = 2), with a regression coefficient of 0.374. This trend appears to be reflected in the increasing body fatness during this period.

Absolute abundance of food may be affected by environmental factors (for example, water temperature, currents affecting productivity). Thus, investigating the annual abundance of prey from plankton recording during the feeding season of the whales may only be a weak indicator of actual availability of food to the whales. In 1981, however, ships reported that the sea areas of the whaling grounds during July appeared pink from the profuse swarms of krill.

Another obvious criticism of using a general euphausiid abundance as an indication of food supply is that whales consume mainly swarming euphausiids of a particular size, the predominant food species being *M. norvegica*, although fin whales are known for their opportunistic feeding behaviour (Kawamura 1980). The size of euphausiid consumed in 1977 was frequently recorded as a small larval form, different from the larger form normally observed in later years of sampling.

Ovulatory Activity as a Measure of Potential Fecundity

Figure 6 shows the proportion of nonlactating mature females in the catch, with a corpus luteum present in the ovaries, for each season from 1976 to 1982 inclusive. Despite an apparent 2-yr oscillation, there is an upward trend, and 1981 shows a large increase in proportion over 1978. Calculating a regression on the running means to dampen the oscillations, the slope of the linear regression, 0.0448, is significant at $p < 0.01$ ($t = 5.7488$, df = 4). It thus appears that there has been an increase in potential fertility in females over this time period.

Theoretical Prediction of Interdependence between Food Supply, Fat Storage, and Fecundity

Over a short period of consecutive seasons off Iceland, food supply, body fat condition, and fecundity have all increased significantly. The conclusion therefore is that improved body fat condition resulting from increased food resource may be the cause of increased ovulation rate.

I have calculated (Lockyer 1978, 1981b, 1981c) that the energy drain of the reproductive cycle, especially lactation, is considerable to the female. Production of a viable calf probably depends on the success of the summer feeding for adequate fat storage to cover these reproductive costs, because of the seasonal variations in the pattern of feeding.

The relative fatness of pregnant females observed here, compared with other classes, may be the result of energy storage necessary to meet such reproductive energy drain. Presumably, if feeding conditions and consequentially fat storage are poor in any one season, the female has few options: she may fail to ovulate, or fail to conceive, or fail to suckle the calf should pregnancy go to term; alternatively, the basic reserves normally required for maintenance may be preferentially chanelled into reproduction in order to carry a fetus and to complete lactation. This latter alternative might prolong the period of anoestrus and hence the reproductive interval while the female rebuilds her energy reserves — a situation that should be apparent in the proportion in the catch of ovulating females (females with a corpus luteum), assuming most such females become pregnant. Conversely, it may be speculated that the 2-yr cycle could be reduced in years of high food availability, the ultimate time-limiting factor being the length of gestation.

While variations in body fatness cannot yet be translated into actual quantitative energy reserves for individual whales because blubber fat, muscle, and internal organs were not weighed, future studies will investigate intraseason variation in body fatness, covering the entire summer feeding period, and will monitor the interrelationship of body fatness, food supply, and fecundity.

Acknowledgements

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