PARASITES OF SKIPJACK TUNA, *KATSUWONUS PELAMIS*: FISHERY IMPLICATIONS

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ABSTRACT

The numbers of 26 types of parasites were counted in 878 fish, of which all but 3 were from 14 areas in the Pacific. Data from the 22 most reliable parasites gave no evidence of discrete stocks of skipjack tuna in the Pacific, either when analyzed singly or when using combinations of parasites in multivariate analyses. New Zealand fish carried many tropical parasites, particularly didymozoids, in numbers similar to fish caught in the tropics, indicating that the bulk of these fish had recently migrated from the tropics. The number of *Tentacularia coryphaenae*, a larval tapeworm, was positively correlated to fish size in the tropics. In New Zealand, however, fish over 55 cm carried about the same number of *T. coryphaenae* as fish 45 to 55 cm, suggesting they had left the tropics when they were 45 to 55 cm and had not returned.

Analysis of the numbers of parasites from particular schools suggested that school members stayed together for several weeks but not for life.

The use of parasites to delineate stocks for management purposes is a well-established technique. For a comprehensive review of the many examples see MacKenzie (1983).

The skipjack tuna, *Katsuwonus pelamis*, is one of the most valuable fishery resources of the central and western Pacific. At least 50 species of parasites have been reported from it. The distribution of only one, the hemiuroid digenean *Hirudinella ventricosa*, has previously been investigated. In the Atlantic, Watertor (1973) found it in 7% of skipjack tuna off West Africa, 40% off Brazil, and < 1% off Florida. In the Pacific, Nakamura and Yuen (1961) found it in 21% of skipjack tuna off the Marquesas and 34% of fish from Hawaii. Sindermann (1961) pointed out that analyzing the distributions of combinations of parasites may provide more information than the examination of individual species. That, in general, has been our approach here.

In addition, school-school variation in parasite numbers was studied to determine how long schools stayed together, and secondarily to evaluate the degree of permanence of the parasites.

MATERIALS AND METHODS

Of the 878 fish dissected, 386 were collected by the *Hatsutori Maru* on charter to the South Pacific Com-

mission (SPC), 246 by the New Zealand Ministry of Agriculture and Fisheries (NZ), and the remainder by other governments and fishing companies (see Acknowledgments). Fish were obtained from 15 areas (Fig. 1, Table 1).

Gills and viscera were frozen and flown to Brisbane for dissection. The SPC and NZ fisheries officers sampled 5 fish/school from a maximum of 3 schools/d. Commercial companies were unable to sample from individual schools and usually supplied the head and the anterior ventral body, removed from frozen fish by a single slanting cut using a band saw. Fork length, if not supplied, was calculated

TABLE 1.—Sources of fish dissected.

	Area	Date	No. fish	Avg. length (cm)
A	Palau, Helen R.	Aug. 1980	35	41
B	Ponape	July 1980	45	59
C	Papua New Guinea	June 1981	30	50
D	Papua New Guinea	Nov. 1981	60	41
E	Solomon Is.	June 1980	30	46
F	Coral Sea	Jan. 1982	19	57
G	Fiji	Feb., Mar., Apr., May 1980	100	50
H	Norfolk Is.	Mar. 1980	21	57
I	New South Wales	Jan. 1981	103	47
J	New Zealand, west	Mar. 1980; Jan., Feb. 1982	69	52
K	New Zealand, east	Jan. 1980; Jan., Feb. 1982	163	49
L	Marquesas	Dec. 1979; Jan. 1980	150	47
M	California	Aug. 1981	30	47
N	Ecuador	Jan. 1982	20	48
O	Atlantic (Puerto Rico)	Mar. 1981	3	50

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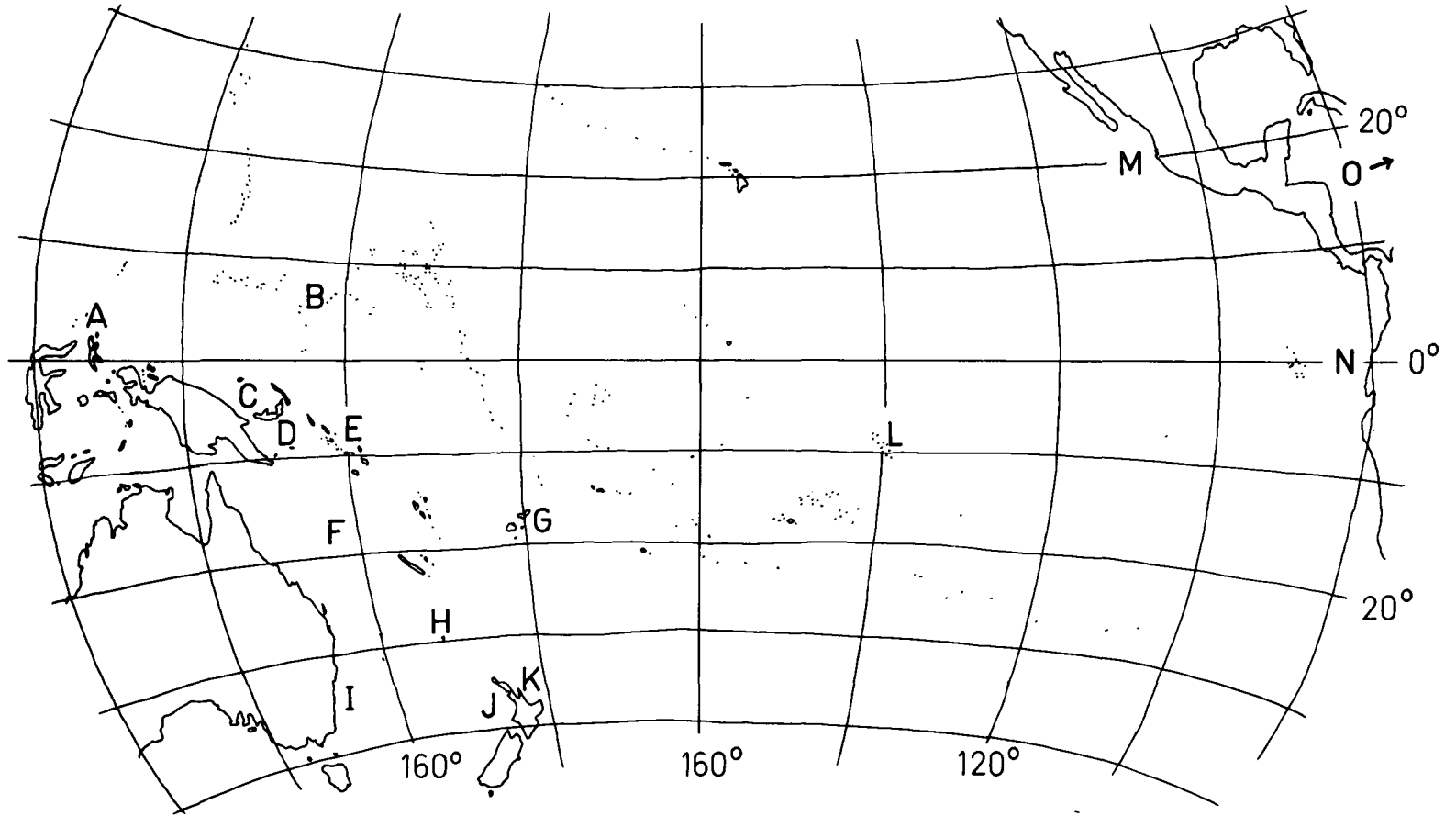
FIGURE 1. – The 15 sites, A to O, from which fish were received for parasitological analysis.   A = Palau, Helen Reef; B = Panape; C and D = Papua New Guinea; E = Solomon Islands; F = Coral Sea; G = Fiji; H = Norfolk Island; I = New South Wales; J = New Zealand West; K = New Zealand East; L = Marquesas Islands; M = California; N = Ecuador; O = Atlantic (Puerto Rico).

from head length using the formula 7.8 + 2.75 × (head length) for heads under 14.5 cm and − 1.7 + 3.3 × (head length) for larger heads (from measurements of 80 and 83 fish, respectively). Prior to dissection, fish were thawed overnight at 6°C. In general, all viscera parasites were counted whereas gill parasites were counted on one side only and the numbers doubled in the final tables. A didymozoid capsule was counted as one parasite though most contained two individuals. Representative parasites were fixed and stored in 10% Formalin[4] except for nematodes which were fixed and stored in 70% alcohol.

An additional set of data on the abundance of the larval cestode *Tentacularia coryphaenae* was collected at sea by SPC and NZ fisheries officers. They recorded the number of *Tentacularia* visible through the peritoneum in the wall of the body cavity of 1,529 fish.

Besides some summary statistics, two types of statistical analysis were done: 1) investigation into the similarities and dissimilarities of the parasite fauna between the various areas sampled, and 2) a study of school integrity.

The similarities and dissimilarities between areas were examined using a series of cluster analyses and multivariate canonical analyses (Mardia et al. 1979). Strictly speaking, canonical analyses require data which are normally distributed and which have a common variance. However, the frequency distributions of the parasites were not normal. They showed considerable differences from one parasite to

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another and most appeared to have two components: one which could be adequately approximated by a negative binomial distribution; and a second component consisting of a disproportionately large zero category, presumably arising because some schools had not been exposed to infection. Precise transformations to normalize the data would thus have been complex and of doubtful accuracy considering the small size of the samples from each school. A single transformation for all species was therefore used: the natural logarithm of the number of parasites plus 1.0.

To avoid possible biases due to associations between parasite numbers and fish length, such as that shown in Figure 2, the transformed counts were then adjusted for fish length. This was done for each species by regressing log (parasite number + 1.0) on fish length, for all Pacific tropical fish (489), to estimate the magnitude of any relationship. This was used to adjust the transformed parasite numbers, except where this was zero, to that expected for a fish of a standard length of 50 cm. (This length was very close to the overall mean length of the fish.) The method could not be trusted to eliminate all effects of length, so, as an added safeguard, only fish 39.5 to 57.5 cm were used in the multivariate analyses (83% of the total). These are likely to have been 1 yr old (Uchiyama and Struhsaker 1981; Wankowski 1981).

In a few instances a parasite was absent from all fish in one area. To allow matrix inversion in the canonical variate analyses, a random number between − 0.005 and + 0.005 was added to the data. This did not influence the outcome. The results of the canonical variate analyses were displayed graphically as plots of the first versus the second canonical
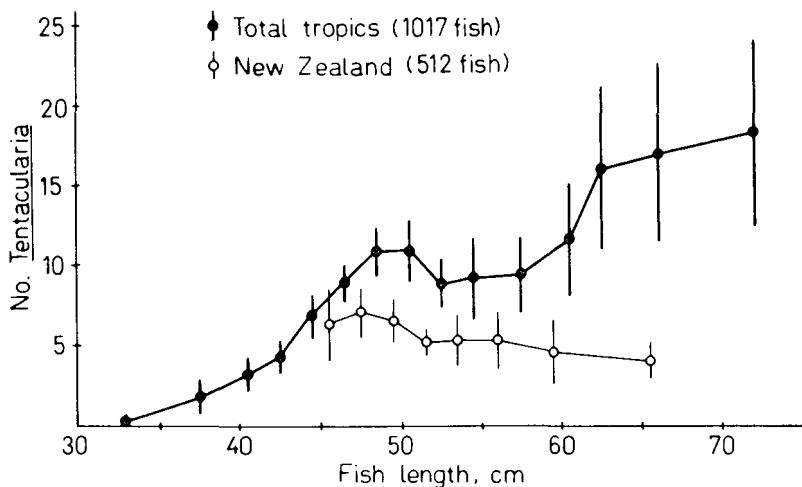

FIGURE 2. — Relationship between number of *T. coryphaenae* and fish length. Mean ±2 SE. Each mean from minimum of 19 fish. In the tropics the number increased with length but this was not reflected in the New Zealand samples.

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axes. Confidence limits (95%) for the positions of different areas on these plots are presented as circles with radius equal to the square root of 5.99/number of fish in sample (Mardia et al. 1979).

Analyses on the same combinations of parasites were also done by calculating minimum spanning trees (Gower and Digby 1981), and dendrograms from nearest neighbor and centroid cluster analyses (Clifford and Stephenson 1975), basing similarity measures on logarithms of area means. Areas were grouped in a similar way by all methods. Using clustering algorithms which either ignored or allowed for matches between areas where parasites were not recorded did not significantly influence results. For these reasons, and because only canonical variate analysis provided some measure of reliability for its conclusions (confidence rings), only the results of the canonical analyses are presented below.

School integrity was examined by comparing the variability in parasite numbers per fish between schools, to that within schools, for the two areas (Marquesas and east New Zealand) where the largest numbers of schools were sampled. This showed which parasites were strongly linked to schools, and also allowed tentative estimation of the length of time schools remained intact. In theory, for parasites to show strong school associations two conditions need to be met: the parasite must heavily infect some schools and not others, and its life span in the fish must be equal to or shorter than the life of the school. Parasites which showed strong school-school association were therefore likely to be shorter lived than those not showing such associations, and other evidence being equal, were considered less reliable as population markers than related species.

Two methods were used to compare within and between school variability in each of the two areas. First, a series of univariate analyses of variance of log (parasite numbers + 1.0) were done to calculate the ratio of between school to within school variances. The magnitude of these ratios, and the corresponding probabilities that they do not differ from 1.0, were interpreted as measures of school integrity. A limitation of this method was that the data . were only approximately normally distributed, particularly for rare parasites, and thus the derived probabilities were also approximations.

The second method, a median test, was based on the binomial distribution. The number of parasites of a particular species in each fish was transformed to a zero if it was less than or equal to the median number per fish for the area, and to a one otherwise. The zeros and ones of each school were then considered

as a binomial sample. If these samples showed evidence of greater variation than expected by chance (i.e., too many schools with nearly all zeros or nearly all ones), then the schools differed with respect to the distribution of the parasite. A statistic, approximately distributed as a χ^2 random variable, was calculated using GLIM (Baker and Nelder 1978) to determine whether the binomial samples showed evidence of differences. Its associated probability was used as a measure of school integrity. The method had the useful property of being independent of the distribution of parasite numbers. For parasites with a median per fish of <1, the test was based on the presence or absence of the parasite, though obviously the rarer the parasite the less sensitive the test.

It is possible that some schools were sampled twice. If this did happen, the results of both methods err on the conservative side. Only those species that gave consistent results by both methods were used to draw conclusions about school integrity.

RESULTS

Evaluation of Parasite Species

Information was collected on 26 different types of parasites (species or species complexes) from 15 areas. A summary of the raw data unadjusted for fish length is given in Table 2.

The parasite species were evaluated for their probable longevity on or in skipjack tuna. For them to be useful as markers they needed to be relatively long-lived, preferably surviving for the life of the fish. Nothing was known specifically about their longevity in skipjack tuna, though data were available on related forms (Table 3). In general, intestinal lumen dwellers appear to be more easily lost than larval forms encapsulated in the tissues. The 26 skipjack tuna parasites were divided into four groups, those considered "temporary", "semi-permanent", and "permanent", and those not used at all.

Four parasites were not used in any analyses. Two of the nematodes, Ctenascarophis sp. and Spinitectus sp. (Nos. 23 and 24 in Table 2), were found in the gut of virtually every fish in which they were sought, from every area. Their small size meant that the number recovered was a function of the time spent searching. They were only counted in every fifth fish, as were the two larval cestodes from the large intestine, Scolex polymorphus (large) and S. polymorphus (small) (Nos. 25 and 26). Counting these was time consuming, their apparent abundance may have been inversely related to the state of preservation of

TABLE 2.—Average numbers of parasites per fish in all skipjack tuna (878) from the areas listed in Table 1, unadjusted for length. The last column gives the correlation coefficient (r) for length against log (parasite number + 1) for Pacific tropical fish.

No.	Parasites	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	r
1	Caligus spp.	5	17	5	5	10	36	4	3	3	3	1	7	0	1	7	0.37
2	Didymocylindrus filiformis	16	5	2	3	4	4	7	3	6 ,	8	10	4	4	3	10	−0.14
3	Didymocylindrus simplex	16	7	4	6	13	11	14	12	18	26	18	14	15	6	3	−0.08
4	Didymoproblema fusiforme	4	1	0	1	1	1	4	1	4	2	3	3	3	1	1	−0.06
5	Lobatozoum multisacculatum	0.1	0.1	0.0	0.0	0.0	0.0	0.1	0.5	0.0	0.1	0.4	0.2	0.3	0.1	0.0	0.03
6	Syncoelium filiferum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	13.1	0.0	0.0	0.0	0.0	0.0	0.0	—
7	Philometra sp.	1	3	4	29	5	P[1]	2	2	3	3	1	6	6	1	8	0.02
8	Anisakis type I	1.0	0.2	2.7	1.0	0.7	1.6	0.2	0.5	0.9	2.1	1.5	0.6	0.2	0.1	2.7	0.13
9	Anisakis type II	0.2	0.0	0.0	0.1	0.0	0.1	0.0	0.4	0.1	0.8	0.2	0.0	0.4	1.2	2.3	−0.02
10	Terranova sp.	0.0	0.1	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.2	0.1	0.0	0.0	0.06
11	Coeliodidymocystis sp.	1.3	2.1	0.3	0.2	0.9	0.2	1.2	0.5	0.3	0.7	1.3	0.8	0.1	0.7	0.0	0.03
12	Tentacularia coryphaenae	3	22	P[1]	3	4	19	8	6	4	5	6	10	3	P[1]	P[1]	0.48
13	Oesophagocystis dissimilis	12	6	8	7	8	12	9	3	6	3	9	8	8	9	11	−0.05
14	Kollikeria / Didymocystis spp.	13	4	1	5	9	4	7	7	8	4	5	6	11	5	6	−0.11
15	Dinurus euthynni	55	9	19	35	66	1	2	3	0	0	0	15	0	0	0	−0.34
16	Didymocystoides intestino-muscularis[2]	30	27	26	37	49	39	54	18	15	12	16	44	134	17	64	−0.14
17	Hirudinella ventricosa	0.4	0.6	0.4	0.2	1.1	0.7	0.4	0.3	0.1	0.0	0.0	1.1	0.1	0.2	1.0	−0.10
18	Raorhynchus terebra	22	16	13	17	15	18	25	65	4	2	4	12	3	1	0	−0.00
19	Didymocystoides intestino-muscularis[2]	14	3	3	9	3	8	5	8	6	6	6	7	13	3	2	−0.24
20	Lagenocystis / Univitellannulocystis spp.	76	40	29	29	22	45	43	16	38	17	30	61	178	34	41	−0.11
21	Tergestia laticollis	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.8	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.00
22	Rhipidocotyle sp.	0.0	0.3	0.0	0.2	0.2	2.3	2.4	0.0	1.3	0.0	0.0	0.1	0.0	0.0	0.0	0.08
23	Ctenascarophis type	35	7	6	2	18	22	38	49	7	17	21	33	4	1	108	
24	Spinitectus type	10	7	20	2	12	5	9	10	5	6	18	13	5	3	10	
25	Scolex polymorphus (large)	4	0.4	0.2	0	7	166	33	P[1]	122	101	27	10	161	9	7	
26	Scolex polymorphus (small)	200	124	1,089	287	8,900	257	463	140	211	53	24	206	495	153	105	

[1]P = present.
[2]No. 16—stomach; No. 19—intestine.

the fish, and their longevity was doubtful. *Philometra* sp. (No. 7) was found predominantly in developed ovaries, which were present in less than half of the fish sampled. The data were used for comparing school-school variability only.

Seven parasites were considered "temporary". They appeared to be short-lived or easily lost from the fish. The caligoid copepods (No. 1, primarily *Caligus productus* in the tropics and *C. bonito* in temperate waters) were not permanently attached and probably moved from fish to fish (Kabata 1981). *Syncoelium filiferum* (No. 6) was common on the gills in New South Wales and New Zealand samples (I, J, and K), but was not recovered from anywhere in the tropics. It is common on fish endemic to New Zealand (D. Blair[5]). It was considered possibly a temperate short-lived parasite, at least on skipjack tuna, and this was verified by the school integrity study and by conventional tagging data (see later).

Some hemiurids are known to be readily lost from the gut of other species of fish (Table 3). Margolis and Boyce (1969) observed that over half the *Lecithaster gibbosus* were lost from salmon fingerlings

within 3 wk of bringing the fish into captivity. We found *Dinurus euthynni* (No. 15) in all tropical samples from the central and western Pacific but not in the temperate samples I, J, and K. As it showed strong school associations and as the didymozoid data described later showed that New Zealand fish had a recent origin in the tropics, *D. euthynni* was evidently a short-lived tropical parasite that was lost as the fish migrated south. This also appeared to be true for *Hirudinella ventricosa* (No. 17) and possibly for two relatively rare gut-lumen digeneans, *Tergestia laticollis* (No. 21) and *Rhipidocotyle* sp. (No. 22).

In other fish, adult acanthocephalans may be short lived (Table 3). Möller (1976) found that over half the *Echinorhynchus gadi* in three species of fish were lost within 2 wk of the fish being brought into captivity. In our data, *Raorhynchus terebra* (No. 18) was present in reduced numbers in I, J, and K, suggesting it was lost in southern waters. All these parasites then were labelled "temporary".

Didymozoid digeneans were considered "semipermanent" parasites. In other fish, some didymozoids, or at least the remains of them, are believed to stay in the tissues for the life of the fish. Others, including some species found in the gonads or gills, are lost annually (Table 3). In general, therefore, skip-

TABLE 3.—Probable maximum life spans of parasites related to those found in skipjack tuna.

Parasite	Site	Host	Life span	Reference
Acanthocephala				
Echinorhynchus gadi	Intestine	*Zoarces viviparous*	2 wk	Moller (1976)
Echinorhynchus gadi	Intestine	*Gadus morhua*	6 wk	Moller (1976)
Echinorhynchus gadi	Intestine	*Myxocephalus scorpius*	7 wk	Moller (1976)
Echinorhynchus gadi	Intestine	*Platichthys flesus*	11 wk	Moller (1976)
Acanthocephalan sp.	Intestine	*Sparus aurata*	< 8 wk	Paperna et al. (1977)
Hemiurid Digenea				
Lecithaster gibbosus	Int. and caec.	*Oncorhynchus gorbuscha*	< 9 mo	Boyce (1969)
Lecithaster gibbosus	Int. and caec.	*Oncorhynchus gorbuscha*	> 5 mo	Margolis and Boyce (1969)
Lecithaster gibbosus	Int. and caec.	*O. keta*	8 mo	Margolis and Boyce (1969)
Tubulovesicula lindbergi	Stomach	*O. keta*	> 31 mo	Margolis and Boyce (1969)
Lecithophyllum botryophorum	Stomach	*Argentina silus*	10 mo	Scott (1969)
Didymozoid Digenea				
Nematobothrium texomense	Ovary	*Ictiobus bubalus*	> 8 mo	Self et al. (1963)
Neometadidymozoon helicis	Buc. cav.	*Platycephalus fuscus*	1 yr	Lester (1980)
Nematobothrium spinneri (eggs)	Muscle	*Acanthocybium solandri*	> host	Lester (1980)
Larval Cestoda				
Gilquinia erinaceus	Mesentery	*Melanogrammus aeglefinus*	> host	Lubieniecki (1976)
Trypanorhynch sp.	Mesentery	*Clupea harengus*	> 1 yr	Sindermann (1961)
Triaenophorus crassus	Mesentery	*Oncorhynchus* spp.	> host	Margolis (1965)
Larval Anisakinae				
Larval anisakid	Mesentery	*Clupea harengus*	> 1 yr	Sindermann (1961)
Larval anisakid	Mesentery	marine fish	several years	Margolis (1970)
Porrocaecum decipiens	Mesentery	*Gadus morhua*	several years	Platt (1976)

jack tuna didymozoids were thought to be in the fish probably for at least several months. However, there was some suggestion that 3 of the 10 skipjack tuna didymozoids had a shorter adult life span than the others. Didymozoid No. 16 was much less common in New Zealand waters than in the tropics (Table 4), and didymozoid Nos. 19 and 20 were also less common and, in addition, showed strong school associations (see later). These three didymozoids (possibly representing four species) were omitted from the analysis for Figure 3.

The remaining four parasites (Nos. 8, 9, 10, and 12) were classed as "permanent". Larval cestodes and nematodes, particularly those found in the tissues, are generally believed to survive for several years, often for the life of the fish (Table 3). They

have been used successfully many times as fish population markers (see MacKenzie 1983). In skipjack tuna, the larva of a trypanorhynch cestode, *Tentacularia coryphaenae*, was found in the wall of the body cavity and occasionally in the viscera. No degenerating forms were seen, suggesting that it survived for an extended period and hence could be an excellent population marker, though counts were not available from areas C, N, and O. Larval anisakids were found on the wall of the stomach or in the mesentery. The literature suggested that they should also be good long-term markers (Table 3). They were counted in all areas.

Protozoan parasites have been used successfully to separate stocks of several species of fish. However, none has been reported from skipjack tuna, and we found none in this study.

TABLE 4.—Average number of didymozoids in New Zealand fish (all lengths) compared with fish caught in the tropical western Pacific (areas A, B, C, D, E, F, G, and L). In parentheses, $\log (x + 1)$ length-adjusted means for fish 40 to 57 cm only.

No.[1]	Parasite	New Zealand		Tropics	
2	*D. filiformis*	9	(1.1)	6	(0.8)
3	*D. simplex*	20	(1.7)	12	(1.3)
4	*D. fusiforme*	2.7	(0.6)	2.5	(0.5)
5	*L. multisacculatum*	0.3	(0.1)	0.1	(0.0)
11	*Coeliodidymocystis* sp.	1.1	(0.4)	0.9	(0.3)
13	*O. dissimilis*	7	(1.3)	9	(1.9)
14	*Kollikeria / Didymocystis* spp.	5	(1.2)	6	(1.5)
16	*D. intestinomuscularis*[2]	15	(1.8)	41	(3.3)
19	*D. intestinomuscularis*[3]	6	(1.3)	7	(1.4)
20	*L. katsuwoni / U. katsuwoni*	26	(1.9)	47	(2.3)
	No. of fish	232	(213)	469	(364)

[1]Code no. from Table 2.
[2]Stomach.
[3]Intestine.

Relationships Between Areas

Analyses of individual distributions of permanent and semipermanent parasites showed that the abundances of individual parasites varied across the Pacific. However, these differences were inconsistent, the pattern established by one parasite being in conflict with that of a second, and so on.

The data from the three anisakid nematodes and the seven didymozoids considered longest lived were therefore analyzed using canonical variate analysis. Because of the more permanent nature of these parasites and the completeness with which they were recorded from all areas, these data were considered the most reliable for statistically assessing the similarities and dissimilarities between areas. The first three canonical axes accounted for 75% of the

FIGURE 3.—Results of multivariate analysis using 3 "permanent" and 7 "semipermanent" parasites (Nos. 2, 3, 5, 8, 9, 10, 11, 13, and 14). Values for first two cannonical vectors plotted, and 95% confidence rings indicated for samples of more than 24 fish. The letters refer to the sampling sites indicated in Figure 1.

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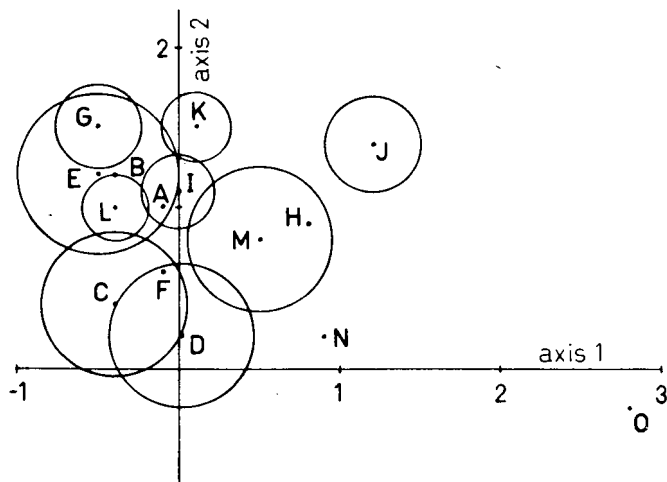
variation in area-to-area differences in parasite numbers. A plot of the first two, accounting for 58% of the variation, showed the Atlantic fish (O) to be distinct from all the Pacific ones, even though only three fish from the Atlantic were dissected (Fig. 3). However, fish from California (M) and Ecuador (N) fell close to the western Pacific samples. They were separated out on the third axis (not shown), but nevertheless it is evident that they had a somewhat similar parasite fauna. The fish from western New Zealand (J) appeared distinct, and so too, to a less extent, were the Papua New Guinea samples (C and D). There is no suggestion that fish from Ponape (A), Palau (B), Solomon Islands (E), Fiji (G), and the Marquesas (L) had distinct faunas of these long-lived parasites.
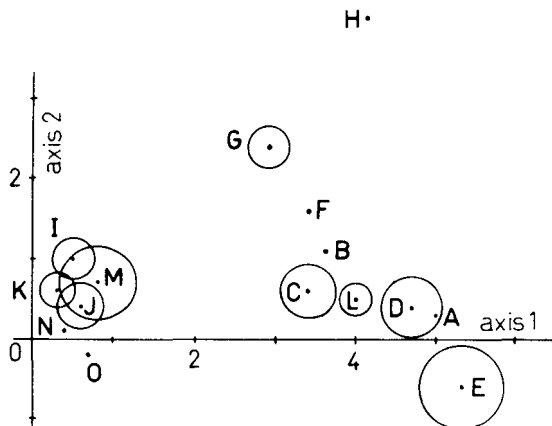
FIGURE 4. – Results of multivariate analyses using 7 "temporary" parasites (Nos. 1, 6, 15, 17, 18, 21, and 22). 95% confidence rings given for samples of more than 24 fish.

In this analysis, *Anisakis* II had the most powerful discriminating properties, though at least 7 of the 10 parasites used were capable of substantial discrimination in their own right.

An analysis based on the 7 "temporary" parasites (Nos. 1, 6, 15, 17, 18, 21, and 22) produced a much greater separation of areas (Fig. 4). They are grouped into two broad classes: one containing New South Wales (I), New Zealand (J, K), and the eastern Pacific (M, N); and the other the western tropical areas. Each area in the latter group had a temporary parasite fauna that was distinct from most other areas. Over 83% of the variation was accounted for by the first two axes, and 90% by the first three. It is interesting to note that New South Wales (I) is more similar to east New Zealand (K) than to west New Zealand (J) (this was much more marked on the third axis, not shown, where I and K were pulled to one side), and that west New Zealand is similar to California (M) and Ecuador (N).

Taken together, Figures 3 and 4 indicate that several distinct skipjack tuna parasite faunas existed within the tropical Pacific, and the longer lived parasites were more evenly distributed than the shorter lived ones.

To check these results and to look for links between the New Zealand fish and the tropical areas, the west Pacific data were reanalyzed using first the 10 "semipermanent" parasites (the didymozoids) and second the 4 "permanent" parasites (anisakids and *T. coryphaenae*).

The average numbers of didymozoids in the New Zealand fish were almost identical to the overall average for the central and western tropics (Table 4). In the multivariate analyses, the temperate water samples fell to one side of the tropical samples (Fig. 5
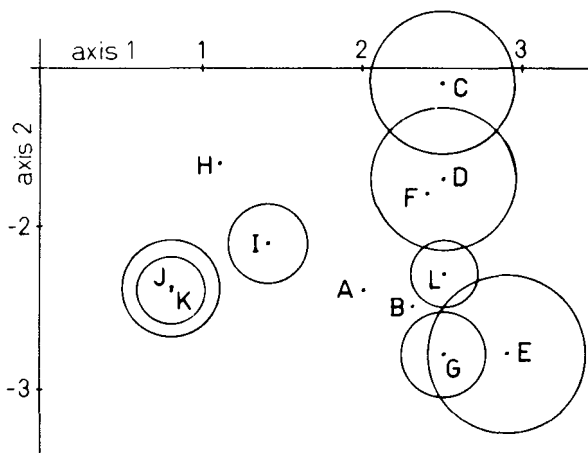

FIGURE 5. – Results of multivariate analysis using 10 didymozoids only (Nos. 2, 3, 4, 5, 11, 13, 14, 16, 19, and 20). 95% confidence rings given for samples of more than 24 fish.

– H, I, J, K), possibly because of the three didymozoids suspected of being relatively short-lived (Nos. 16, 19, and 20). The east and west New Zealand samples (J, K) were identical on the first two axes, and separated only slightly on the third axis (not shown). There was no obvious link between New Zealand and any particular tropical area.

Similarly, the larval nematodes and *T. coryphaenae* (Nos. 8, 9, 10, and 12) did not suggest a link between New Zealand fish and those from any particular tropical area (Fig. 6). However, west New Zealand (J) now appeared distinct from east New Zealand (K) and New South Wales (I). The separation was due to areas having either high *Anisakis* I and II and low *Terranova* and *T. coryphaenae* or low *Anisakis* I and II and high *Terranova* and *T. coryphaenae*. West New Zealand (J) was at one extreme (high *Anisakis*) and the three most northwestern areas – Ponape (B), Fiji (G), and Marquesas (L) – at the other. *Tentacularia coryphaenae* and probably *Terranova* were picked up in the tropics. It seems likely that one or both of the *Anisakis* larvae were picked up predominantly in temperate waters, particularly in west New Zealand. This may explain the separation of west New Zealand from the other areas in Figure 4.

In summary, the New Zealand fish were not closely aligned with any particular tropical sample, and the eastern and western New Zealand fish were probably carrying similar parasite faunas when they arrived in New Zealand.

Tentacularia coryphaenae

Data on this parasite are presented in detail because we had more than for any other parasite and because potentially it was our most valuable marker. It also was the subject of many queries from skipjack tuna processors. The parasite was common throughout the south, central, and west Pacific (Table 3, parasite No. 12). The means of samples of over 22 fish within the length range 44 to 53.9 cm suggested an east-west cline across the Pacific, with twice as many parasites being found in fish from around the Marquesas (L) as around Papua New Guinea (C and D) (Fig. 7). A regression analysis of number of parasites against longitude using tropical data on the number of parasites in 972 fish, transformed and adjusted for differences in host length (data collected independently by the SPC), showed that the relationship was statistically significant, though it only accounted for about 7% of the fish-to-fish variation.

Considering fish of all sizes, the number of *T. coryphaenae* in the tropics increased with the size of the
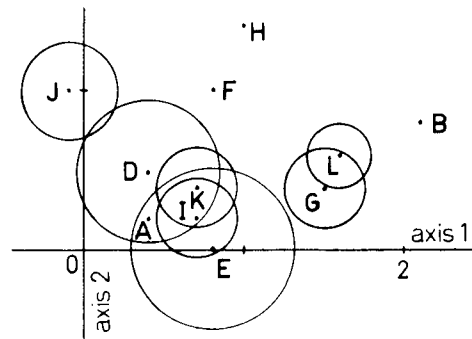

FIGURE 6. – Results of multivariate analysis using the four "permanent" parasites (anisakids and *T. coryphaenae*, Nos. 8, 9, 10, and 12). 95% confidence rings given for samples of more than 24 fish.

fish (Fig. 2, solid circles). The increase around 47 cm is due to many of the Marquesas fish being this size and Marquesas fish tended to have more *T. coryphaenae*. In New Zealand, smaller fish had about the same average number as fish from the tropics. However, this number did not increase with size (Fig. 2, open circles). Thus, the 58+ New Zealand fish had fewer parasites than their peers in the tropics, and about the same number as the 45 to 50 cm fish.

School-to-School Variation

An analysis of variance, and a median test, were carried out on 30 schools from the Marquesas and 19 schools from eastern New Zealand (areas L and K, respectively, Table 5). The results of the two methods on each data set show close agreement.

In the Marquesas, five parasites showed strong evidence of association with particular schools, i.e., the probability that schools differed was at least 0.95 with both methods. The parasites were *Caligus* spp. (No. 1), *D. euthynni* (No. 15), *H. ventricosa* (No. 17), *D. intestinomuscularis* (No. 19), and *Lagenocystis/ Univitellannulocystis* spp. (No. 20). For these parasites to show significant differences, they must have heavily infected some schools and not others, and their life span in the fish must have been equal to or shorter than the life of the school. The literature review suggested that the first three species could possibly be readily lost from fish, and this is vindicated by their strong school association. The evident impermanence of the last two, however, was unexpected. It was as a consequence of this finding that they were not included in the analysis for Figure 3.
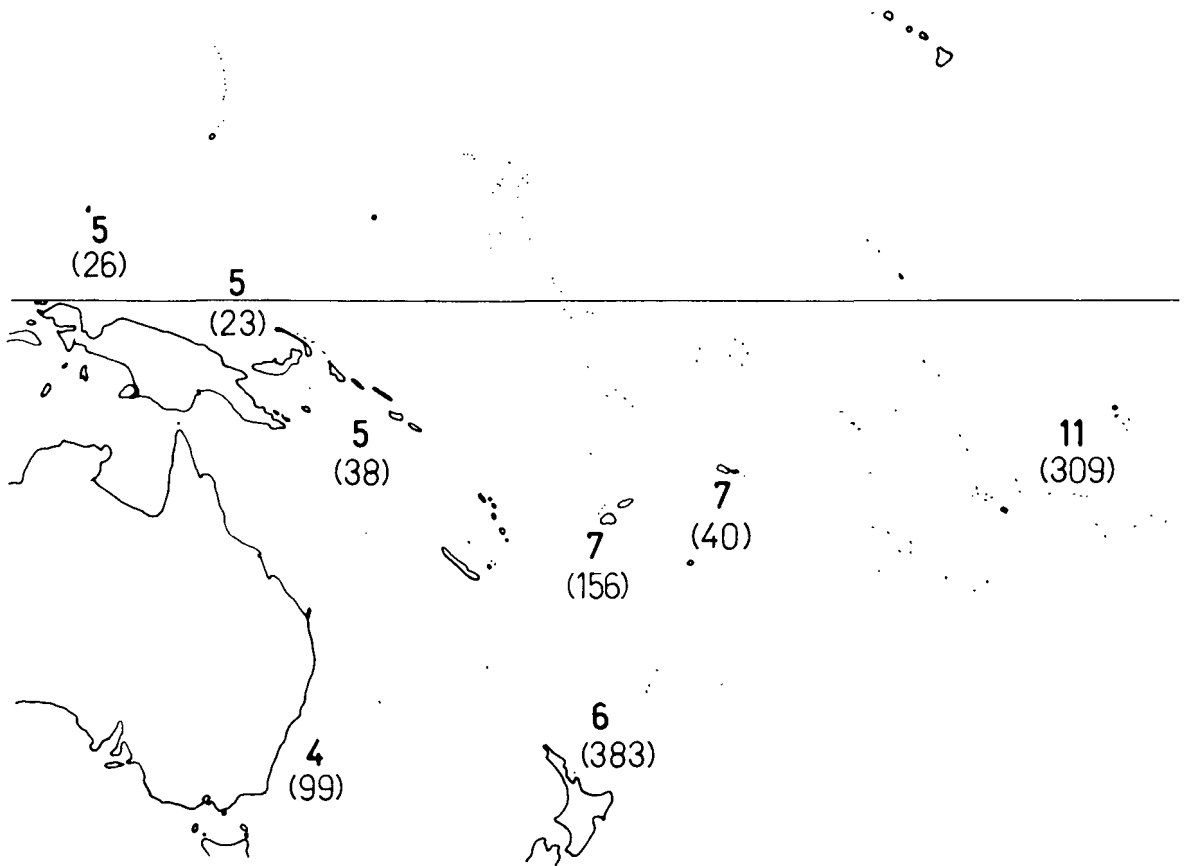
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FIGURE 7. – The average numbers of *T. coryphaenae* in skipjack tuna 44 to 53.9 cm long in samples of over 22 fish. Note that the number in- • creased to the east. (In parentheses, number of fish sampled.)

Several other parasites thought to be short-lived, such as *R. tereba*, did not show up in the test, presumably because their infective stages were relatively evenly distributed in the tropical Pacific.

In New Zealand, parasites showing close association with particular schools (using both tests) were *L. multisacculatum* (No. 5), *S. filiferum* (No. 6), *Philometra* sp. (No. 7), *Coeliodidymocystis* (No. 11), *T. coryphaenae* (No. 12), *R. terebra* (No. 18), and *D. intestinomuscularis* (No. 19). *Syncoelium filiferum* and *R. terebra* were both thought to be temporary parasites that could be gained in New Zealand or adjacent waters (Norfolk Island). The origin of the *Philometra* was unknown. Their number reflected the state of maturity of the fish and this varied between schools. However, we were left with three didymozoids and *T. coryphaenae*, all of which differed markedly between schools in eastern New

Zealand. One of the didymozoids, *L. multisacculatum*, a normally rare tropical parasite, was found on all five fish from one school (numbers per fish 1, 2, 8, 3, and 1). As the three didymozoids and *T. coryphaenae* are essentially tropical parasites, the schools had evidently not fully mixed while in temperate waters.

If this is true, these four parasites could not have been picked up uniformly across the Pacific. Evidence is given above that *D. intestinomuscularis* (No. 19) was not picked up uniformly even within the Marquesas. For the other species, a comparison of their mean numbers per fish per school in different areas of the tropical Pacific showed that *Coeliodidymocystis* sp. and particularly *T. coryphaenae* were indeed more abundant in some areas than others. *Lobatozoum multisacculatum* was too rare for any conclusions to be drawn in this respect.

TABLE 5.—Comparison of within and between school variability in numbers of parasites per fish for two areas.

Parasite no. (see Table 3)	Marquesas		New Zealand	
	Analysis of variance[1]	Median test[2]	Analysis of variance	Median test
1	***[3]	***		
2		**		
3		*		
4				
5			***	**
6	(no parasites found)		***	***
7			*	*
8		*		
9				
10			(no parasites found)	
11			*	*
12			*	***
13				*
14				
15	***	**	(no parasites found)	
16				
17	*	*		
18			***	***
19	***	***	*	***
20	**	***		
21	*			
22				

[1]The probabilities that the ratio of the between and within school variances is no greater than one. (Based on transformed data, i.e., log (parasite no. + 1.0).)

[2]The probabilities that the proportion of fish with more than the area median is the same for all schools.

[3]*** = $P < 0.001$; ** = $P < 0.01$; * = $P < 0.05$; blank = $P > 0.05$.

Rate of Mixing of Schools

To estimate the rate of mixing of schools we needed to know the distribution of the parasites among schools before, and after, some known time interval. This we did not have for any of the Marquesas samples.

In New Zealand, however, some approximate calculations could be made because schools arrived from the tropics at different times. Sixteen of the 19 east New Zealand schools were of similar-sized fish and were all caught within 1 mo. These schools were divided into two groups: "early arrivals" and "recent arrivals". (This was done by ranking the schools using a combination of four parasites whose prevalences were positively correlated with each other, Nos. 16, 18, 19, and 20, and which were thought to be relatively short-lived parasites picked up in the tropics. Thus high numbers indicated a recently arrived school.) From catch data (Habib et al. 1980), we calculated that there was an average of 3 to 4 wk between the capture of 25% and 75% of the annual catch. This interval was taken as the approximate period between the arrival times of the early group and the recent group. If mixing was occurring, one would expect that the school-school

differences for tropical parasites would be greater when the fish first arrived (the recent arrivals) than after they had been there for a few weeks (the early arrivals). However, this we could not demonstrate. Our sample sizes at this point were rather small (eight schools in each category), and in fact the reverse appeared to be the case, the early schools having a generally higher variability than the recent arrivals. This suggested that the early arrivals had come from several areas (and still had not fully mixed), whereas many of the later arrivals had perhaps come from one area.

DISCUSSION

Ten of the 26 parasites counted were species of didymozoid trematodes. These are almost exclusively a tropical group. Yamaguti (1970), for example, found 84 different species of didymozoid in fish around Hawaii. None were recorded in checklists of parasites from New Zealand (Hewitt and Hine 1972) or Canada (Margolis and Arthur 1979). Thus, although skipjack tuna are caught in both tropical and temperate waters, their didymozoid infections are evidently picked up primarily in the tropics.

Larval didymozoids have been found in small fish and in invertebrates. It is almost certain that the definitive host becomes infected by feeding on an infected intermediate host (Cable and Nahhas 1962; Nikolaeva 1965). In the tropics skipjack 40 to 60 cm in length feed largely on fish, squid, and stomatopods (Argue et al. 1983). In New Zealand, however, they feed almost exclusively on euphausids (Habib et al. 1980, 1981). This completely different diet in New Zealand, together with the fact that no endemic New Zealand fish are known to carry any didymozoids, lead us to the conclusion that few, if any, didymozoids are picked up in New Zealand waters.

The occurrence of 10 species of didymozoids in skipjack tuna caught in New Zealand, in numbers very similar to fish of the same size caught in the tropics, thus indicates that New Zealand and tropical fish were found until recently in a similar tropical environment. Almost certainly, the New Zealand fishery is based on fish that have recently migrated from the tropics, and not on fish recruited as post-larvae in temperate waters. This disagrees with tagging data which show that the bulk of New Zealand skipjack tuna of known origin were off New South Wales 10 mo earlier. However, the tagging inference is applicable to < 4% of the total New Zealand fish (Argue and Kearney 1983). Our conclusion is in agreement with Argue et al. (1983) who found no juvenile skipjack tuna in the stomachs of adults from

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subtropical waters, though juveniles formed a significant component of the adult diet in the tropics.

The absence of degenerating *T. coryphaenae* and the positive correlation of parasite number and host length suggest that the parasite was long-lived and accumulated in the fish with age. The low numbers of *Tentacularia* in the 57+ cm fish caught in New Zealand indicate that these fish have had a different history from their peers in the tropics. The bulk of the skipjack tuna caught in New Zealand are 45 to 55 cm long. Less than 10% measure 60 cm or more (Habib et al. 1980, 1981). We have concluded above that the majority of New Zealand fish recently arrived from the tropics. The *T. coryphaenae* data indicate that the 57+ cm fish left the tropics at 45 to 55 cm long and have not returned. Evidently as fish age, they become less migratory. This was hypothesized by Kearney (1978).

Large fish were not necessarily permanent residents in New Zealand, however. Of 17 57+ cm fish on which full dissections were carried out, 2 were carrying the acanthocephalan *R. terebra*, a parasite thought to be relatively short-lived (see above) and not picked up in New Zealand. *Raorhynchus terebra* was common in fish from Norfolk Island (area H). Thus some of the large fish may have recently come from areas as far away as Norfolk Island.

The first two canonical variate analyses comparing all areas sampled suggested that fish 40 to 57 cm long had moved between areas and carried the longer lived parasites with them. Parasitologically, there was no evidence of more than one stock of skipjack tuna in the Pacific. Richardson (1983) observed an east-west cline in the gene frequency of two enzymes across the Pacific. From an analysis of 200 gene frequencies he proposed an "isolation by distance" model for skipjack tuna. In this, the degree of mixing of skipjack tuna genes was inversely proportional to the distance between the spawning areas. Tagging data have confirmed that there is some mixing of adult skipjack tuna in the central and western Pacific (Kleiber and Kearney 1983), though more than 95% of the tagged fish recovered during the SPC program were caught within 1,000 mi of their point of release (Kearney 1982).

Schools of skipjack tuna have been observed to break up when feeding (Forsberg 1980). This and observations from aircraft where schools have been seen to merge and later separate (Habib unpubl. obs.) have led to the hypothesis that skipjack tuna do not remain in a particular school for more than a day or so. Certainly the pattern of recovery of SPC tags suggested that tagged skipjack tuna underwent considerable mixing amongst schools soon after release

(Argue and Kearney 1983). However, using Marquesas data we found that several parasites showed strong school associations, particularly didymozoid Nos. 19 and 20 (*D. intestinomuscularis* and *Lagenocystis/Univitellanulocystis* spp.). In another didymozoid, *Neometadidymozoon helicis* from the gills of *Platycephalus fuscus*, it takes up to a year for the worms to migrate through the tissues, pair up, mature, and die (Lester 1980). Though only a short migration is needed for didymozoids 19 and 20, as they are intestinal parasites, the worms are still likely to be in the skipjack tuna for a period of weeks. Thus, their strong association with particular schools suggests that school half-life is likely to be in terms of at least weeks rather than days.

In New Zealand, the large school-school differences observed in the numbers of *T. coryphaenae* and several other tropical parasites, especially in the early arrivals, indicate that at the time of catching, the New Zealand schools had not mixed sufficiently to mask their previously distinct tropical faunas.

Do schools remain intact for an extended period, perhaps for the life of the fish? Sharp (1978) found evidence of genetic similarity between individuals in core schools, suggesting that some members of the school were siblings. However, none of *L. multisacculatum*, *Coeliodidymocystis* sp., or *T. coryphaenae*, three long-lived parasites that showed significant school-school differences in New Zealand, showed any significant differences in the Marquesas. This suggests that within the probable long life of these parasites, fish caught in the Marquesas had changed schools and had thus obscured any patchiness in the distribution of the infective stages of the parasites. The parasitological data, then, do not support the hypothesis that fish stay in the same school for life.

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BEHAVIOR OF BOWHEAD WHALES, *BALAENA MYSTICETUS*, SUMMERING IN THE BEAUFORT SEA: A DESCRIPTION[1]

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ABSTRACT

Behavior of bowhead whales summering in the Canadian Beaufort Sea was observed from an airplane and occasionally from shore during 1980-82, mainly during August. Behavior varied between years. In 1980, whales alternated periods of socializing with periods of feeding in several different ways: near the bottom (as evidenced by surfacing with mud), in the water column (suspected during long dives), and skim-feeding at the surface. In 1981, more time was spent apparently feeding in the water column, with some socializing and skim feeding. In 1982, almost all activity appeared to be feeding in the water column. In 1980, most whales studied were in water only 10-40 m deep. In 1981 they were farther from shore and in > 20 m depth, and in 1982 long (10-30 min) dives were common in depths of 40-600 m. Variability in distribution and behavior presumably was related to availability of prey.

Besides feeding and socializing, we saw sporadic bouts of aerial activity (breaches, tail slaps, etc.) and log play. During 1981 and 1982 we observed young-of-the-year calves apparently waiting at the surface while adults fed below. In 1982, two such lone calves played with debris in the water.

During near-surface skim feeding, whales often associated in V-shaped or echelon formations, with up to 14 animals staggered behind and to the side of each other, all moving in the same direction at the same speed, with mouths wide open. We hypothesize that such coordinated movement may increase the efficiency of feeding on concentrations of small invertebrates.

In recent years, much has been learned about behavior of several species of baleen whales (e.g., Payne 1983). Most long-term studies of whales have been carried out during winter, when social interactions, mating, and calving occur more often than feeding. Recently, however, detailed studies have been conducted in summer, when whales are primarily feeding (e.g., Dorsey 1983).

This paper describes the general behavior of bowhead whales, *Balaena mysticetus*, in the summers of 1980-82. A companion paper gives a quantitative description of the surfacing, respiration, and dive patterns (Würsig et al. 1984). This study was done to provide background data necessary to interpret observations of bowhead behavior in the presence of offshore industrial activities (Richardson et al. in press).

The Western Arctic population of bowheads winter in the Bering Sea, and migrate north and east to the eastern Beaufort Sea in spring. During summer (late June to early September), most are off northwestern Canada in Amundsen Gulf and the eastern part of the Beaufort Sea (Fig. 1). In the commercial whaling era in the 19th century, many bowheads apparently summered in the Chukchi and western Beaufort Seas off Alaska (Townsend 1935), but bowheads are no longer present in significant numbers off Alaska in summer (Dahlheim et al. 1980). The eastern Beaufort Sea is believed to be a major feeding area for bowheads (Fraker and Bockstoce 1980), but previous to 1980 there had been no comprehensive studies of bowheads in that area.

METHODS

Aerial Observations

We observed from a Britten-Norman[6] Islander aircraft based at Tuktoyaktuk (Fig. 1). The Islander has two piston engines, high wing configuration, and low

[6] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.
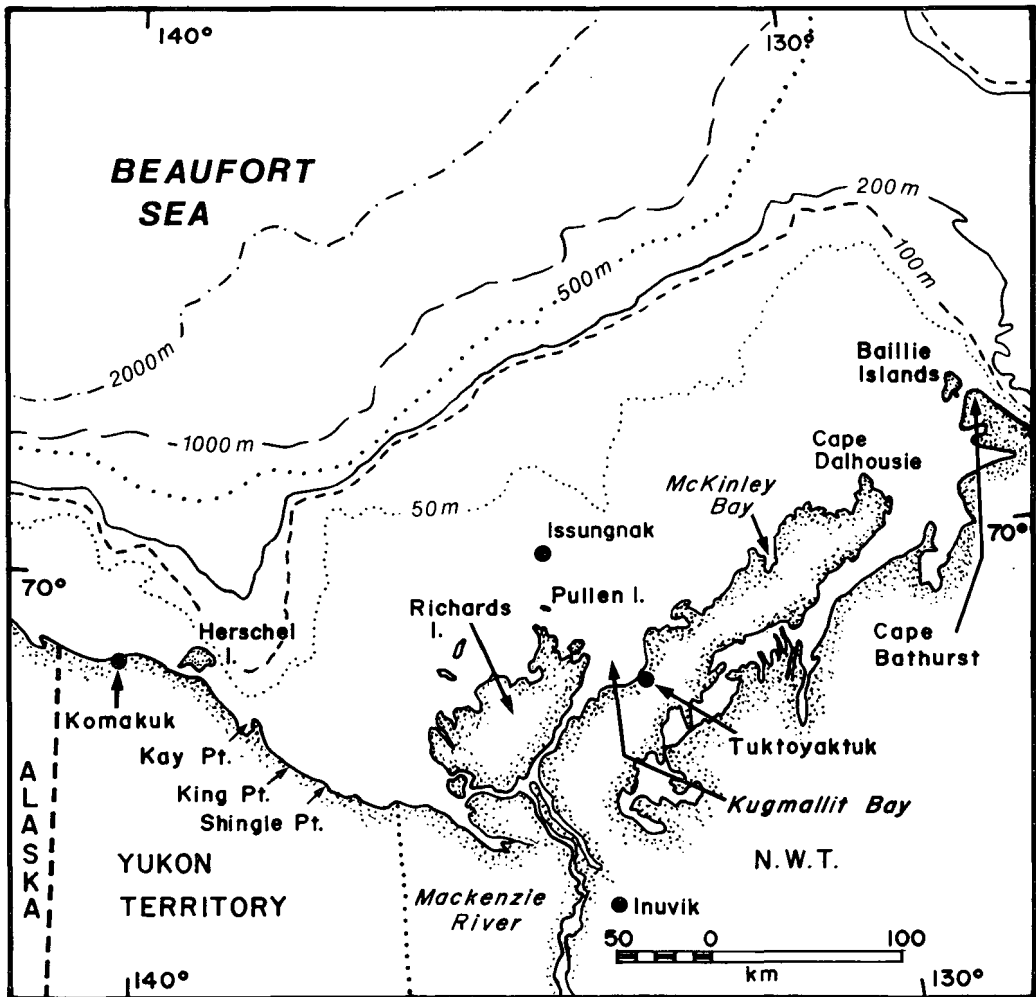
FIGURE 1.—The eastern Beaufort Sea.

stall speed. An OnTrac VLF/Omega navigation system indicated the latitude and longitude. A hand-held color video camera (JVC-CV-0001 in 1980 and 1981, Sony HVC-2000 in 1982) connected to a portable video cassette recorder (Sony SLO-340 in 1980 and 1981, Sony SL-2000 in 1982) was used through the side windows to record oblique views of bowheads.

Our usual strategy was to search until we encountered bowheads, and then circle over them as long as possible while making observations. If contact was lost, we searched for another group. We created a fixed reference point about which to circle when bowheads were below the surface by dropping a fluorescein dye marker. Near the start of most periods of circling above whales, a sonobuoy

(AN/SSQ-41B or AN/SSQ-57A) was dropped to broadcast underwater sounds to the aircraft, where they were recorded.

In 1980-82, we flew for a total of 340 h during 71 offshore flights. Of this time, we circled over bowheads for 97.7 h during 46 flights. Flight duration was typically 4-5.5 h. Flights were made between 3 and 31 August 1980, 31 July and 8 September 1981, and 1 and 31 August 1982. We encountered bowhead whales during every day we flew in 1980, and during the majority of days in 1981 and 1982.

We usually did not fly when wind speed exceeded 25 km/h; in more severe conditions whales are difficult to detect and behavior cannot be observed reliably. While searching for whales, we usually flew at 457-610 m (1,500-2,000 ft) above sea level (ASL),

and at 185 km/h. While circling over whales, we reduced speed to 148 km/h. Bowheads rarely appeared to be disturbed by the aircraft when it remained at or above 457 m (Richardson et al. in press).

The aircraft crew usually consisted of four biologists and the pilot. Three biologists were seated on the right side of the aircraft, which circled clockwise during behavioral observations. Biologists seated in the right front (copilot's) seat and in the seat directly behind it described behaviors. These descriptions were recorded onto audiotape, onto the audio channel of the video recorder, and, in 1981, directly onto data sheets by a biologist in the left rear seat. The biologists in rear seats videotaped whales, handled sonobuoys, and kept records. All personnel on board were in constant communication through an intercom.

While circling bowheads, we usually were able to obtain consistent records of 12 variables and types of behavior:

1) Location of sighting (and, therefore, water depth);
2) Time of day;
3) Individually distinguishing features, if any, on whales;
4) Number of individuals visible in area and number of calves;
5) Headings and turns of each whale in degrees true;
6) Distances between individuals (estimated in whale lengths);
7) Length of time at surface, and sometimes length of dive;
8) Timing and number of respirations or blows, including underwater blows;
9) Possible indications of feeding: mouth open, defecation, mud streaming from mouth;
10) Socializing, possible mating, probable nursing by calves;
11) Aerial activity: breaches, tail slaps, flipper slaps, lunges, rolls;
12) Type of dive: flukes out, peduncle arch, pre-dive flex.

Descriptions of these behaviors appear later.

In most parts of this paper we consider only the observations under "presumably undisturbed" conditions. Bowheads were considered "potentially disturbed" if our aircraft was at < 457 m ASL, if a boat was underway within 4 km, or if sonobuoys showed that industrial noise was readily detectable in the water. The "presumably undisturbed"
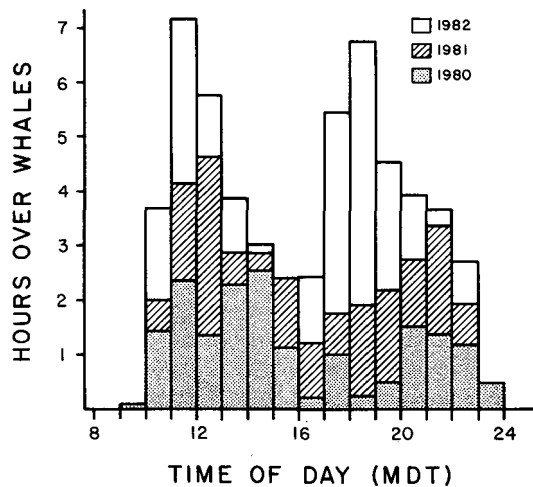

FIGURE 2. – Hourly distribution of behavioral observation time from the air of bowhead whales.
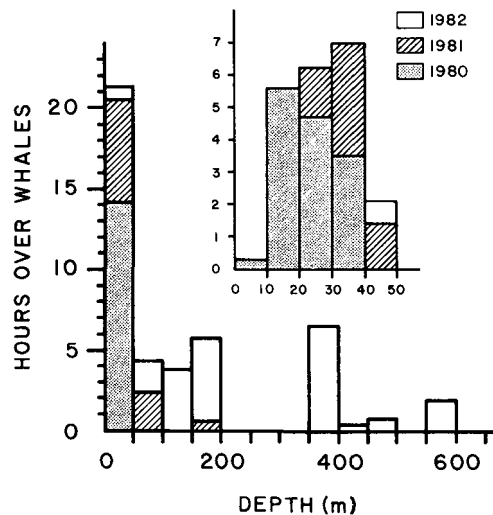

FIGURE 3. – Distribution of behavioral observation time from the air by depth of water of bowhead whales. The inset shows effort for the 0-50 m range by 10 m intervals.

behavioral observations were distributed by hour of day and water depth as presented in Figures 2 and 3.

Shore-Based Observations

Shore-based observations were obtained in 1980 and 1981 from the east end of Herschel Island, Yukon (lat. 69°35'N, long. 138°51'W), and about 225 km west of Tuktoyaktuk (Fig. 1). A surveyor's theodolite was used from a high point (50 m ASL in 1980,

90 m ASL in 1981) on the coast. We used a Wild T1 theodolite with 6-s accuracy and 30-power optics in 1980, and a Nikon NT-2A with 20-s accuracy and 30-power optics in 1981. Horizontal and vertical bearings were later translated to x and y map coordinates. This transiting technique, developed by R. Payne, is described by Würsig (1978). The station was in use from 19 August to 1 September 1980, and 23 August to 13 September 1981.

Locations of most whales within a 10 km radius of the theodolite station during fair weather and daylight hours were documented. Unfortunately, whales rarely approached Herschel Island closer than 5 km during the 1980 field season, so details of behavior were difficult to discern. In 1981, fewer whales were seen, but they were closer to shore, allowing more detailed behavioral observations.

RESULTS

The Surfacing-Dive Cycle

In the Beaufort Sea in summer, nonmigrating bowhead whales typically alternate between dives of variable length, depending on activity, and surfacings within which there are several respirations. This pattern differs slightly from that during migration, when sounding dives (around 15 min long) are separated by periods when several brief surfacings, each with a single respiration, alternate with "series" dives about 15 s long (Rugh and Cubbage 1980; Carroll and Smithhisler 1980). Presumably, migrating animals dive between respirations to avoid hydrodynamic drag imposed by the air-water interface. No such submergence is necessary for a whale that is not moving rapidly through the water. However, the basic repertoire of breathing several times in relatively, closely spaced series and then not breathing for many minutes (during the long dive) is similar during both prolonged directed movement and more stationary activity. The pattern extends to some degree even to whales that remain at the surface for long periods (up to 30 min or more during surface skim feeding, socializing, or play). They generally breathe several times within a few minutes, and then cease breathing for a longer time, despite their near proximity to the surface and the availability of air. Similar patterns are seen in other whales, including right whales, *Eubalaena glacialis*, (Kraus et al. 1982) and gray whales, *Eschrichtius robustus*, (Sumich 1983). Durations of surfacings and dives, intervals between successive blows, and number of blows per surfacing are described in Würsig et al. (1984).

Surfacing and Respiring

Whales in water deeper than about 30-45 m usually surface head and blowhole first after a sounding dive, with the body oriented at some angle (such as 30°) from horizontal. When whales do not dive very deeply (as in shallow water), the surfacing is less due to active swimming upward, and the head and tail surface at approximately the same time.

A blow is an exhalation of air by a whale. Blows can occur above or below the surface. Surface blows are usually visible as a white cloud of water spray, but may be so weak as to be undetectable. The first blow after a surfacing usually appears strong, probably because it is a more forceful exhalation and because water is present above the blowholes during or just after surfacing. On calm days and when whales lie at the surface with the blowholes exposed, the blowholes are relatively dry, and blows may be difficult to detect. Blows of calves can also be difficult to see.

Surface exhalations of gray; humpback, *Megaptera novaeangliae*; fin, *Balaenoptera physalus*; and southern right whales, *Eubalaena australis*, are almost always followed immediately by an inhalation (B. Würsig, pers. obs.). Hence we suspect, following Scoresby (1820), that exhalations and inhalations generally occur together in bowhead whales as well.

Diving and Associated Behavior

The predive flex is a distinctive concave bending of the back seen several seconds before many dives. The whale flexes its back by about 0.5-1 m, so that the snout and tail disrupt the surface. Considerable white water is created at these two points. The whale then straightens its back and lies momentarily still before arching the back convexly as it begins its roll forward and down. The predive flex is seen from low vantage points as an abrupt lifting of the head, because the flukes apparently only touch the water surface from below.

The predive flex was seen more often during 1980 than during 1981 or 1982. Although it occurred previous to dives well over 50% of the time in 1980, it occurred in only 8% of the observations (before 29 of 352 dives) in 1981. For 1982, we have especially detailed analyses of predive flexes. In that year, predive flexes occurred in presumably undisturbed noncalves before 32 of 132 dives (24.2%); flexes occurred more often in late August than earlier (Table 1). Dives following predive flexes were, on the average, about twice as long as dives without predive flexes (19.00 ± SD 7.877 min, n = 13, vs. 10.15 ±

TABLE 1.—Dives preceded by a predive flex among noncalf bowheads early and late August 1982. The frequency of occurrence is significantly higher after 19 August (chi-square = 4.29, df = 1, 0.025 < P < 0.05).

	Up to 19 Aug. 1982	After 19 Aug. 1982	Total
Dives with predive flex	9	23	32
Dives without predive flex	49	51	100
Total	58	74	132

7.465 min, n = 36; Mann-Whitney U = 97.5, P < 0.01). Five dives were preceded by two predive flexes, with the flexes separated by a blow. Two dives were preceded by three flexes. We have no data on durations of dives following multiple flexes.

During the dive, which can at times be predicted by the predive flex, the whale makes its body convex and pitches forward and down. If the angle of submergence is steep, the tail is usually raised above the surface; if not, the tail may remain below or just touch the surface. Rarely do bowheads sink down without visibly arching the back.

In 1982, 59 of 138 dives (42.8%) were preceded by raised flukes. Of the 32 dives preceded by one or more predive flexes, 21 also showed raised flukes. These two predive behaviors tended to occur together (χ^2 = 3.94, P < 0.05, df = 1), and dives with raised flukes were significantly longer than those not preceded by raised flukes (18.67 $\pm$ SD 9.966 min, n = 12, vs. 10.05 $\pm$ 6.956 min, n = 38; Mann-Whitney U = 114, P < 0.01).

There was no difference in durations of surfacings concluded with and without raised flukes. However, surfacings including predive flexes tended to be longer than those without predive flexes (3.09 $\pm$ SD 1.038 min, n = 14, vs. 1.79 $\pm$ 1.284 min, n = 52; t = 3.50, df = 64, P < 0.001), probably because durations of surfacings and dives are correlated (Würsig et al. 1984).

The function of the predive flex is unknown. Flexes occur more often before longer dives (which may take the whales deeper in the water column). Raising the flukes before a dive appears related to the steepness of the dive; whales that roll forward while dropping the front of the body at least 30° below the water surface usually raise their flukes. The weight of the raised tail stock in the air must help propel the animal downward (much as human skin divers raise their legs above the surface during the initiation of a steep dive). Although raised flukes are common during steep dives in many whales, the predive flex has not been reported in other species.

The Underwater Blow

The underwater blow is a burst of air emitted underwater. The bubble burst is circular and up to 15 m in diameter when it arrives at the surface. Release of air underwater was recorded about 10 times via nearby (< 1 km away) sonobuoys; the noise was detectable for 3-4 s, but the white water and expanding concentric wave were visible much longer. On one occasion, we definitely saw that the air came from the blowhole rather than the mouth, and we believe that this is always true. We saw underwater blows immediately after whales dove and just before they surfaced, but more usually in the middle of the dive, when the whales were out of sight.

Underwater blows were most frequent in 1980 during periods of pronounced feeding in water < 14 m deep (see Feeding section). In 1980, we saw 158 underwater blows in 30.4 observation hours; in 1981, 57 blows in 30.8 observations hours; and in 1982, only 6 blows in 36.5 observation hours. (The difference between years is statistically significant; χ^2 = 189, df = 2, P < 0.001.) Concurrently, whales tended to be found in progressively deeper water from 1980 to 1982.

Underwater blowing occurred more often in the morning and evening than around solar midday in both 1980 and 1981 (Fig. 4; solar noon occurs about 1500 MDT in the eastern Beaufort Sea). The midday "lull" in underwater blowing coincided with a peak in frequency of socializing, the main nonfeeding behavior observed (see Social Behavior section below). Nemoto (1970) suggested that baleen whales in general show a high level of feeding activity in the
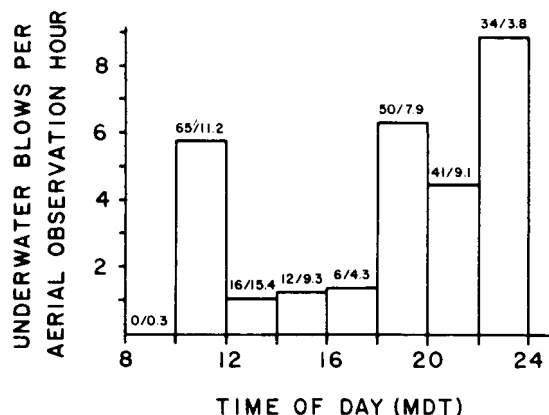

FIGURE 4.—Number of underwater bowhead whale blows per aerial observation hour in relation to time of day, 1980 and 1981 combined. There were few underwater blows in 1982. The numbers at the top of each column are number of blows seen/number of observation hours.

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morning and a lower level during midday, but we have no direct evidence of this in bowheads.

Although underwater blows seem to occur more often in shallow water when whales may be feeding, we have not included this behavior as a definite part of feeding. There is only a general similarity to bursts of bubbles associated with feeding humpback whales in the North Atlantic (Hain et al. 1982), and the bubble nets reported for humpbacks by Jurasz and Jurasz (1979) are very different.

Social Behavior

Behavior was termed social when whales appeared to be pushing, nudging, or chasing each other, or when they were within half a body length of one another. Whales within half a body length almost always stayed close to each other, and oriented towards each other or interacted in some manner. Thus, our use of proximity as an indication of sociality was appropriate. Interactions between mothers and calves, and between whales skim feeding in close proximity, were not included as social interactions in this analysis. Whales may, of course, communicate by sound, and thus may socialize over far greater distances than those described here. Our sonobuoys often detected bowhead calls while socializing was underway. However, we could not verify whether acoustic communication was occurring between any particular whales, so we restricted our definition of socializing to visible behavior. Synchronous diving and surfacing over areas many kilometers in diameter (see below) may represent a different form of social interaction from what we discuss in this section. Because groups of whales usually could not be reidentified positively from one dive to the next, we treated observations of social behavior at intervals of > 5 min as independent for the purpose of counting number of interactions. Conversely, we did not score social behavior by one group more than once in 5 min when counting frequency.

Frequency of Socializing

Social behavior was seen less frequently in late August-early September than in early August, both in 1980 and 1981 (Table 2). Rugh and Cubbage (1980) and Carroll and Smithhisler (1980) reported a higher incidence of social interactions during the spring migration around Alaska than we saw at any time. The apparent waning of social activity from early to late August may be part of a continuing decrease from a higher level in spring.

Little socializing was observed in 1982. In presumably undisturbed whales, we observed only seven cases, all on 8, 19, and 23 August. Throughout August 1982, most whales were alone and making long dives. The overall socializing rate for each year (Table 2) demonstrates the dramatic decrease in socializing in 1982 compared with the two previous years. This decrease may be related to the increase in 1982 in the average distance from shore and depth of water at locations where bowheads were studied. However, we found no consistent trend for socializing to occur more often in shallow water than in deep water within 1 yr.

There was some indication of hour-to-hour variation in amount of social activity in all 3 yr (Fig. 5). In 1980 and 1981, it peaked around 1400-1600 MDT, the noon period by sun time. In 1982, the few (7) cases were recorded from 1600 to 2000 MDT, somewhat after solar noon (Fig. 5). In both 1980 and 1981, there was another peak after 2000 MDT. Why whales should engage in more social activity around noon (and possibly in the evening) than at other times is unknown. However, diel rhythms are well known in several mammals (e.g., Saayman et al. 1973 for bottlenose dolphins; Matsushita 1955 for sperm whales; Schevill and Backus 1960 for humpback whales). The increased level of socializing around noon may reflect a lowered level of feeding at that time, which Nemoto (1970) suggested for baleen whales in general.

Physical Interactions

During surface interactions with nearby whales, socializing whales often turned. In contrast, non-socializing whales often surfaced and dove again without changing direction. In the 3 yr, turns oc-

TABLE 2.—Number of social interactions per aerial observation hour, divided into about 10-d periods, in 1980, 1981, and 1982. Only presumably undisturbed periods are included.

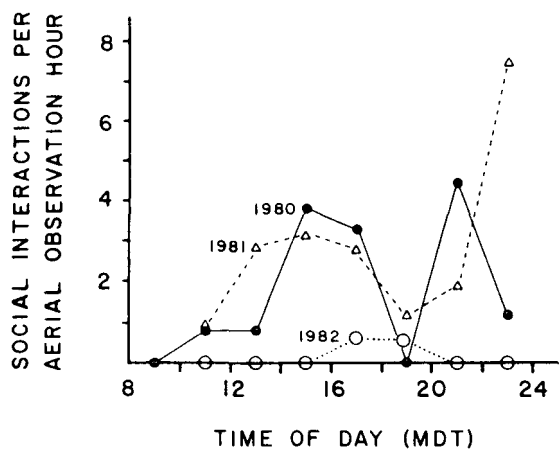| Year	1-10 Aug.	11-20 Aug.	21-31 Aug.	1-10 Sept.	Overall
1980	28/7.0 = 4.0	6/2.9 = 2.1	8/7.7 = 1.0	—	42/17.6 = 2.4
1981	14/4.3 = 3.3	12/5.5 = 2.2	9/3.3 = 2.7	4/4.0 = 1.0	39/17.1 = 2.3
1982	1/1.5 = 0.7	3/7.6 = 0.4	3/12.8 = 0.2	—	7/21.9 = 0.3

FIGURE 5. – Number of bowhead whale social interactions per aerial observation hour in relation to time of day.

curred during 53 of 133 (40%) surfacings with socializing, and in 128 of 484 (26%) without socializing (χ^2 = 9.04; df = 1, P < 0.005).

When bowhead whales touched, they often appeared to push each other. Pushing or touching was usually done with the head, while oriented head to head, or head to tail. However, we also saw whales of adult size dive under the bellies of other whales and apparently nudge or push the other whales near their genital areas. At other times, whales dove under each other at very close range without any indication that they were touching.

Apparent chase sequences involved two or three whales in a line, usually < 2 body lengths apart. During these chases one whale often turned abruptly left or right, and the second (and third) followed. Movement was faster during chases than at all other times when we saw presumably undisturbed whales at the surface.

Both touching and chasing may at times represent low levels of sexual activity, but this is unproven because we cannot determine the sex of a bowhead whale from a distance. Payne and Dorsey (1983) and Tyack and Whitehead (1983) described physically interacting right and humpback whales, respectively, which appeared to be engaging in social-sexual activity.

Possible Mating

In 1981, we twice observed apparent mating. The more prolonged observation was on 10 August 1981, within a 25 km² area where there were 20-30 whales whose main activity was socializing. Two whales

interacted for over 1 h with chases, flipper caresses, belly-to-belly orientation, rolls toward and away from each other, head nudges to the genital area and to the rest of the body, tail slaps, and flipper slaps. One whale, a recognizable animal that we termed "Whitespot", was about 1-2 m longer than the other ("B") and was the more aggressive. Although B originally nudged the genital area of Whitespot, it was Whitespot who appeared to initiate flipper caressing and rolls toward B. The two whales rolled their ventral surfaces together for about 5 s, but B then rolled its ventrum in the air in an apparent attempt to avoid ventral contact with the larger animal. As it rolled away from Whitespot, B defecated, and when Whitespot moved its head toward the genital area of B, B defecated two more times in rapid succession. B then dove away from Whitespot, and Whitespot followed it at the surface in an apparent chase. Whitespot then stopped and, alone at the surface, rolled two times and tail slapped while on its back. It then dove, and the two appeared together again at the surface 4 min later, with no further energetic surface interaction.

We do not know the sex of either animal, but it appeared that Whitespot was attempting to copulate with the reluctant animal. Some of us (Würsig and Payne) have observed southern right whale females frequently roll their ventra away from aggressive males, leaving their genital areas above the surface of the water, where the males cannot reach them. Everitt and Krogman (1979) photographed very similar behavior of a group of six bowheads off Barrow, AK, in May. Our observations here were highly reminiscent of such behavior. Although adult females are slightly larger than adult males in both right and bowhead whales, we commonly see large southern right whale males in pursuit of smaller females, which attempt to avoid the males.

On 25 August 1981, two bowheads briefly placed their ventral surfaces together and clasped each other with their flippers. After 1 min, they rolled apart, blew, and dove slowly as a third whale approached. The mutual rolling and leisurely diving indicated that, if this was copulatory behavior, it was mutually undertaken by the two whales in contrast to the previous example.

Group Structure and Stability

Two observations of recognizable bowheads provided evidence about group structure and stability. We observed a distinctively marked pair of adults, one accompanied by a calf, at about lat. 70°10′N, long. 133°50′W on 7 August 1980. We saw a similar-

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ly marked group of two adults and a calf, almost certainly the same whales, on 20 August at lat. 70°07'N, long. 131°30'W, which is about 85 km from the place they had been seen 2 wk earlier. This observation suggests that some groups of bowheads are maintained for at least a few weeks. The observation also suggests that females with calves may sometimes be accompanied by escorts, as has been observed for wintering humpback whales (Herman and Antinoja 1977).

Feeding

Feeding appeared to occupy much of the time of the bowheads that we observed, but we had to rely on indirect clues, such as observations of swimming with open mouth, mud streaming from the mouth, or presence of feces in the water, to indicate that feeding had taken place. The four possible types of feeding behavior that we identified were 1) water-column feeding; 2) near-bottom feeding; 3) skim feeding; and 4) mud tracking. Of these, the first three rather clearly represented feeding, whereas the function of the last was less certain. As noted above, underwater blowing showed some association with feeding, but the connection was uncertain.

In 1980, certain feeding behaviors occurred in particular areas: only water-column feeding was seen near the Issungnak artificial island site (Fig. 1), whereas only skim-feeding was seen off the Tuktoyaktuk Peninsula near McKinley Bay. In 1981, there was less evidence for feeding, although we suspect that most feeding occurred in the water column. In 1982, when whales dove for long periods (up to 30 min), we suspected water-column feeding to be occurring at almost all times.

Water-Column Feeding

Water-column feeding could not be observed directly. Whales were scored as feeding in the water column when they dove for long periods, and when, between long dives, there was much defecation and only slow forward motion. Defecation is simply an indication of prior feeding. However, particular behaviors such as a series of long dives usually continued for many hours, so occurrence of defecations between long dives was considered indicative of ongoing feeding in the water column.

The frequency of apparent water-column feeding was not constant. In 1980, we saw bowheads water-column feeding from 3 to 22 August. Thereafter, few whales were present in the area where we had observed this behavior, and whales seen elsewhere did

not seem to feed in the water column. In 1981, when we saw less defecation, we only scored as water-column feeding some adult whales that dove for prolonged periods on 24 August, while calves remained at the surface. In 1982, most whales made long dives. These whales probably were feeding in the water column, even though we saw little defecation at the surface. Feeding below the surface may have occurred during many other dives besides those that we classified as dives with water-column feeding.

Observations on 3 August 1980 typify water-column feeding behavior. On this date, bowheads were north of Kugmallit Bay where water depth was 18-38 m. The surface water was turbid, brackish water from the Mackenzie River, but beneath this surface layer, there was a second layer of clearer, saline Beaufort Sea water (Griffiths and Buchanan[7]). The whales occurred in groups of 2-10 animals, and occasionally as individuals without others nearby. Group members showed a high degree of synchrony, often surfacing very close together and remaining close at least until they dived again. Not only did the members of a group surface and dive synchronously, but various groups spread over an area several kilometers in diameter all tended to be at the surface or beneath it at the same time.

While the animals were at the surface, they moved slowly forward while taking a series of breaths. As each individual dived, it raised its tail clear of the water, and disappeared from view in the turbid water. Thus, these dives must have taken the whales well below the surface. When the whales were at the surface, they often disturbed the turbid surface layer, exposing dark patches of seawater from deeper depths. However, while submerged after a dive that was preceded by raised flukes, they did not affect the thin surface layer, indicating that they were probably feeding in the underlying clearer ocean water. Defecation was frequent, suggesting that feeding may have taken place recently. The feces clouds were red-orange.

Bottom Feeding

On 12 August 1980, we noticed clouds of mud suspended in the water about 25 km west of Issung-

nak artificial island (Fig. 1). The clouds represented suspended mud and not plankton because the material was of the same color as mud dredged up by industrial activities. Whales surfaced with large amounts of muddy water streaming from their mouths, indicating they had been feeding from or near the bottom. This behavior occurred in 24-29 m of water and seemed very localized. We saw no indication of bottom feeding in the same area on 22 August 1980, but we had observed similar mud clouds nearby on 9 August, when prolonged observations were not possible. On 25 August 1981, whales again surfaced with mud streaming from their mouths. The location was 15 km south of the position where we observed such behavior in 1980; water depth was only 10-13 m.

These are, to our knowledge, the first published behavioral observations of apparent near-bottom feeding by bowhead whales. However, Johnson et al. (1966), Durham (1972), and Lowry and Burns (1980) detected pebbles and bottom-dwelling species in bowhead stomachs.

Bottom-feeding whales were usually separated from other whales by 150-300 m when at the surface. On 12 August 1980, at least 10 whales were bottom feeding within an area of 3 km radius. Whether they were feeding on inbenthic or epibenthic invertebrates we do not know. In the eastern Beaufort Sea, the average biomass of inbenthic animals greatly exceeds that of epibenthic animals (Griffiths and Buchanan footnote 7). However, the latter may occur in dense swarms in certain places. For a balaenid whale, such swarms would seem to be a much more suitable type of food than inbenthic organisms. Mud might be taken inadvertently along with epibenthic animals.

Skim Feeding

The only feeding type that we observed directly was skim feeding. In the third week of August 1980, we observed whales moving slowly and deliberately at the surface with their mouths open wide. Usually the rostrum just broke the surface of the water, and was parallel to it. In these cases, the lower jaw was dropped to varying degrees, as could be seen from the depth of the white chin patch. In 1980, skim feeding was observed along the Tuktoyaktuk Peninsula in water 12-22 m deep. Whales occasionally skim fed alone, but more often did so in groups of 2-10 or more individuals. During any one observation period, they stayed in the same general area by repeatedly turning and did not appear to make any net geographic movement. However, we found groups of skim-feeding whales in different locations on different days.

During 1981, we witnessed skim feeding on a large scale only on the evening of 18 August, 32 km NNW of Pullen Island in water 25 m deep. About 20-30 whales in the 25 km² area were swimming with mouths open; they travelled slowly, usually just below the surface (∼ 2-3 m deep). Copepods were unusually abundant in near-surface waters at this location and time (Griffiths and Buchanan footnote 7). On 23 and 24 August 1981, we saw one isolated example on each day of a whale feeding at the surface briefly (observed for < 1 min) in approximately the same area as on 18 August.

Typically, skim-feeding whales were oriented with their backs at the water's surface. However, they occasionally swam on their sides with mouths open at an angle of about 60°, and once we saw two whales separated by three body widths swimming on their sides, belly to back. In one instance, a skim-feeding whale swam inverted for at least 3 min, with the underside of its chin at the surface.

Frequently, the skim-feeding whales swam in echelon formation, each whale swimming just behind the preceding whale, but offset laterally by one-half to three body widths, reminiscent of geese in V formation (Fig. 6). At other times, they swam abreast and parallel to one another. Videotape from 18 August 1981 showed that whales within the echelons were a mean of 0.53 whale lengths apart (SD = 0.599, n = 66), or about 8 m. These distances were measured from different echelons or from the same echelon at intervals of at least 5 min. We videotaped a recognizable whale for almost 3 h on this day as it skim fed in changing echelon formations, usually taking the lead position. Echelons were clearly dynamic in terms of membership, size, and organization. In 1981, the mean echelon size was 4.7 animals (SD = 4.05, n = 23). While the largest such formation observed in 1980 contained 5 individuals, the largest in 1981 contained 14 animals.

We suspect that echelon feeding increases the feeding efficiency of those animals staggered behind and to the side of other individuals, perhaps by helping them to catch prey that escape or spill from the mouth of the whale in front, or by reducing the ability of prey to escape to the side. Skim feeding in echelon may allow more effective exploitation of concentrated patches of small prey than would be possible if whales were feeding alone. If so, the change in efficiency that accrues when echelons are formed may have an important cost/benefit effect on energy expended per whale. The predominant prey types of bowheads include copepods and euphausiids (Lowry
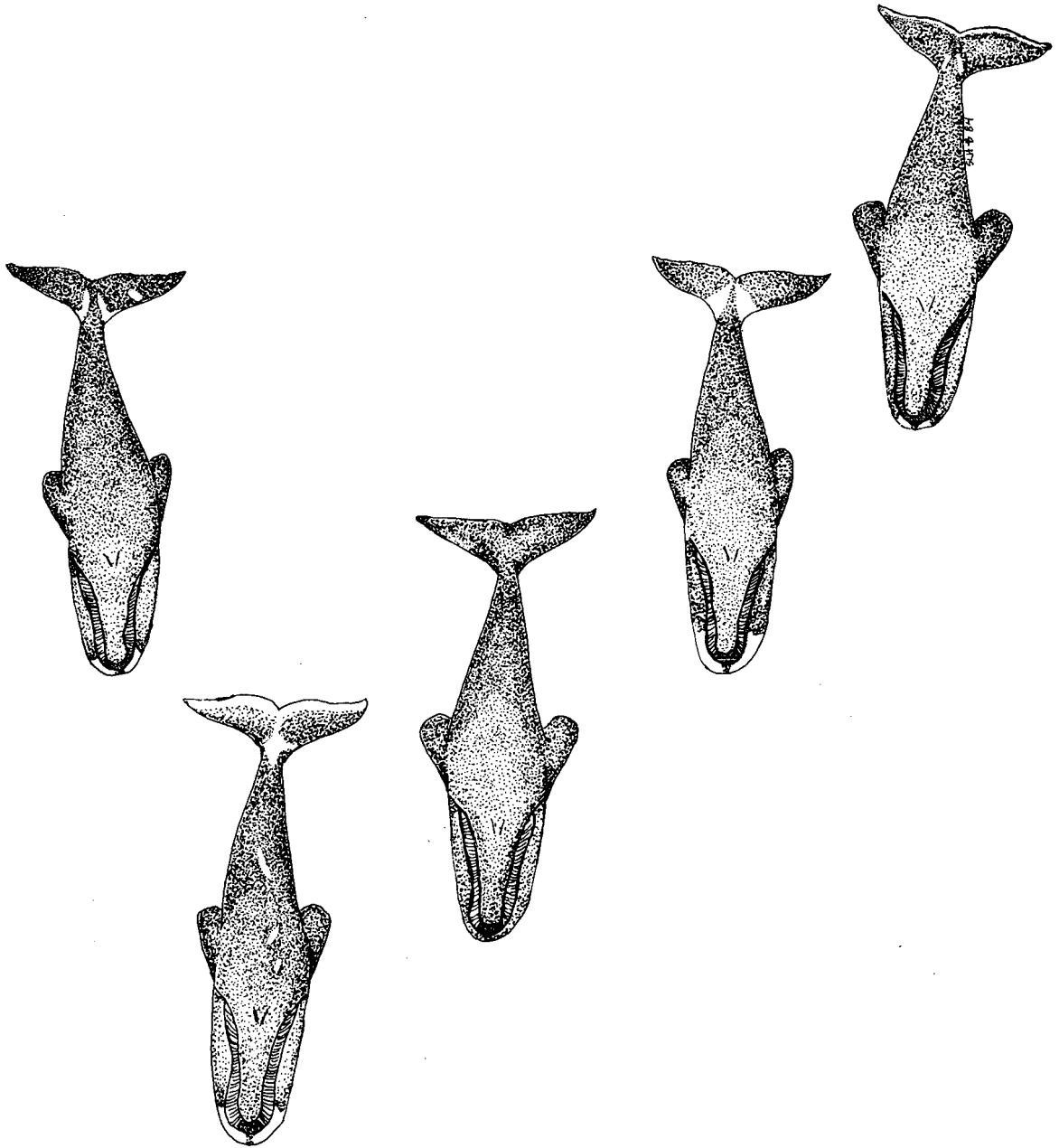
FIGURE 6. – Five bowhead whales skim feeding in echelon formation. Drawing after a 35 mm photograph and video footage from the air.

and Burns 1980). The latter are adept at avoiding most sampling gear because of their rapid movement. However, bowheads at times collect euphausiids in very large numbers, despite the bowhead's slow swimming speeds relative to the better known euphausiid predators such as rorquals. Perhaps

echelon feeding is especially helpful in catching fast-swimming prey such as euphausiids.

During 1982, little direct evidence for feeding was noted. We saw no skim feeding at the surface, and noticed only nine isolated instances when a whale's mouth appeared to be open slightly. These brief, slight

openings of the mouth contrasted sharply with the sustained large gapes observed in 1980 and 1981, and probably did not represent feeding. In southern right whales, Payne (pers. obs.) has observed mouth opening that he interprets as yawning following sleep.

Mud Tracking

Mud tracking occurred when whales swimming in shallow water (< 12 m depth) disturbed the bottom sediments with each fluke beat, producing clouds of mud joined by a narrower trail of muddy water. These elongated clouds of mud were different from mud clouds produced during presumed bottom feeding. Although we often could not see the whales, in at least a few instances their mouths were open. We saw mud tracking during only three flights in the third week of August 1980.

Mud tracking probably represented incidental disturbance of bottom sediments by a whale feeding near the bottom in shallow water. We saw no evidence that bowheads ever turned and swam back along a mud track made previously. The mud tracks tended to be straight, and some extended for well over 1 km. At certain times, clouds of mud streamed from the whale's body as it swam near the surface. In this case, we suspect that the whales had contacted the bottom, and that the mud had stuck to their bodies. Sometimes, mud-tracking whales exhaled while submerged, producing a characteristic burst of bubbles (see section on The Underwater Blow).

Defecation

Defecation usually was evident as a cloud (2-3 m diameter) of red-orange feces near the surface. Whales almost invariably were moving forward or diving when they defecated, and over 50% of the bowheads observed defecating in 1980 did so while the tail was arched up high out of the water just before the dive. The anus was thus close to or at the surface. No part of the body appeared to touch the feces cloud, which was visible at the surface for up to 10 min. When whales moved forward while defecating, the feces were more dispersed and disappeared within 1-2 min. Brown (1868) noted that feces of eastern arctic bowheads were also red. Renaud and Davis[8] observed red clouds of feces off the Tuktoyaktuk Peninsula in 1980.

Defecation was seen more often in 1980 (23 cases during 30.4 h over whales) than in 1981 (11 cases during 30.8 h over whales). The difference is statistically significant (χ^2 = 4.39, df = 1, 0.025 < P < 0.05), and may be related to year-to-year differences in feeding patterns. In 1982, we saw only one defecation (by a lone whale playing with a log). Because we can only observe defecations by whales at the surface, we compared the rates in reference to the number of whale-hours of observation at the surface. In 1980, there were 2.29 defecations/whale-hour at the surface, as opposed to 0.73 in 1981, and 0.09 in 1982 (χ^2 = 27.58, df = 2, P < 0.001). This decrease could result either from decreased defecation (indicative of less feeding), or from an increasing tendency to defecate under the surface where we could not observe it. During 1982, dives were longer than in the 2 previous years (Würsig et al. 1984), and we suspect that much water-column feeding was taking place.

Adult-Calf Pairs

Calves of the year are a light tan color, distinct from the dark black of noncalf bowheads. An adult that remained close to a calf was assumed to be the calf's mother. For the closely related southern right whale in winter, Payne and Dorsey (1983) found that in unambiguous adult-calf pairs, the adult was always a female, and that identified calves were always seen with the same individually identified female. At times, we saw apparent nursing as calves submerged briefly, oriented toward the teat region of the adult. In 1982, we made longer observations of calves than in either 1980 or 1981.

The relative lengths of six calves measured from videotape sequences recorded during August 1981 were a mean of 0.57 ± SD 0.052 adult body lengths. Many of the calves we observed in August 1982 appeared to be smaller, about one-third adult size. This is corroborated by the fact that 14 calves measured via photogrammetry in August-early September 1982 were 4.1-7.6 m long, or 33-45% (mean 41%) of the length of the accompanying adult (Davis et al.[9]). It may be that births occurred earlier in the year in 1981 than in 1982, or that the females videotaped in 1981 were smaller, on average, than those measured in 1982.

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[8]Renaud, W. E., and R. A. Davis. 1981. Aerial surveys of bowhead whales and other marine mammals off the Tuktoyaktuk Peninsula, N.W.T., August-September 1980. Unpubl. Rep., 55 p. LGL Ltd., Toronto, for Dome Petroleum Ltd., Box 200, Calgary, Alberta T2P 2H8, Canada.

[9]Davis, R. A., W. R. Koski, and G. W. Miller. 1983. Preliminary assessment of the length-frequency distribution and gross annual reproductive rate of the western arctic bowhead whale as determined with low-level aerial photography, with comments on life history. Unpubl. Rep., 91 p. LGL Ltd., Toronto, for National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., BIN C15700, Seattle, WA 98115.

When an adult and calf were both at the surface, they were usually within one adult-length of each other. Videotape sequences showed the mean distance apart to be 0.61 adult whale lengths (SD = 0.564, n = 8, range = 0.1-1.5), or about 9 m. The calves spent most of the time lying beside the adult, and facing in the same direction as the adult. At times, the calf strayed up to two whale lengths from the adult, and then oriented toward the adult. While the adult lay at the surface, the calf often submerged near the belly of the adult with its tail close to the adult's tail. This position is probably indicative of nursing. The calf then often swam under the adult, surfaced on the other side, respired one or two times, and submerged again toward the adult's belly, alternating sides with each surfacing. The calf also appeared at times to rest, lying quietly on the back and tail of the adult.

Calves were sighted at similar frequencies in all 3 yr (Table 3). However, durations of surfacings by calves were longer in 1982 than in 1980-81. Because of this, calves accounted for 15% of whale-hours of observation in 1982, but only 3% in 1981, and 4% in 1980 (Table 3).

Calves Alone

In 1982, calves spent almost 40% of their time at the surface unaccompanied by an adult. This was comparable with their behavior in 1981, but unlike 1980 when they were rarely seen alone. (Table 3).

On 24 August 1981, we saw three calves separated from each other and from the closest adults by 100 m to more than 300 m. It was, therefore, often not possible to assign calves to particular females. The nearest adults spent much time submerged, but the calves remained stationary at the surface. At one point, we videotaped an adult that surfaced 4.9 adult lengths from a calf lying stationary at the surface. During another videotaped sequence, an adult-calf pair, 0.2 lengths apart, was separated from a lone calf by 7.6 adult lengths. We suspect that the adults were feeding in the water column while calves waited at the surface.

In 1982, we observed four lone calves at the surface, on 18, 19, and 23 August, and on three of these occasions we saw the calf rejoin its presumed mother. On 18 August, a lone calf surfaced and oriented straight toward an adult at a distance of 1.6 km. When it came within 75 m of the adult, the adult also began to swim rapidly toward the calf. During a second incident on the same day, a calf and adult swam rapidly toward each other from at least 300 m distance. In both cases, the two dove simultaneously after coming together. On 23 August 1982, an adult surfaced 180 m from a lone calf, and the adult oriented toward the calf. When the two whales were ~ 120 m apart, the calf also oriented toward the adult, but the adult was mainly responsible for closing the distance between them, as it swam at medium speed toward the calf. When the two whales were ~ 20 m apart, the calf dove and reappeared 18 s later, reoriented by 180°, lying to the right of the adult, and facing in its direction. The calf then

TABLE 3.—Calf sightings and observation time in 1980, 1981, and 1982. Only flights with behavioral observations are considered, and both presumably undisturbed and potentially disturbed periods are included. The number of sightings of calves is an approximate count because multiple counts of the same calf were possible in cases where the calf and its mother were not individually recognizable.

	1980	1981	1982
No. sightings of calves	12	16	16
No. flights	14	18	14
Calf sightings/flight	0.86	0.89	1.14
Hours in plane over whales	30.4 h	30.8 h	36.5 h
Calf sightings/hour	0.39	0.52	0.44
Calf time at surface with mother	20.4 min	17.5 min	63.1 min
Calf time at surface alone	1.6 min	12.7 min	38.2 min
Total calf time at surface	22.0 min	30.2 min	101.3 min
% of calf surface time alone	7.3%	42.1%	37.7%
Whale-hours of observation at surface	10.03 h	14.98 h	10.95 h
Calf-hours of observation/ whale-hour of observation	0.037	0.034	0.154
Calf time at surface/ sighting	1.57 min	1.89 min	6.33 min

submerged several more times toward the belly of the adult, probably nursing.

Our observations of adults and calves orienting accurately toward one another at distances up to 1.6 km apart suggest that there was acoustic communication between the two. There is possible evidence for this from the incident on 23 August 1982. The rate of low-frequency tonal frequency-modulated calls, which we suspect to be long-distance contact calls, increased while the mother and calf were swimming toward each other from some distance apart, and then ceased altogether once the two whales were joined. Several unusual higher pitched calls of undetermined origin were also recorded by a sonobuoy near the calf while the two whales were separated.

Nursing

When the lone calf of 23 August 1982 joined its mother after a separation of at least 71 min, we observed the longest probable nursing bout seen during the study. As the two animals approached each other head on, the calf dove out of sight for the first apparent nursing dive when they were still about 22 m apart. The calf dove toward the teat region of the adult six times in all, with submergences lasting 18, 11, 27, 17, 12, and 10 s (mean = 15.8 ± SD 6.37 s). These brief dives were separated by brief surfacings lasting 6, 6, 9, 11, 23, and 17 s (mean = 12.0 ± SD 6.75 s). Each surfacing included a single respiration. Nursing ended as the calf and adult dove out of sight at the same time. Although there was no apparent progression in the durations of the calf's nursing dives over the entire nursing bout, surfacings tended to lengthen, suggesting an appeasement of the calf's eagerness to nurse. The duration of the probable nursing bout from the start of the first nursing dive to the start of the deep dive by both mother and calf was 2.78 min.

The other bouts of probable nursing were shorter, sometimes < 1 min, and involved adult-calf pairs that had not recently been separated, as far as we knew. Usually, all that we could see was one or two short dives by the calf toward the teat region of the mother at the end of a surfacing sequence, followed immediately by a dive by both animals.

Other Behaviors

Aerial Activity

Bowhead whales sometimes leaped or breached from the water, forward lunged, or slapped the tail or a pectoral flipper onto the water. During breaches, 50-60% of the body length left the water. The whale emerged head first at a small angle from the vertical, usually with the ventrum down. It then twisted and fell back onto the water on its side or back. Forward lunges differed from breaches in that the body came out of the water at a shallower angle and did not twist; the whale reentered belly first. The forward lunge had a larger forward component than did the breach.

Breaches, tail slaps, and flipper slaps sometimes occurred in bouts. Within bouts, intervals between successive breaches were generally greater than those between tail or flipper slaps. For example, breaches, tail slaps, and flipper slaps by one whale that engaged in all three behaviors on 6 August 1980 were at average intervals of 46, 8, and 4 s, respectively.

The incidence of aerial activity was comparable in the 3 yr (0.60, 0.93, and 0.82 bouts/whale-hour in 1980, 1981, and 1982), but much lower than reported for spring migration. Rugh and Cubbage (1980) saw breaching by 23% of all bowheads (n = 280) observed passing Cape Lisburne, AK, in spring.

Play

Although many social interactions may involve play, we could not distinguish low levels of mating activity or aggression from play. We scored play behavior only when whales spent some time at the surface associating with an object other than a conspecific. We saw no such behavior in 1980, but several incidents in 1981 and 1982. Few such interactions have been described for other baleen whales.

LOG PLAY. – We witnessed whales playing with logs in the water on two occasions in 1981, and once in 1982. Log play, which consisted of a whale nudging, pushing, or lifting a log, lasted 5 s, 10 min, and at least 1.5 h during these three observations. In 1981, other researchers saw bowheads playing with logs twice in the same general area as our 1981 observations (C. R. Evans and J. Hickie[10]). During two of our three observations the water was ensonified by noise pulses from distant seismic exploration (Richardson et al. in press). However, there was no proof of a connection between log play and seismic noise.

Some elements of log play by bowheads were similar to play with seaweed observed in southern

right whales (Payne 1972). Both involved lifting the object with the head, moving the object along the back, and patting it with the flippers. Two log-playing bowheads attempted to push the log under water with the head. This action was reminiscent of a motion commonly made by male right whales when attempting to mate with uncooperative females (Payne, pers. obs.).

CALF PLAY.—On two occasions in 1982, lone calves at the surface interacted with debris in the water, and the actions had the appearance of play.

The first incident occurred over 12.3 min on 19 August 1982, when a lone young-of-the-year calf followed a line of surface debris ∿ 2 m wide, probably composed mainly of invertebrates. The calf stayed at or just below the surface and oriented directly along the windrow, changing course as the line meandered left or right. Although the calf appeared to have its mouth open slightly for brief periods, it did not appear to feed extensively, if at all. However, its movements thoroughly disrupted and dispersed the line of debris. The movements were rapid and jerky, reminiscent of any uncoordinated young mammal. The calf lunged forward while in the debris on three occasions, and slapped its tail onto the water surface twice. For ∿ 30 s, it moved rapidly along the line, ventrum up, with rapid up-and-down movements of the tail for the entire time. The sequence ended when the calf dove out of sight at the end of the windrow; we did not see it with an adult. Although the incident did not seem to represent concerted feeding, this "play" by the calf may have been practice in skills required for feeding.

A second incident of "calf play" occurred on 23 August 1982. This calf was first encountered hanging quietly just below the surface, or moving forward very slowly. During slow movement, it entered an area marked by dispersed fluorescein dye from one of our dye markers (see section on Methods). The dye covered an area about 40 m by 100 m. Immediately upon entering the area of bright green water, the calf became active. During the 22.3 min of association with the dye, the calf rolled ventrum up eight times for 5-20 s each time, and moved back and forth within, and to the edge of, the dye-clear water interface. Although not as active and not beating its tail as fast as the calf in the windrow, this calf made abrupt turns of > 90° on 25 occasions during its stay in the dye, reorienting itself at the dye's edge in order to remain within the dye. The calf ultimately moved out of the dye and oriented toward an approaching adult. When the two joined, the calf apparently began nursing.

Synchrony of Activity and Orientations

There was often an impressive degree of synchrony of basic behaviors among members of quite widely spaced groups. We observed apparent synchronization of behaviors on time scales ranging from seconds to days.

Synchrony in General Activity

During 1980, we found that all or most bowheads in various areas did the same thing for up to several days. Some days later, the whales had usually moved, and whales were then found elsewhere engaged in different activities. For example, on 3 and 5 August 1980, whales north and east of Issungnak artificial island were mainly engaged in water-column feeding, with frequent defecation. By 6 and 7 August, whales in this area shifted to more surface-active behavior, interacting in groups with pushes and apparent chases. We saw little defecation at this time. On 12 August, at least 15 animals about 30-40 km west of this area were all apparently bottom feeding.

Whales were encountered in two additional areas in 1980: east of Pullen Island (19 and 20 August) and just west of McKinley Bay (19-22 August). In the Pullen Island area, all whales were mud tracking as described above. In the second area, mud also was evident, but there was much less underwater blowing. Some animals had mouths open at the surface. On 22 and 23 August 1980 almost all whales we encountered were skim feeding in groups of 10-30 animals north of McKinley Bay. However, in the Issungnak area farther west, substantial numbers of whales were still water-column feeding. On 27, 29, and 31 August 1980, whales interacted in small groups of 2-5 individuals. Some small groups oriented SSW, perhaps indicating the beginning of migration.

In summary, during 1980 (but not 1981 or 1982) we found that whales in various areas did much the same thing for up to ∿ 5 d, but then shifted location, activity, or both. A partial explanation for the synchrony of behavior seen in 1980 may be that whales moved to exploit new food resources, and that the most appropriate feeding mode changed according to site-specific conditions. In the subsequent 2 yr, it appeared that whales were doing more water-column feeding in deeper water, perhaps because of a more consistent food supply.

Synchrony in Dives and Surfacings

We sometimes had the impression that all whales

in an area were synchronizing their surfacings and dives. Many were too far apart to be in visual contact. Ljungblad et al (1980) also reported synchrony among whales engaged in water-column feeding ~75 km east of Kaktovik, AK. They reported that ". . . whales were observed on the surface almost at regular intervals and gave the impression of resting between dives; then, suddenly, no whales would be seen in any quadrant for several minutes."

Although synchrony in surfacings by animals far apart suggests acoustic contact between animals, it is not proof of communication over that distance. The synchrony could be established through independent responses to common external cues. It could also occur if the animals were close together and visually synchronized before observations began; the observed synchrony would then be a residual phenomenon that persisted because of whales diving and surfacing for similar lengths of time. None of these possible explanations – acoustic communication, common external cues, or residual phenomenon – can be either proven or discounted at this time.

Synchrony in Orientations

Analysis of orientations provides additional evidence that widely separated whales at times synchronize their behavior during summer. Our best data were from three flights in 1980 when we flew in a straight line. At these times, we counted each individual only once. Rayleigh and χ^2 tests (Batschelet 1972) show that whale orientations were significantly nonrandom (Table 4).

For flights when we circled to make detailed behavioral observations, we analyzed orientations using the first heading noted for each surfacing of a whale. Because we were making repeated observations on the same animal in some cases, any consistency in orientations during those flights is attributable in part to different whales, and in part to subsequent surfacings of the same whale. In 1980 and 1981, the whales were oriented nonrandomly during 7 of the 11 flights with enough data for analysis (Table 4). The headings changed from day to day, however, and bore no apparent relationship to the general behavior of the whales. In 1982, no significant departures from uniformity were found during any of the five flights with sufficient data for analysis.

The headings on the latest day with observations in 1980 and 1981 usually were not in the direction to be expected at the beginning of the westward migration. On 31 August 1980, most bowheads observed while we circled north of the Tuktoyaktuk Peninsula were oriented north, east, or south (mean 121°T (true), Table 4). However, later that day on a direct flight, we found other bowheads to be oriented toward the south (mean 189°T). In this same general area, Renaud and Davis (footnote 9) also recorded a slight eastward tendency for bowheads seen on 21-24 August 1980, but a significant southwestward tendency (236°T) on 3-4 September 1980. On 8 September 1981, most whales west of Herschel Island were oriented toward the northeast (62°T), again not the direction to be expected at the beginning of westward migration. These results support our impression that most of the whales we observed were not migrating.

TABLE 4.—Bowhead orientations, judged relative to true north from the air, 1980-81. Only during the direct flights was each observation known to represent different animals. During the circling flights, each whale was scored an unknown number of times (but only once per surfacing).

| Date | No. of animals with these orientations | | | | | | | | | Vector mean direction | Rayleigh test | Chi-square test P |
	N	NE	E	SE	S	SW	W	NW	Total			
Direct flights												
11 Aug. 1980	16	1	3	0	5	2	10	6	43	321°	<0.001	<0.001
12 Aug. 1980	7	5	16	5	7	6	9	2	57	bimodal	n.s.	<0.025
31 Aug. 1980	1	1	1	3	8	8	0	1	23	189°	<0.001	¹/
Circling flights												
31 Aug. 1980	4	4	6	3	11	1	0	2	31	121°	<0.05	/
10 Aug. 1981	0	3	0	2	0	4	0	1	10	—	n.s.	/
10 Aug. 1981	3	1	7	2	1	6	0	1	21	bimodal	n.s.	/
13 Aug. 1981	12	9	11	1	1	0	1	1	36	43°	<<0.001	/
18 Aug. 1981	2	5	10	5	6	1	2	1	32	111°	<0.001	/
18 Aug. 1981	3	0	0	0	0	1	6	0	10	289°	<0.005	/
23 Aug. 1981	0	4	1	1	0	0	0	0	6	62°	<0.02	/
24 Aug. 1981	1	0	3	2	5	8	10	5	34	243°	<0.001	/
6 Sept. 1981	1	7	2	1	0	2	3	3	19	—	n.s.	/
7 Sept. 1981	2	5	1	1	0	2	2	3	16	—	n.s.	/
8 Sept. 1981	1	8	3	1	1	0	0	0	14	62°	<0.001	/

¹/ means cell sizes too small for a chi-square test.

We do not know whether consistent orientations represented a type of social synchrony, or whether the whales independently reacted to environmental stimuli (such as currents or wave orientations). Norris et al. (1983) and Braham et al. (1984) reported gray and bowhead whales, respectively, that may have been feeding by stationing themselves against a current. Shane (1980) has reported a similar stationing against the current for bottlenose dolphins in Texas. Gray whales in lagoons have been observed to move in the same direction as the tidal current (Norris et al. 1977), but in that case movement may have been related to avoiding shallow water as the tide receded.

Miscellaneous Observations

Speed of Travel

In 1980 and 1981, some data were gathered on bowheads visible from Herschel Island. The whales were usually > 3 km from shore, and detailed behavioral observations were infrequent. However, speed was sometimes measurable with a surveyor's theodolite. Whales rarely changed direction within any one 30 s period, so we calculated speeds from theodolite readings taken within 30 s of each other. This criterion was changed to 60 s for 30 August 1981, when a whale was followed at the surface for a long period, and changed direction relatively little.

For 1980, average speed was 5.1 km/h ($n = 18$, SD = 2.93) at the surface, and 4.3 km/h ($n = 4$, SD = 0.79) below the surface. The 1980 speeds are comparable with the most reliable estimates derived by Braham et al. (1979) and Rugh and Cubbage (1980) for migrating bowheads: 4.8-5.9 km/h and 4.7 $\pm$ SD 0.6 km/h, respectively. However, based on additional data, Braham et al. (1980) estimated the mean speed at Point Barrow in spring to be 3.1 $\pm$ SD 2.7 km/h. Speeds during active migration along the coast of Baffin Island in fall were 5.0 $\pm$ SD 1.3 km/h ($n = 22$) based on theodolite observations from a cliff (Koski and Davis[11]).

On 30 August 1981, an adult whale traveling east was observed continuously for 1.52 h. Its behavior was unusual – it did not submerge during the entire time. Its mean speed was 2.3 $\pm$ SD 1.26 km/h, considerably slower than the speeds mentioned above. Its mean blow interval was 10.0 $\pm$ SD 13.55 s ($n =$

420), significantly lower than the mean for all other undisturbed whales observed from Herschel Island (14.6 $\pm$ 9.56; $n = 60$; $t = 2.54$, $P < 0.02$).

On 8 September 1981, a mother-calf pair was observed by theodolite for 1.8 h. The average speed of the calf was 8.9 $\pm$ SD 5.57 km/h ($n = 28$). During this rapid movement, the calf exhibited breaches, forward lunges, tail slaps, and flipper slaps.

Associations of Bowheads with Other Species

We saw several marine mammal species in the same general areas in which we observed bowheads: ringed seals, Phoca hispida; white whales, Delphinapterus leucas; and a gray whale. There was no obvious interaction between these species and bowhead whales. The gray whale was about 500 m from the closest bowhead. The Canadian Beaufort Sea is the extreme northeastern limit of the gray whale's summer range (Rugh and Fraker 1981).

Flocks of up to 50 phalaropes (Phalaropus sp.) were often present near skim-feeding bowheads. These birds often alighted on water that had been disturbed by the whales, sometimes only a few meters from the whales. Phalaropes and bowheads probably feed on some of the same plankton species. The whalers used the presence of phalaropes as an indicator of where "whale feed" was present and, therefore, where whales were likely to be found (J. R. Bockstoce in press). Aside from phalaropes, we noticed glaucous gulls, Larus hyperboreus; arctic terns, Sterna paradisaea; and unidentified gulls circling briefly over whales on eight occasions.

DISCUSSION

Activities of Bowheads in Summer and Other Seasons

From 1980 through 1982 we observed a steady progression in the August distribution of bowhead whales near Tuktoyaktuk from shallow water nearshore to deeper water farther from shore (Fig. 3; Richardson et al.[12]). Such a dramatic difference in distribution over the 3 yr may be due to many different ecological and behavioral factors. Disturbance

[11]Koski, W. R., and R. A. Davis. 1980. Studies of the late summer distribution and fall migration of marine mammals in NW Baffin Bay and E Lancaster Sound, 1979. Unpubl. Rep., 214 p. LGL Ltd., Toronto, for Petro-Canada Explorations, Calgary. Available from Pallister Resource Management Ltd., 700 - 6th Avenue S.W., Calgary, Alberta T2P 0T6, Canada.

[12]Richardson, W. J., R. A. Davis, C. R. Evans, and P. Norton. 1983. Distribution of bowheads and industrial activity, 1980-82. In W. J. Richardson (editor), Behavior, disturbance responses and distribution of bowhead whales Balaena mysticetus in the eastern Beaufort Sea, 1982. Unpubl. Rep., p. 269-357. LGL Ecological Research Associates, Inc., Bryan, TX, for U.S. Minerals Management Service, Reston, VA. Available from Minerals Management Service Alaska OCS Region, P.O. Box 101159, Anchorage, AK 99510.

by industrial activity in nearshore waters is also a possibility (see footnote 12). The fact that predominant feeding modes shifted from year to year is consistent with the "variable food supply" explanation. In 1980, whales in shallow water exhibited bottom feeding and skim feeding, while whales in slightly deeper water apparently fed in the water column. In 1981, most feeding appeared to be water-column feeding and skim feeding. In 1982, whales made long dives and presumably were often feeding in the water column.

Bowhead whales have finely fringed baleen, the longest of any whale species, and are adapted to strain small zooplankters from the sea. Stomach contents indicate that, at least in Alaskan waters, bowheads feed mainly on copepods, euphausiids, and amphipods (Marquette et al. 1982). Summering bowheads tend to occur at locations where copepod abundance is above average (Griffiths and Buchanan footnote 7). Lowry and Burns (1980) examined five whales killed off Barter Island, AK, in autumn and found about 60% copepods and about 37% euphausiids in their stomachs. However, all five whales may have fed at least partially near the sea floor; about 3% of the stomach contents consisted of mysids, amphipods, other invertebrates, and fish. Durham (1972) also suggested, based on stomach content analyses showing mud-dwelling tunicates, vegetation, silt, and small pebbles, that bowheads feed at times near the bottom. Lowry and Burns concluded from stomach content analyses that "... a feeding dive probably involves swimming obliquely from surface to bottom and back, feeding the entire time." Although this may be true at times, there is no direct information on underwater feeding behavior. We suspect that bowheads can detect concentrations of prey and open their mouths when appropriate. The bowhead whale is perhaps a more catholic feeder than once thought, capable of taking advantage of many different types of prey items at various positions in the water column and near the bottom. Year-to-year changes in distributions and availability of prey may account for the distributional changes that we have observed, but data on yearly changes in prey are lacking.

During spring migration around Alaska, bowhead whales appear to do little feeding; their stomachs usually are nearly empty (Marquette et al. 1982). On the other hand, feeding continues in autumn after bowheads have moved from the Canadian to the eastern part of the Alaskan Beaufort Sea (Lowry and Burns 1980; Marquette et al. 1982). Some feeding occurs in autumn as far west as the Point Barrow area (Lowry et al. 1978; Braham et al. 1984),

and perhaps farther west off the Soviet coast (Johnson et al. 1981).

Feeding is not the only activity of bowheads in summer. Socializing, perhaps with occasional sexual activity, is also important. In 1982, however, there was less socializing than in 1980-81. Whales were in close proximity to each other less in 1982. This year-to-year difference in proximity may be related to the difference in type of feeding. While skim feeding at the surface, whales are often in close echelons. The proximity necessary for echelon feeding offers more chance for socializing, and socializing before or after feeding in echelon may be important to that mode of feeding. When whales appear to feed in the water column, however, they usually do not stay as close together. Thus, this type of feeding may neither require nor stimulate aggregations of animals, and the suspected predominance of water-column feeding in 1982 may explain the low socializing rate that year. Even when there is no close socializing, however, animals are often in a dispersed group within which acoustic communication is probably possible. Our observations of surfacing and dive synchrony by whales spread over distances of several kilometers indicate that they may have been in touch by acoustic communication.

The primary mating period of bowhead whales occurs in spring, including the spring migration (Everitt and Krogman 1979; Carroll and Smithhisler 1980; Johnson et al. 1981; Nerini et al. 1984). We saw some evidence for sexual activity in the Canadian Beaufort Sea in both 1980 and 1981, but not in 1982. Even the active rolling at the surface that we observed in 1981, however, was not as boisterous as observed by Everitt and Krogman in spring. Also, we found an indication of less social activity in late August-early September than in early August. This apparent waning in social activity may be a continuation of the waning of sexual activity that started in late spring.

Many calves are born in winter or spring before the whales reach Point Barrow, although some may be born in early summer (Davis et al. footnote 9). During summer, the activities of female bowheads with accompaning calves are closely coordinated with those of their calves, and differ in some details from the activities of other adult bowheads (this study; Würsig et al. 1984). At least some calves remain with their mothers for the fall migration (Davis and Koski 1980). We know of no information concerning the age of weaning of bowhead calves, but in the closely related right whale, at least some calves remain with their mothers for 1 yr and ultimately separate from their mothers after returning to the

wintering area (Taber and Thomas 1982).

Aerial activity similar to what we observed in the eastern Beaufort Sea–breaches, tail slaps, pectoral flipper slaps, and rolls–has been observed in bow-heads during spring migration (Rugh and Cubbage 1980; Carroll and Smithhisler 1980). It appears that aerial behavior is more frequent during spring migration than on the summer feeding grounds, and this may be related to the high levels of social-sexual activities during spring.

Comparisons with Other Baleen Whales

Bowhead whales spend their entire lives in arctic and near-arctic waters. This habit separates them from all other baleen whales, which may move into temperate or subtropical waters (Lockyer and Brown 1981). However, behavior is in large part determined by feeding mode and related ecological factors (Gould 1982), and here similarities between bowhead whales and several other species are evident.

Gray, bowhead, and right whales are often found in shallow water, and all three species feed on small invertebrates. Gray whales usually feed near the bottom (Bogoslovskaya et al. 1981; Nerini and Oliver 1983), whereas right and bowhead whales may skim their food at or near the surface (see Watkins and Schevill 1976, 1979 for right whales). But all three species are adaptable in feeding behavior. Gray whales apparently will feed on mysids associated with kelp (Darling 1977) or on crab *Pleuroncodes* in the water column (Norris et al. 1983). Right whales also feed below the surface, probably straining swarms of copepods and other small invertebrates in the water column (Pivorunas 1979). While it has long been known that bowhead whales feed at the surface and in the water column (Scoresby 1820), it was recently established from stomach content analyses (Durham 1972; Lowry and Burns 1980), and by observing bowhead whales surfacing with muddy water streaming from their mouths (this study), that bowheads sometimes feed near or on the bottom. It is not surprising that there are many similarities in the behavior of these species. Bowhead and right whales, in particular, are morphologically and tax-onomically quite similar, and appear to obtain their food in very much the same ways. In fact, Rice (1977), mainly relying on a detailed comparison of morphology of bowhead and right whales, suggested that they be put in the same genus, *Balaena.*

The sleeker rorquals (Balaenopterid 'whales) generally gather their food more actively by lunging through concentrations of prey, and at least in the case of humpback whales, have developed compli-cated behavioral strategies for confining and concen-trating their prey (Jurasz and Jurasz 1979; Hain et al. 1982). The rorquals are more often found in deeper water far from shore, and their behavior in general appears to be less similar to that of the bowhead whale than its behavior is to that of gray and right whales.

Gray whales spend part of the winter in warm water, near the shores of Baja California, and most of the summer they feed in the northern Bering and southern Chukchi Seas. Western Arctic bowheads make much shorter migrations, spending their winter in the pack ice of the Bering Sea and their summer predominantly in the Beaufort Sea. The two species thus use the Bering Sea at different seasons and for different purposes–gray whales to feed in summer and bowheads apparently to mate and calve in winter. Like bowhead whales summering in the Beaufort Sea, the primary activity of gray whales summering in the Bering and Chukchi Seas is feeding. However, both bowheads and gray whales (Sauer 1963; Fay 1963) occasionally socialize during summer.

Right whales, like bowhead whales, often appear to feed in the water column or at the surface (Watkins and Schevill 1976, 1979) and may stay in the same general area for days. While skim feeding, both species at times aggregate into echelons. In right whales, these echelons usually consist of only 3-6 whales (Payne, pers. obs.), while up to 14 bow-head whales have been seen skim feeding in echelon. However, Payne observed right whales during winter when little feeding occurs, so apparent dif-ferences in feeding details may be due to seasonal factors.

Apparent differences between the social activity of bowheads and right whales may also be largely attri-butable to the different times of year when they have been studied. The same kinds of nudges and pushes have been observed for interacting whales of both species, but the winter-spring social activity of right whales is much more boisterous than the summer social activity of bowheads. Observations of bowhead whales in spring indicate that their social-sexual acti-vity at that season can be as boisterous as is seen in mating groups of right whales (Everitt and Krogman 1979; Carroll and Smithhisler 1980; Rugh and Cub-bage 1980; Johnson et al. 1981). The belly-up posi-tion of a female bowhead photographed in spring in the Alaskan Beaufort Sea (Everitt and Krogman 1979) indicates that females may attempt to evade potential mates who pursue them in large mating aggregations in the same way that female right

whales evade males in Argentine waters (Payne and Dorsey 1983). A photograph showing a remarkably similar mating group of right whales is shown in the article by Payne (1976). The fact that similar-looking social aggregations are seen in both species argues for a similar social system, although it does not show that the social systems are similar in all details.

Female right whales have young only at intervals of 3 yr or more (Payne, pers. obs.). The same appears to be true of bowheads (Davis et al. footnote 9; Nerini et al. 1984). This long calving interval may help to explain why bowhead and right whales have not made as dramatic a recovery from commercial exploitation as has, for example, the gray whale. Payne also found that right whale females that calve along the shore of southern Argentina in winter are usually not present in the years between calving. Each winter, a different segment of the population of mature females is present, in a 3-yr cycle. It is not known whether this cycling extends to the summer feeding grounds of these right whales. During the present 3-yr study, year-to-year variation in feeding and social behavior was dramatic, but we do not know whether this was due in part to some cyclic and synchronized activity of individual whales. We suspect that variable prey distibution was largely responsible.

ACKNOWLEDGMENTS

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