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Evaluation of Male Reproductive Features as Maturity Indices for Short-finned Squid (*Illex illecebrosus*)

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Abstract

Various aspects of maturation in male *Illex illecebrosus* were examined in an attempt to find evidence for a more realistic maturity scale than that currently in use. Simple indices, based on morphology of the hectocotylized arm, failed to provide satisfactory relationships, but the observed variation in hectocotylus measurements may provide useful insights into the population ecology of the species. The earlier maturation of males than females and the observed premature release of spermatophores cast doubt on the usefulness of spermatophore counts as the basis for developing a reliable maturity scale for male *I. illecebrosus*. Preliminary examination of spermatophores and spermatozoa with light and scanning electron microscopes have so far failed to reveal any difference between material from early and late "mature" males.

Introduction

Basic information on maturation and size at maturity is fragmentary for many cephalopods. In the case of the short-finned squid (*Illex illecebrosus*), which has been the object of a significant fishery in the Northwest Atlantic since the early 1970's, information on the reproductive cycle throughout its distributional range is incomplete. Such studies are difficult because the migratory pattern of the species is still obscure. Although a considerable amount of data has been collected during the presence of short-finned squid (late juveniles and maturing adults) on the continental shelves in summer and autumn over several years, coverage has not been consistent from year to year because of fluctuations in abundance and distribution.

Male and female *I. illecebrosus* exhibit marked dimorphism in relation to the maturation process. Females are still classified as immature in the autumn when they begin their migration from the continental shelves to yet unknown spawning areas (Mercer, MS 1973; Lange and Sissenwine, MS 1981; Amaratunga, MS 1982). However, most maturity scales which are now in use indicate that males are fully mature at the time of migration. The simple presence of spermatophores in Needham's sac, which is the usual criterion of full maturity, is an inadequate one, because laboratory observation have indicated that mating behavior, even in the presence of mature females, occurs only in males which contain several hundred spermatophores (O'Dor *et al.*, MS 1980; O'Dor, 1983). The apparent early maturation in males may simply result from use of a truncated maturity scale, which fails to distinguish the latest stages of maturation. The use of such a truncated scale makes it difficult to compare the maturation process in populations of squid from different areas, because males are considered to be fully mature for perhaps half of their life cycle.

The number, size and shape of spermatophores and the amount of sperm in them has been used widely to distinguish maturity stages in male cephalopods (Dragovich and Kelly, 1962; Mangold, 1963; Austin *et al.*, 1964; Haefner, 1964; Fields, 1965, Hamabe and Shimizu, 1966; Summers, 1968; Hayashi, 1970; Vovk, 1972; Mercer, MS 1973; Zuev and Shevchenko, 1973; Araya and Ishi, 1974; Cohen, 1976; Arnold and Arnold, 1977; Lipinski, MS 1979). Spermatophores have also been suggested to represent, to some extent, clues to the degree of reproductive isolation (Voss, 1977) and to be a more reliable character than other structures, such as suckers and beaks. All of these aspects emphasize interest in providing further information on the characteristics of spermatophores.

Although the authors have observed spermatophores in maturing and mature *I. illecebrosus* males and, after transfer, in a few mated females, no studies on spermatophores of this species have been reported. There are suggestions that spermatophores vary in size, probably in relation to animal size, as for other species (Mangold, 1963). The most detailed information on spermatophores in cephalopods pertains to the genus *Loligo* (Drew 1919) and to some octopodids (Franzen, 1966) but it relates primarily to morphology. The formation and storage of spermatophores and their relationship to the maturation process are still unclear.

Although male squid are usually considered to be mature when spermatophores are found in Needham's

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sac, there are indications that the first spermatophores may be incompletely developed and that their production occurs over a considerable period of time (Grieb and Beeman, 1978; Coelho *et al.*, MS 1982; Voss, 1983). Because the basic process of spermatogenesis in males is apparently continuous from an early stage, other aspects of the reproductive cycle need to be examined. Three aspects which have been suggested are spermatophore morphology (Voss, 1983), spermatophore number (O'Dor *et al.*, MS 1980), and degree of hectocotylization (Schuldt, 1979). In this paper, data on hectocotylization of *I. illecebrosus* from natural and captive populations are compared, spermatophores and spermatozoa are described on the basis of scanning electron microscopy, and evidence for the accidental release of spermatozoa and spermatophores is discussed.

Materials and Methods

The squid, which provided the main body of information for this study, were obtained from the inshore fishery in St. Margaret's Bay, near Halifax, Nova Scotia, in the summers of 1982 and 1983 and were maintained alive in the 15-m circular pool at the Aquatron Laboratory, Dalhousie University, Halifax, until they were sampled in autumn (October–November). After death, the squid were measured as dorsal mantle length (mm), weighed (g) and sexed according to standard procedures (Mercer, MS 1973; Durward *et al.*, 1979). The hectocotyli of males were preserved in Bouin's solution. Mantle lengths and hectocotyli measurements were obtained from two additional samples. One sample consisted of squid which were captured off Newfoundland in October 1982 and preserved in a frozen state until examined, and the other sample consisted of animals which were captured in St. Margaret's Bay and preserved in 10% formalin since July 1979.

Standard measurements of hectocotylized arms (HA) and hectocotyli (HP) (Fig. 1), according to the methodology of Roper and Voss (1983), were made on all squid in the three samples (Appendix Tables A, B and C). Additional observations on the squid in one sample (Appendix Table A) included the number of non-transformed suckers (NTS), number of folds or transformed suckers on the hectocotylus (TS), diameters of largest (SD1) and smallest (SD2) suckers, diameter of arm at the base of first transformed sucker (HD), a tracing of the perimeter of the arm at its base (AP), and a tracing of the irregular cross-section at the base of the first transformed sucker (SA). These measurements were taken as alternative ways of expressing the size of the hectocotylus. A 48K Apple II computer with a graphics tablet was used to determine the areas of the arm tracings, and the results are reported in arbitrary units for comparison only.

Occasionally, small samples of sperm were collected from the water surface in the tanks that were used in the field (August, 1983) to transfer the live squid to the laboratory pool. This usually occurred within a few seconds after the transfer of squid from the net to the tanks. Two similar samples were obtained later (November) from the water surface in the pool. These pieces of whitish tissue were suspended in phosphate-buffered formalin, washed in distilled water, stained with osmium tetroxide, and dehydrated in acetone. After critical-point drying, they were affixed to aluminum stubs and sputter-coated with gold. Micrographs were obtained with a scanning electron microscope (Bausch and Lomb ARL NANOLAB 2000). Identically-prepared tissues of testis, vas deferens and spermatophores of squid (Fig. 2) from sample A were used for comparative observations of spermatozoa.

Results

Spermatophores and sperm release

The recovery of sperm masses from seawater during operations to capture live *I. illecebrosus* and subsequently from seawater in the Aquatron Laboratory pool indicate that males can expel sperm independently of copulation. Consequently, exclusive use of the number of spermatophores in Needham's sac may not be a reliable indicator of maturity in males.

Scanning electron micrographs were made to document some aspects of the morphology of spermatophores and spermatozoa. Sections of a spermato-

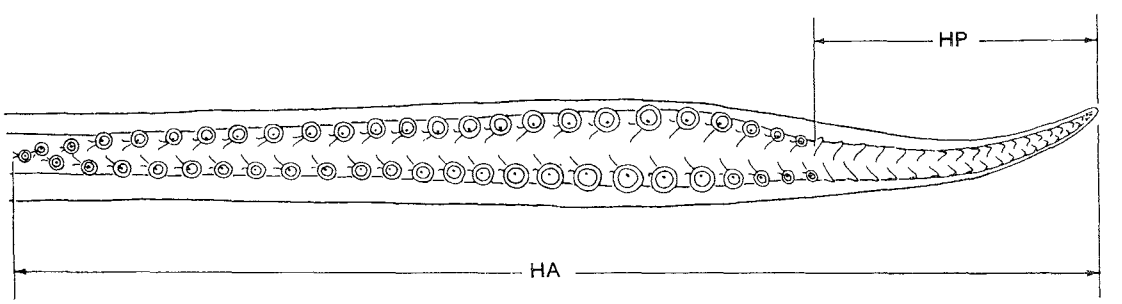

Fig. 1. Schematic representation of the hectocotylized arm of *I. illecebrosus* (adapted from Roper and Voss, 1983).

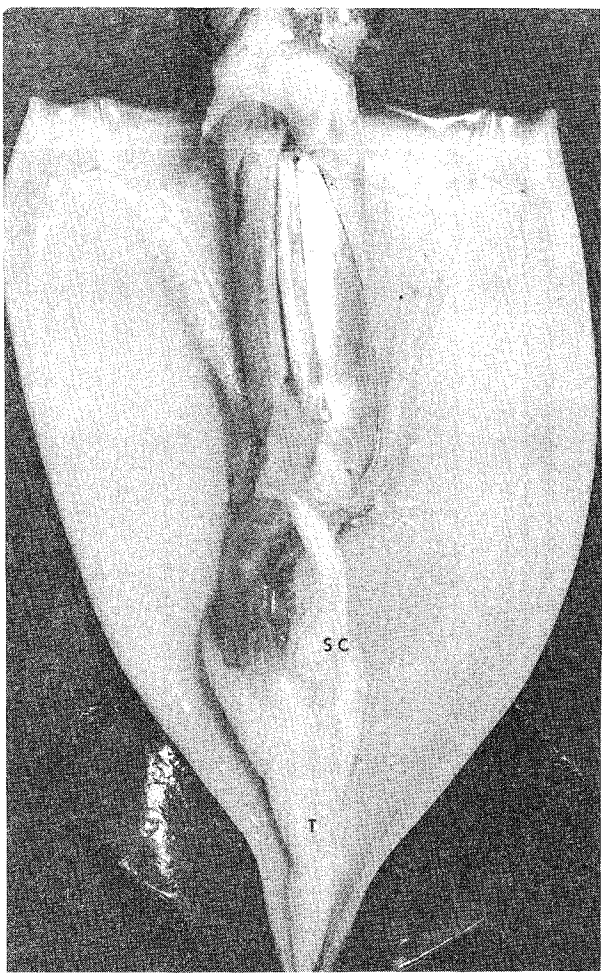

Fig. 2. Testis and spermatophore complex of a mature male *I. illecebrosus*.

phore from a mated female indicate distinct biflagellate spermatozoa with spherical to pear-shaped heads about 3 μm long (Fig. 3, A–E). The field samples of sperm in late summer did not clearly show individual intact spermatozoa (Fig. 3H), but those from the pool in November did (Fig. 3F). The structure of these spermatozoa was comparable to those from gonad tissues of mature males (testis, vas deferens and spermatophores).

It is interesting to note the spiral structure in the external tunic of the spermatophore (Fig. 3, A and B), which shows how the spermatozoa are packaged. This spiralization and the density of packing of the spermatozoa inside the spermatophore might be a potential indicator of the degree of maturity in male squid.

Hectocotylus

The means and standard deviations of the measurements and indices in Appendix Tables A, B and C are given in Tables 1 and 2. There was no consistent relationship between hectocotylus length index (HLI) and mantle length (ML) insofar as progression of maturation through stages 2, 3 and 4 are concerned (Fig. 4). In sample A (preserved in Bouin's solution), the mean HLI declined with increase in length from maturity stage 3 to stage 4; in sample B (frozen specimens), the mean HLI declined with a slight increase in length from stage 2 to stage 3 but increased substantially in stage 4 squid which were considerably smaller on the average; in sample C (preserved in formalin), the mean HLI increased slightly with a significant increase in length from stage 2 to stage 3, but stage 4 animals were smaller and had a lower mean HLI.

TABLE 1. Mean dorsal mantle length (ML) and hectocotylus length index (HLI) by maturity stage (MAT) for *I. illecebrosus* specimens listed in Appendix Tables A, B and C (SD = standard deviation).

Sample	MAT	No. of squid	ML (mm) Mean	ML (mm) SD	HLI (%) Mean	HLI (%) SD
A	2	—	—	—	—	—
	3	4	213	9.0	32.5	6.9
	4	24	238	6.7	29.2	4.2
B	2	8	219	7.6	23.2	10.6
	3	13	223	10.6	18.4	3.6
	4	4	208	10.4	26.0	4.2
C	2	9	182	16.9	20.8	6.9
	3	4	223	10.4	22.6	2.2
	4	5	214	18.6	20.8	2.1

TABLE 2. Mean weight (TW), number of transformed suckers (TS), diameter at base of hectocotylus (HD), perimeter of hectocotylized arm (AP) and section area at base of hectocotylus (SA) for *I. illecebrosus* in Appendix Table A (SD = standard deviation).

Parameter	1983 MAT 3 Mean	1983 MAT 3 SD	1983 MAT 4 Mean	1983 MAT 4 SD	1982 MAT 4 Mean	1982 MAT 4 SD
No. of squid	4		20		4	
TW(g)	231	10.7	351	34.9	360	62.6
TS (number)	18.0	7.2	25.8	6.0	—	—
HD (mm)	3.7	0.5	4.2	0.7	—	—
AP[a]	20.3	2.3	23.4	2.6	19.8	6.4
SA[a]	0.7	0.0	1.1	0.3	0.8	0.3

[a] Arbitrary units from computer output.

The other variables from sample A, which are related to hectocotylus development but not strictly to length (Table 2), also failed to correspond well with the change in maturity from stage 3 to stage 4 (there were no stage 2 animals in this sample). However, positive trends are evident in all cases when the mean values of the variables (SA, AP, HD and TS) in the 1983 data are plotted against mean weight of squid at stages 3 and 4 (Fig. 5). Plots of individual values of AP and SA against hectocotylus length (HP) (Fig. 6) show great variability but there is some degree of proportionality for the October 1983 data. While the October and November 1983 data appear to follow a common pattern, the November 1982 data for the same variables deviate markedly.

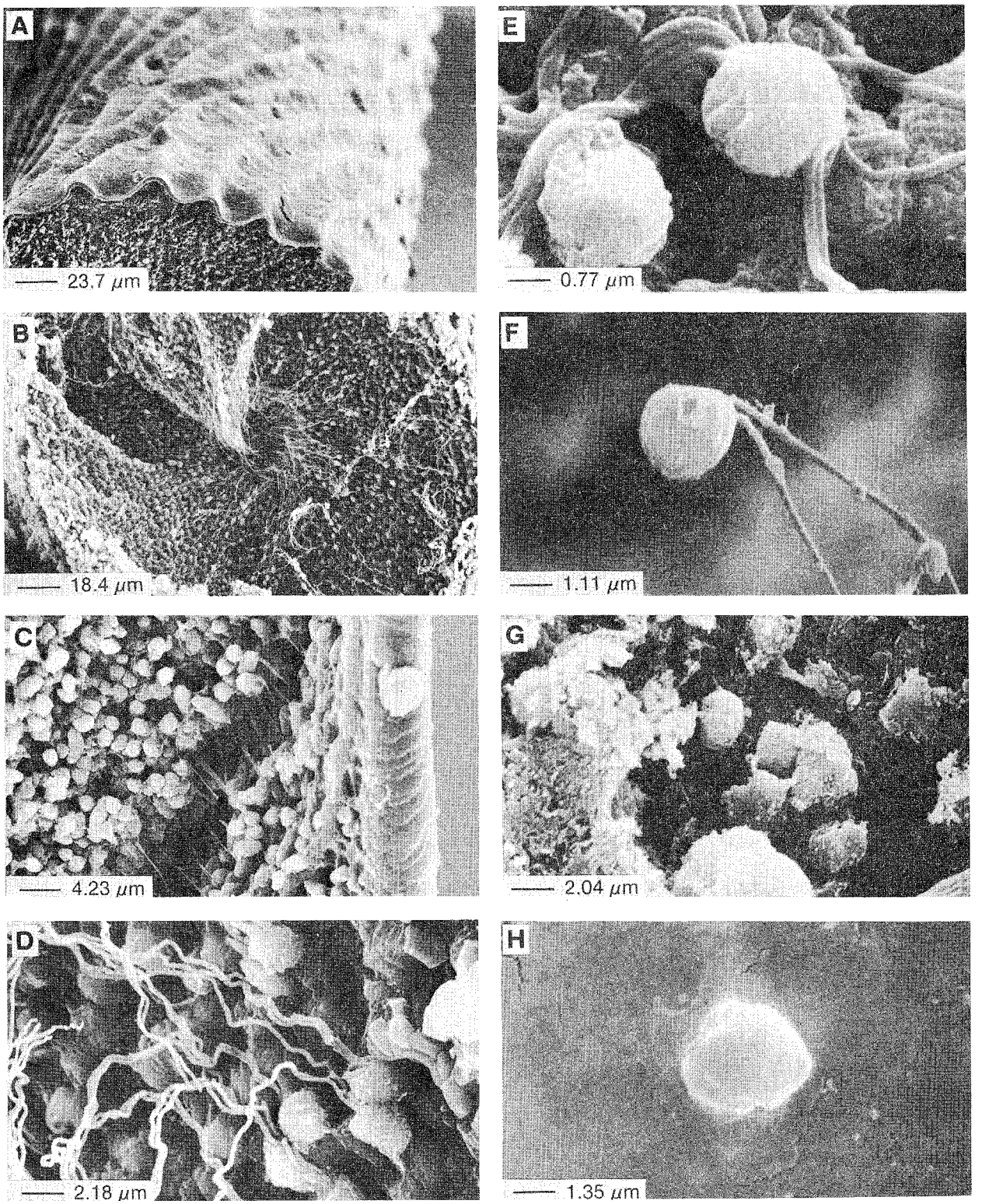

Fig. 3. Micrographs of *I. illecebrosus* spermatophores and spermatozoa: **A–E**, spermatozoa in the spermatophore of a mated female; **F**, spermatozoa in sperm mass from the Aquatron Laboratory pool in November 1983; **G–H**, spermatozoa in sperm mass from water surface of tank used during the capture of live squid at St. Margaret's Bay in August 1983.

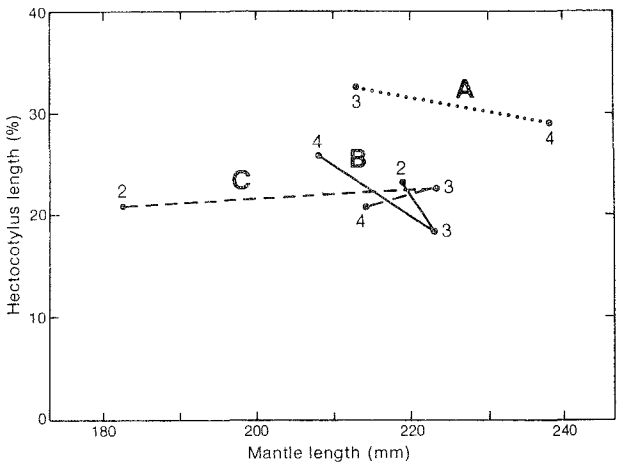

Fig. 4. Plot of mean values of hectocotylus length index against mantle length by maturity stage for male *I. illecebrosus* from samples A, B and C.

Discussion

The hectcotylus length index (HLI), as defined above, would be expected to be the most convenient index of maturity in male squid, but the measurements in this study indicate that it is unreliable for *I. illecebrosus* when it is considered in relation to the present scale of denoting the maturity stages. Before considering interpretations of the variability in the index, a brief review of the limited information on factors which control hectocotylization is needed. In *Octopus vulgarus*, differentiation of the hectocotylus is genetically controlled in males and does not require gonadal hormones (Wells and Wells, 1977). However, hectocotylized arms in maturing males with active optic glands regenerate at nearly three times the rate of other arms (O'Dor and Wells, 1978). The fact that the optic gland hormone is required to promote spermatogenesis (Wells and Wells, 1972) and may also affect hectocotylization is the major reason for expecting a close relationship between maturity stage and hectocotylus length. The environmental factors which activate the optic glands in *I. illecebrosus* in nature are unknown, but there is evidence from laboratory experiments that both photoperiod changes (O'Dor *et al.*, 1977) and fasting (Rowe and Mangold, 1975) may be stimulatory. These environmental cues could lead to maturity in two ways: (a) seasonal triggering of the maturation process and the steady progression of growth and maturation in well-fed populations, as illustrated by the advanced maturity that is associated with the largest squid (sample A); and (b) early triggering of maturation in small squid which competed unsuccessfully for food, as may be the case for the advanced maturity (stage 4) of smaller squid early in the season (samples B and C).

Such an intermix of cues may also account for the variability of HLI. If hectocotylization is stimulated at

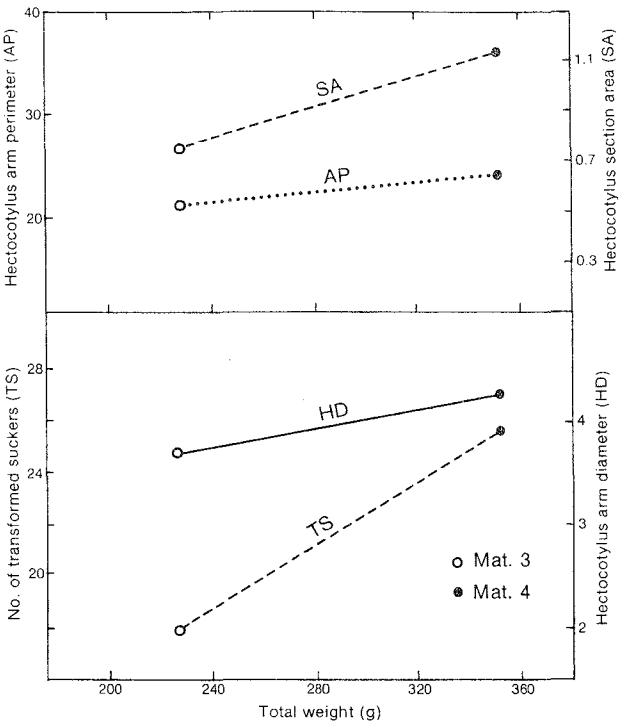

Fig. 5. Plots of mean values of AP, SA, TS and HD against total weight (TW) by maturity stage for male *I. illecebrosus* from sample A (see Appendix for definitions of abbreviations).

the same time as spermatogenesis between maturity stages 2 and 3, this would explain why HLI variability is highest at stage 2 (Table 1) or during the transition from stage 2 to stage 3. Presumably, a minimum effective length is required for the hectocotylus to function effectively in spermatophore transfer (Wells and Wells, 1977). However, the actual value of HLI may depend on growth during the period before optic gland activation. Thus, a squid that matured during a period of fasting early in the season would have a lower HLI than one that grew and matured in the normal season.

It is clear that development of the hectocotylus is a complicated process, with several morphological changes in addition to length. These changes are undoubtedly linked to the process of maturation, but the change in hectocotylus length is not well correlated with maturity stage. A combination of indices related to animal weight (HD, TS, SA and AP) seem to improve the relationship with maturity stage, but it does not meet the goal of finding a simple method for maturation staging of male *I. illecebrosus*.

The high variability in HLI may have been due, in part, to the different methods of preserving the samples, but it is unlikely that a particular fixative would differentially affect the hectocotylus and the hectocotylized arm of animals in different stages of maturation. Rather, there are at least two hypotheses about the nature of the sampled populations that could explain why *I. illecebrosus* failed to show the relationship

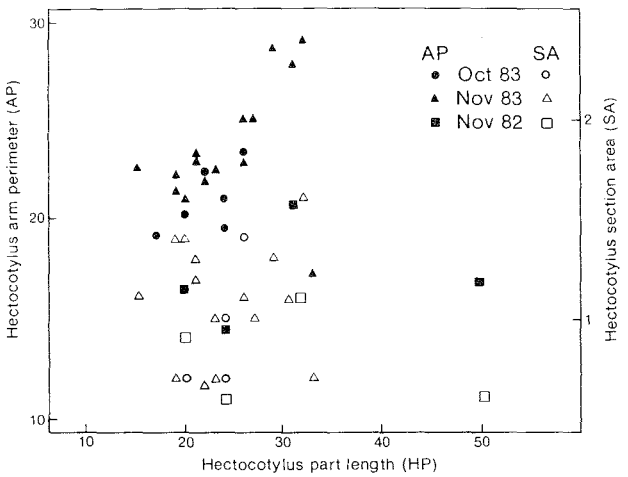

Fig. 6. Plots of individual values of AP and SA against HP for male *I. illecebrosus* from Appendix Table A.

between HLI and maturity stage, which has been reported for *I. argentinus* (Schuldt, 1979). The first hypothesis is that the squid in samples B and C, which were taken in different areas, were derived from spawning at different places or at different times. The comparatively small stage-4 animals may, for example, have been immigrants from a more southerly population which was exposed to higher temperature and different photoperiod. Further collection and analysis of data are required to determine whether such population differences exist. If such differences can be established, HLI may prove to be a useful distinguishing character. Alternatively, it may be hypothesized that differing combinations of intrinsic and extrinsic factors result in varying maturation rates in squid from the same population. In 1983, when squid were very scarce and arrived late in St. Margaret's Bay, they were large and reached maturity late in the season. There was no evidence of individuals having matured early as a result of limited access to food. Squid were much more abundant in 1979 and 1982 when samples B and C were taken than in 1983, and the likelihood that some squid encountered limited food conditions in 1979 and 1982 was much greater. In such a situation, the least competitive squid might be closer to starvation and mature earlier than usual at a small size. Thus, the variation in maturity pattern among samples need not reflect mixed populations. In this case, the hectocotylus length index may provide some insights into the conditions to which squid are exposed in different areas and years, even if it cannot be used as a maturity index.

Another interpretation of the data in this study is the possible mixing of *I. illecebrosus* with another species of the genus *Illex*. However, the apparent distinction between long and slim *versus* short and thick hectcotyli, which might support this hypothesis, is also not consistent in sample A, which was presumed to consist only of *I. illecebrosus*.

In conclusion, it is apparent that several factors are involved in producing the variation in hectocotylus morphology, in contrast to the more consistent changes that have been reported by Schuldt (1979) for *I. argentinus*. Thus, the HLI cannot be used alone as an indicator of maturity in *I. illecebrosus*. Furthermore, observations on the accidental loss of sperm and/or spermatophores indicate that spermatophore counts would not be the basis for an adequate index. Such a criterion would be questionable in unmated males, and males which have mated once would certainly have reduced spermatophore numbers. Examination of the morphology of spermatophores and spermatozoa is still incomplete, but it has failed so far to distinguish between spermatophores from early maturing males and those from males which are ready to mate or have mated.

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Appendix

The three tables below provide detailed information on hectocotylus morphology of *I. illecebrosus*, which is summarized in the text. The following definitions pertain to abbreviations in the table headings.

ML	Dorsal mantle length
TW	Total weight
MAT	Maturity stage (Mercer, MS 1973)
HA	Length of hectocotylized arm
HP	Length of hectocotylized part
HLI	Hectocotylus length index (HP/HA)
NTS	Number of non-transformed suckers
TS	Number of folds (transformed suckers)
SD1	Diameter of largest sucker on hectocotylized arm
SD2	Diameter of smallest sucker on hectocotylized arm
HD	Diameter of arm at base of hectocotylized part
AP	Perimeter of hectocotylized arm at its base
SA	Section area at base of hectocotylized part

TABLE A. Measurements of hectocotylized arm and associated features from *I. illecebrosus* samples that were captured in St. Margaret's Bay in late summer and maintained alive until death in the autumn (**sample A** in text).

ML (mm)	TW (g)	MAT	HA (mm)	HP (mm)	HLI (%)	No. of suckers NTS	TS	Total	SD1 (mm)	SD2 (mm)	HD (mm)	AP[a]	SA[a]
November 1982													
205	275	4	48	24	50	35	29	64	1.9	0.5	4.6	14.5	0.6
210	297	4	94	31	33	40	30	70	3.2	1.0	5.0	28.8	1.1
220	326	4	120	50	42	33	21	54	2.0	1.5	5.2	18.3	0.6
223	440	4	50	20	40	29	23	52	3.0	1.0	4.0	16.5	0.9
October 1983													
200	246	3	77	22	29	40	13	53	2.5	1.0	3.0	22.3	0.7
214	221	3	62	24	39	38	26	64	2.3	1.0	4.0	19.7	0.7
230	294	4	77	17	22	51	29	80	1.0	0.8	3.0	19.2	0.9
230	311	4	70	20	29	48	25	73	3.0	0.7	4.3	20.2	0.7
235	328	4	65	24	37	46	26	72	3.0	1.0	5.0	21.1	1.0
235	371	4	83	26	31	58	10	68	3.0	0.3	4.0	23.3	1.4
240	402	4	85	26	31	50	22	72	3.0	0.9	5.0	23.5	1.2
November 1983													
218	227	3	79	23	29	48	22	70	2.7	0.5	4.0	21.8	0.7
220	231	3	100	33	33	27	11	38	3.0	1.2	3.8	17.3	0.7
225	340	4	71	15	21	52	27	79	3.0	0.9	3.5	22.5	1.1
227	310	4	75	23	31	43	34	77	2.9	1.0	4.2	22.5	1.0
230	299	4	70	20	29	50	37	87	3.0	1.0	4.0	22.0	1.4
234	360	4	81	26	32	45	30	75	3.0	1.0	5.2	23.8	1.0
234	334	4	97	26	27	53	26	79	2.5	0.5	4.0	25.1	1.0
236	328	4	90	27	30	44	33	77	2.4	1.0	3.2	25.0	1.0
240	367	4	97	29	30	54	24	78	3.0	0.5	4.6	28.7	1.3
240	365	4	72	21	29	33	20	53	3.3	1.0	3.5	23.3	1.2
242	405	4	68	21	31	50	28	78	3.0	1.0	5.0	22.9	1.3
243	361	4	102	31	30	46	28	74	3.5	1.0	5.0	27.9	1.1
243	385	4	86	22	26	49	23	72	2.8	0.7	4.0	22.1	0.7
244	323	4	90	19	21	44	28	72	2.7	0.7	3.3	22.3	0.7
245	390	4	90	32	36	35	23	58	4.0	1.0	—	29.1	1.6
246	350	4	83	26	31	47	25	72	3.0	1.0	4.6	22.9	1.1
250	400	4	65	19	29	51	17	68	3.0	0.9	4.5	21.4	1.4

[a] Uncalibrated arbitrary units from computer output.

TABLE B. Measurements of hectocotylized arm of *I. illecebrosus* in a sample from Newfoundland, September 1982 (**sample B** in text).

ML (mm)	MAT	HA (mm)	HP (mm)	HLI (%)
195	4	125	30	24
200	3	100	18	18
205	4	75	22	29
210	2	110	15	14
210	2	110	15	14
210	4	130	27	22
215	2	115	15	13
215	2	145	40	28
215	3	120	20	17
215	3	95	20	21
215	3	110	25	23
220	3	135	22	17
220	3	120	20	17
220	4	165	50	30
223	2	75	15	24
225	2	100	40	40
225	2	115	20	17
225	3	135	25	19
230	2	110	40	36
230	3	125	30	24
230	3	110	12	11
230	3	130	23	18
230	3	105	24	23
235	3	140	25	18
240	3	130	20	15

TABLE C. Measurements of hectocotylized arm of *I. illecebrosus* in a sample from St. Margaret's Bay, July 1979 (**sample C** in text).

ML (mm)	MAT	HA (mm)	HP (mm)	HLI (%)
140	2	60	13	22
175	2	85	22	26
183	2	70	10	14
185	2	70	12	17
185	2	77	27	35
190	2	68	8	12
190	2	78	18	23
190	4	105	22	21
195	2	72	14	19
195	2	83	17	20
210	4	110	25	23
210	3	112	22	20
215	4	125	23	18
220	3	110	23	21
225	3	100	22	22
225	4	110	23	21
232	4	110	20	18
235	3	96	24	25