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MONTHLY DIFFERENCES IN DISTRIBUTIONS OF SEX AND ASYMMETRY IN A LOOKING-GLASS COPEPOD, *PLEUROMAMMA XIPHIAS*, OFF HAWAII

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ABSTRACT

We studied frequencies of several attributes of the reproductive cycle of *Pleuromamma xiphias*, an oceanic, calanoid copepod taken in replicate monthly samples over a 13-month period at a station off Hawaii. Large numbers of late copepodids in these samples allowed us to confidently describe monthly changes in these frequencies despite variability among replicate samples taken within 36 h. The percentage of males among different copepodids of *P. xiphias* decreased from copepodid stage IV to CV and from CV to CVI. The percentage of left females, a sex-limited dimorphism in the condition of asymmetry of an animal, increased from CIV to CV but decreased from CV to CVI. The magnitude of the changes in the percentage of left females was not as great as changes in the percentage of males. Monthly averages for these attributes suggested differential recruitment to CVI males and left females in May when the percentage of CVI females without a dark mass in the genital opening also was high, but when abundances of CVI, CV, and CIV animals were low; the percentage of CVI males with a spermatophore in the spermatophore sac reached a maximum earlier, in February. We compared our data about the percentage of males to similar information for other calanoid copepods, and conclude that documenting the ranges of this attribute among consecutive copepodid stages is more useful in describing the seasonal distribution of sex than calculating an average value for adults.

Among sexually reproducing animals, the seasonal distribution of sex, as reflected in a sex ratio (such as the percentage of males among adult or juvenile animals), is an important descriptor of a species' reproductive cycle. Accounts of such seasonal distributions for calanoid copepods, a widespread group of aquatic crustaceans, include information on sex ratios of 38 species in 11 families (Table 1). In oceanic waters, where calanoids are most speciose, seasonal studies are more common for species restricted to the epipelagic zone. Among deeper water species, seasonal studies of sex ratios are known for *Euchaeta antarctica*, *E. norvegica*, *Metridia longa*, and *Calanus pacificus californiensis*. Fleminger's (1985) study of the trithek/quadrithek antenna 1 in females of the latter species is the only seasonal analysis among calanoid species that combines data on a sex ratio and a sex-limited dimorphism.

Pleuromamma xiphias is a pelagic, calanoid copepod found in warm, oceanic waters above 1,000 m and equatorward of the subtropical convergences (Steuer, 1932). The species exhibits an unusual dimorphism in the concordance of all asymmetrical characters. On each animal, the positions of all asymmetrical characters are fixed relative to one another, so that an animal may exhibit only one of two conditions, a "left" or "right" asymmetry. Males of *P. xiphias* express this concordant asymmetry in a remarkable number of primary and secondary sex characters (Ferrari, 1984). Their asymmetrical skeletal structures include antenna 1 and legs 1–5, the dark organ on the first pedigerous somite, and all urosomal somites. Females express two asymmetrical characters, the dark organ and an internal tubule in the genital complex. Animals of both sexes can be found with left or right asymmetry; however, frequencies of left and right animals differ between sexes. Using the position of the dark organ as an indicator, in *P. xiphias* about two-thirds of females are right while less than one per thousand males is right; in effect, asymmetry in *P. xiphias* is a sex-limited dimorphism.

In studies of related calanoids (Blades and Youngbluth, 1980), several of the homologous, asymmetrical appendages are presumed to have specialized functions during copulation, promoting accurate male-female juxtaposition and aiding precise spermatophore transfer. Giesbrecht (1895) provided an initial description of the internal anatomy of the dark organ of *P. gracilis*. In their study of the ultrastructure of the dark

Table 1. Seasonal studies of sex ratios of calanoid copepods. Numbers refer to copepod families. 1 = Acartiidae, 2 = Calanidae, 3 = Candaciidae, 4 = Centropagidae, 5 = Clausocalanidae, 6 = Diaptomidae, 7 = Euchaetidae, 8 = Metridinidae, 9 = Paracalanidae, 10 = Pseudodiaptomidae, 11 = Temoridae. * indicates studies which include immature stages; # indicates that males were found throughout the year; + indicates that males comprised less than 50% of adults.

Species	Source	Study area
	Marine waters	
Acartia clausii 1	Digby, 1950	English Channel
	Marshall, 1949	northeastern Atlantic Ocean
Calanus finmarchicus 2 # +	Wiborg, 1940	North Sea
	Gibbons, 1936	North Sea
C. helgolandicus 2	Moraitou-Apostolopoulou, 1969	Mediterranean Sea
C. minor 2 # +	Moraitou-Apostolopoulou, 1969	Mediterranean Sea
C. pacificus 2 #	Fleminger, 1985	northeastern Pacific Ocean
C. tenuicornis 2	Moraitou-Apostolopoulou, 1969	Mediterranean Sea
Candacia bradyi 3 #	Saraswathy and Santhakumari, 1982	Arabian Sea
Centropages furcatus 4 # +	Saraswathy and Santhakumari, 1982	Arabian Sea
C. hamatus 4	Marshall, 1949	northeastern Atlantic Ocean
C. typicus 4 # +	Moraitou-Apostolopoulou, 1972	Mediterranean Sea
C. violaceus 4	Moraitou-Apostolopoulou, 1969	Mediterranean Sea
Euchaeta antarctica 7 * # +	Ferrari and Dojiri, 1987	Southern Ocean
E. norvegica 7 * # +	Hopkins, 1982	northeastern Atlantic Ocean
Metridia longa 8 * #	Tande and Grønvik, 1983	Arctic Ocean
Microcalanus pygmaeus 5 # +	Marshall, 1949	northeastern Atlantic Ocean
Paracalanus parvus 9 # +	Marshall, 1949	northeastern Atlantic Ocean
	Digby, 1950	English Channel
Pleuromamma xiphias 8 * # +	This study	northcentral Pacific Ocean
Pseudocalanus elongatus 5 # +	Digby, 1950	English Channel
P. minutus 5 # +	Wiborg, 1940	North Sea
# +	Marshall, 1949	northeastern Atlantic Ocean
*	Grainger, 1959	Arctic Ocean
Temora discaudata 11 #	Saraswathy and Santhakumari, 1982	Indian Ocean
T. longicornis 11	Marshall, 1949	northeastern Atlantic Ocean
	Digby, 1950	English Channel
T. stylifera 11 # +	Moraitou-Apostolopoulou, 1972	Mediterranean Sea
	Moore and Sander, 1983	Caribbean Sea
T. turbinata 11	Saraswathy and Santhakumari, 1982	Arabian Sea
Undinula vulgaris 2 # +	Saraswathy and Santhakumari, 1982	Arabian Sea
# *	Moore and Sander, 1983	Caribbean Sea
	Brackish waters	
Acartia clausii 1 * # +	Lee and McAlice, 1979	Gulf of Maine
A. longiremis 1 * # +	Lee and McAlice, 1979	Gulf of Maine
A. tonsa 1 *	Lee and McAlice, 1979	Gulf of Maine
Drepanopus bispinosus 5 *	Bayly, 1986	Southern Ocean
Gladioferens pectinatus 4 #	Bayly, 1965	Moreton Bay
Limnocalanus grimaldii 4	Lindquist, 1961	Gulf of Finland
Pseudodiaptomus binghami 10	Goswami, 1978	Arabian Sea
P. marinus 10 * #	Uye *et al.*, 1982	Setonaikai, Japan
Sinocalanus tenellus 4	Hada *et al.*, 1986	Setonaikai, Japan
	Fresh waters	
Boeckella propinqua 4 #	Bayly, 1962	Lake Aroarotamahine, New Zealand
Diaptomus arcticus 6	Hebert, 1985	tundra ponds, Canada
D. ashlandi 6	Davis, 1962	Lake Erie, U.S.A.
D. castor 6	Gurney, 1940	temporary pond, England
D. gracilis 6 # +	Chapman, 1969	Loch Lomond, Scotland
D. minutus 6	Davis, 1962	Lake Erie, U.S.A.
D. oregonensis 6	Davis, 1962	Lake Erie, U.S.A.
D. sanguineus 6 *	Hairston *et al.*, 1983	Rhode Island, U.S.A.
D. siciloides 6	Davis, 1962	Lake Erie, U.S.A.
D. tyrrelli 6	Hebert, 1985	tundra ponds, Canada
Heterocope septentrionalis 4	Hebert, 1985	tundra ponds, Canada
Limnocalanus johanseni 4 *	Comita, 1956	Imikouk Lake, Alaska
L. macrurus 4 * #	Carter, 1969	Lake Huron, Canada
	Lindquist, 1961	Gulf of Bothnia
Senecella calanoides 5 *	Carter, 1969	Lake Huron, Canada

organ of *P. abdominalis,* Blades and Youngbluth (1988) suggested that this organ may have a secretory function which is unrelated to secretion of bioluminescent substances.

Here we examine variation in frequencies of sex and this sex-limited dimorphism of asymmetry from several samples taken monthly for 8 months over a 13-month period at a station off Oahu, Hawaii. We compare frequencies of these attributes to frequencies among all adult males of those with a spermatophore in the spermatophore sac and among all adult females of those without a dark mass in the genital opening, two other attributes which we believe useful in describing this animal's reproductive cycle.

Materials and Methods

Specimens of *P. xiphias* were collected at 21°20–30'N, 158°20–30'W, about 20 km off the southwest coast of Oahu, Hawaii, where bottom depths exceeded 2,000 m. The two kinds of gear utilized were described by Clarke (1983), (1) a 3-m Isaacs-Kidd midwater trawl with mouth area 7.7 m^2, lined with 6-mm mesh, whose terminal 5 m consisted of a conical plankton net 1 m in diameter with 0.333-mm mesh and (2) a Bongo net comprised of paired 1.25-m diameter nets, with mouth area of 1.23 m^2 each (times 2 nets = 2.5 m^2) with an initial 5 m of 2.5-mm mesh and a terminal 2 m of 0.505-mm mesh. A flowmeter recorded distance traversed by both devices. In calculating the volume of water sampled, the mouth area of each device was used; this was an approximation, because probably only the fine-mesh, terminal sections of the samplers retained these copepods.

Sampling protocol was similar for both trawl and Bongo net samples (Clarke, personal communication). With a ship speed of about 120 m/min, the gear was lowered as rapidly as possible to about 400 m and then more slowly at about 10 m/min (wire out) until the target depth of 1,000 m presumably was reached. Ship speed then was reduced to about 60 m/min, while wires for trawls were retrieved at about 60 m/min and Bongo nets at about 50 m/min.

Among 43 daytime samples available in the seasonal survey, we studied *P. xiphias* in 29. Two trawls were taken once each month, in the morning and afternoon of the same day, for 8 months over a 13-month period (in August 1978 a third trawl sample taken 27 days earlier than the later 2 was included). During six of those months 2 Bongo net samples (morning and afternoon) complemented the trawl samples taken the preceding day. Series of samples were collected at the beginning of a lunar month (close to new moon) except the series in February 1978 which was taken close to a full moon. Information about samples utilized in this study is given in Table 2. Tow length was not recorded for 780714; we substituted an average value for Bongo net tows in calculating volume of water filtered. Depth was not recorded for 770811; in correcting catch per unit time we substituted 700 m (minimum depth for the study set).

In determining a corrected catch per 100 m^3 of water filtered for each gear type, we assumed maximum and minimum depths of encounter for the following copepodids: CVI 800–300 m; CV 700–200 m; CIV 400–100 m; CIII 400–100 m. These values are based on an earlier study of copepodid distribution by Ferrari (1985) off Cape Verde and are in general agreement with Ambler and Miller (1987) from the Central Pacific and Roe (1972) from off the Canary Islands. We multiplied mouth area of the gear by a tow length (L) which was corrected for the depths of encounter in this way:

$$L = t - (((D\text{-dmax})/D)t) - ((\text{dmin}/D)t)$$

where t is tow length, D is greatest tow depth, dmax is maximum depth of encounter for a given copepodid stage, and dmin is minimum depth of encounter for that copepodid stage. Our formula assumes that copepodids are equally abundant throughout their depths of encounter and distributes tow length equally over depth; these assumptions only approximate the sampling protocol and presumed distribution of the animals.

Copepodids of *P. xiphias* were distinguished from cooccurring congeners, *P. abdominalis* and *P. quadrungulata,* by their low-vaulted and crested head, the 3 proximal segments on antenna 1 with attenuate points, and the dark organ with pointed anterior and posterior margins. Copepodids of *P. abdominalis* and *P. quadrungulata* have more highly vaulted and crestless heads, respectively, 2 or 4 attenuate points on the proximal segments of antenna 1, and the dark organ with rounded margins. Copepodid stages of *P. xiphias* were identified by the number and shape of urosomal somites, and the shape and setal number of leg 5 (Ferrari, 1985). CIII has 2 urosome somites, CIV has 3, and CV has 4. CVI males have 5 distinctly contorted urosomal somites; somites 1 and 2 of CVI females are fused and have a distinctive genital boss with a ventrally centered genital opening. In CV females the terminal segment of leg 5 is no longer than the preceding segment; in males it is longer, and left and right are asymmetrical. CIV females have a number of long setae on the terminal segment of leg 5; all such elements are short on leg 5 of the male. CIII could not be sexed. Asymmetry was defined by the position of the dark organ on pediger 1. In CVI females the presence of a dark mass in the genital opening was easily observed in lateral or ventral views of the genital complex. CVI males were cleared in lactic acid for 1–2 h and the presence or absence of a spermatophore in the spermatophore sac in the posterior prosome was noted. One male from 780213 with reduced leg 5, partially fused urosome 1 and 2, and a protruding boss-like structure on urosome 2 was not considered in this study.

We note in passing that specimens of *P. xiphias* in this study differed in details of secondary sex characters from animals collected off Cape Verde in the Atlantic Ocean (Ferrari, 1985). Hawaiian specimens were smaller; differences in somites included the asymmetrical characters on urosomal somites 2–5, and morphological differences were found on the geniculate A1 and leg 5. Asymmetrically modified legs 1–4 have not been compared, but we also anticipate differences in these appendages.

Our following use of the term "population" is statistical: a group of organisms about which some information is required. Traditional biological definitions of a population which presume a spatial separation of groups of organisms (Lincoln *et al.,* 1982) or their genetic segregation (Mayr, 1963) are inappropriate here

Table 2. Sample information. Depth is greatest depth of tow in m, Begin tow is in local time, Tow time is in min, Tow length is in m, Aliquot 1 refers to the aliquot from which CVI were removed, Aliquot 2 refers to the aliquot from which CV, CIV, and CIII were removed.

Sample	Date	Gear	Depth	Begin tow	Tow time	Tow Length	Aliquot 1	Aliquot 2
770805	10 Aug 1977	Trawl	1,300	0710	258	30,755	0.50	1.00
770806	10 Aug 1977	Trawl	1,030	1215	231	25,667	0.25	0.50
770811	11 Aug 1977	Bongo	700	0716	230	19,181	0.25	0.75
770812	11 Aug 1977	Bongo	950	1127	233	21,610	0.13	0.19
771005	9 Oct 1977	Trawl	1,050	0708	267	30,062	1.00	1.00
771006	9 Oct 1977	Trawl	940	1200	263	35,057	0.25	0.75
771012	10 Oct 1977	Bongo	810	0657	223	16,790	0.13	1.00
771013	10 Oct 1977	Bongo	750	1055	297	18,732	0.13	0.13
780205	22 Feb 1978	Trawl	1,000	0715	270	39,217	0.50	0.50
780206	22 Feb 1978	Trawl	1,000	1215	280	33,961	0.75	0.75
780213	23 Feb 1978	Bongo	1,000	0713	217	22,716	0.50	1.00
780214	23 Feb 1978	Bongo	1,060	1100	137	22,427	0.25	0.50
780405	6 Apr 1978	Trawl	1,060	0724	265	31,503	0.25	1.00
780406	6 Apr 1978	Trawl	1,090	1216	286	32,604	0.50	1.00
780413	7 Apr 1978	Bongo	840	0719	206	15,628	0.25	0.75
780414	7 Apr 1978	Bongo	1,040	1111	224	15,685	0.25	0.75
780505	2 May 1978	Trawl	1,200	0704	269	29,454	1.00	1.00
780506	2 May 1978	Trawl	1,100	1439	214	28,386	0.50	1.00
780513	3 May 1978	Bongo	1,010	0701	180	14,329	0.50	1.00
780514	3 May 1978	Bongo	700	1110	268	19,372	0.25	1.00
780705	4 Jul 1978	Trawl	1,040	0630	275	35,177	0.50	1.00
780706	4 Jul 1978	Trawl	1,200	1123	261	29,378	0.50	0.50
780713	5 Jul 1978	Bongo	730	0628	227	18,216	0.13	0.13
780714	5 Jul 1978	Bongo	1,030	1024	281	18,607	1.00	1.00
780805	3 Aug 1978	Trawl	1,030	0640	290	38,897	0.50	1.00
780905	31 Aug 1978	Trawl	1,030	0710	267	31,733	1.00	1.00
780906	31 Aug 1978	Trawl	1,200	1155	273	27,722	1.00	1.00
781005	28 Sep 1978	Trawl	800	0710	281	32,180	0.25	0.75
781006	28 Sep 1978	Trawl	900	1215	274	25,419	1.00	1.00

because we have no information about the spatial separation of our various samples and the different copepodid stages of *P. xiphias* are not assumed to be segregated genetically.

In standard statistical tests, statistical significance is simply a statement about the likelihood, or chance, of the observed result of a test. The observed probability level provides little information about the magnitude of the observed effect and no information on the substantive nature of the result. In this study we use power and effect size, along with statistical significance, to derive our inferences. We use the power of a statistical test—its probability of detecting a real difference between two populations if that difference exists—to determine a sample size of our study, to assess the discriminating ability of a test, and to increase both the interpretability and generalizability of our empirical findings [values for the power analyses were taken from Cohen (1977)]. We use effect size, which is the magnitude of a difference between two populations, to discover questions for further study. When a test is not significant because sample size is small, power also is low. In these circumstances we believe that an effect size above 0.20 suggests that further study with an increased sample size may discover a statistically significant difference in frequencies of the attribute considered.

A preliminary study of *P. xiphias* off Cape Verde (Ferrari, 1985) showed that a difference in sex ratio between late copepodid stages could be expected in the approximate range of 10–20%. Therefore, we calculated a sample size for the present study which, 90% of the time, would be sufficient to detect a minimal 10% difference if that was the true situation for the population. Using the delta-square coefficient of Sokal and Rohlf (1969: 609), our research design included counting specimens of CVI and CV until a sample size of 500 of each stage was attained. This allowed our test to detect a difference of 10% with a power of at least 90%. Usually a quarter aliquot of each sample was taken initially, and all *P. xiphias* were removed and counted; the remaining quarter or half aliquots were searched to complete the requisite minimum 500 animals of each stage. Because CVI were always more abundant than CV, finding the requisite number of the latter usually required searching a larger aliquot for that stage. All cooccurring CIV and CIII were removed and counted. We treated the paired samples from each Bongo net as a single sample.

Results

We counted 41,389 specimens of *P. xiphias* in this study (Table 3). Corrected catch for Bongo samples was about an order of

Table 3. Numbers of animals of various categories examined from each sample. No mass refers to CVI females without a dark mass in the genital opening; Sperm refers to males with a spermatophore in the spermatophore sac. R = right, L = left.

	CVI female				CVI male					CV female		
Sample	R	L	Total	No mass	R	L	Total	Sperm	Total CVI	R	L	Total
770805	257	148	405	65	—	343	343	134	748	276	126	402
770806	276	128	404	20	—	201	201	81	605	182	114	296
770811	357	177	534	34	—	224	224	110	758	193	109	302
770812	325	181	506	21	—	211	211	99	717	195	105	300
771005	45	16	61	14	—	123	123	9	184	31	15	46
771006	351	178	529	20	—	283	283	39	812	180	88	268
771012	645	349	994	8	—	814	814	57	1,808	135	97	232
771013	307	140	447	12	—	257	257	30	704	163	131	294
780205	406	254	660	86	—	380	380	306	1,040	225	143	368
780206	487	305	792	130	—	425	425	350	1,217	145	91	236
780213	246	146	392	12	—	365	365	182	757	194	121	315
780214	676	407	1,083	80	—	457	457	401	1,540	177	100	277
780405	477	251	728	19	—	468	468	296	1,196	155	75	230
780406	337	178	515	26	—	274	274	104	789	136	89	225
780413	105	62	167	28	—	399	399	281	566	196	124	320
780414	204	107	311	21	—	279	279	164	590	226	132	358
780505	131	75	206	87	—	284	284	160	490	61	43	104
780506	325	194	519	26	—	201	201	97	720	77	44	121
780513	228	113	341	131	—	458	458	291	799	105	55	160
780514	176	105	281	54	—	341	341	167	622	210	97	307
780705	270	174	444	27	—	402	402	136	846	123	82	205
780706	241	149	390	21	—	351	351	207	741	186	109	295
780713	533	297	830	16	—	494	494	189	1,324	152	86	238
780714	144	68	212	21	—	435	435	236	647	133	87	220
780805	294	162	456	18	—	339	339	187	795	122	78	200
780905	293	149	442	35	—	311	311	187	753	36	22	58
780906	190	106	296	20	—	305	305	215	601	21	19	40
781005	541	302	843	18	1	296	297	130	1,140	169	104	273
781006	95	39	134	50	1	214	215	109	349	97	50	147

magnitude greater than the trawl samples. Numbers of copepodids per 100 m^3 of water filtered in Bongo samples increased with increasing age of copepodids and usually varied within an order of magnitude for each stage (0.01–0.06 for CIII, 0.39–4.79 for CIV, 1.73–8.14 for CV, and 8.10–36.93 for CVI). CVI was most abundant in October 1977, CV in July 1978, CIV in August 1977, and CIII in April 1978. Among all animals examined, the percentage of males decreased from 54.7% of CIV to 50.5% of CV to 41.6% of CVI (changes of 4.2% and 8.9%). The percentage of left females increased from 31.5% of CIV to 37.1% of CV, but then decreased to 35.6% of CVI (changes of −5.6% and 1.5%). The percentage of left animals, regardless of sex, was similar for CIII, CIV, and CV (68.8%, 68.9%, 68.9%) but decreased for CVI (62.4%), due to the decrease in the percentage of CVI males which are left. CVI males with spermatophores comprised 49.9% of adult males; CVI females without a dark mass were 8.0% of adult females. Three females had attached spermatophores (a left and a right from 771012, and a right from 771005).

Average monthly values (Table 4) show that the percentage of CVI males with spermatophores was highest in February 1978 (76.2%) and lowest in October 1977 (9.1%). Females without a dark mass were most abundant in May 1978 (22.1%) and least abundant in October 1977 (2.7%). The percentage of CVI males varied among months from 34.4% (September 1978) to 48.8% (May 1978), while variability among CV males was more limited, from 44.9% (September 1978) to 54.6% (August 1978). May 1978 was the only month in which the percentage of CVI males was greater than that of CV males (difference of +1.7%). The percentage of CIV males reached its maximum of 61.1% in August 1978 and its minimum,

Table 3. Continued.

CV male				CIV female			CIV male				CIII			Total all animals
R	L	Total	Total CV	R	L	Total	R	L	Total	Total CIV	R	L	Total	
1	323	324	726	53	18	71	—	78	78	149	10	28	38	1,661
—	292	292	588	69	29	98	—	125	125	223	6	18	24	1,440
—	308	308	610	28	10	38	—	42	42	80	0	3	3	1,451
1	233	234	534	87	38	125	—	165	165	290	0	2	2	1,543
—	56	56	102	17	8	25	—	17	17	42	11	31	42	370
—	281	281	549	4	5	9	—	11	11	20	4	6	10	1,391
—	338	338	570	25	11	36	—	62	62	98	1	2	3	2,479
—	216	216	510	30	10	40	—	51	51	91	0	1	1	1,306
—	492	492	860	45	25	70	—	97	97	167	3	2	5	2,072
—	260	260	496	39	19	58	—	75	75	133	0	2	2	1,848
—	345	345	660	69	31	100	—	102	102	202	0	2	2	1,621
1	287	288	565	40	21	61	—	65	65	126	0	2	2	2,233
—	260	260	490	21	13	34	—	54	54	88	3	10	13	1,787
—	204	204	429	36	17	53	—	67	67	120	3	1	4	1,342
—	338	338	658	15	6	21	—	22	22	43	0	3	3	1,270
—	335	335	693	117	58	175	—	178	178	353	2	6	8	1,644
—	71	71	175	34	14	48	—	44	44	92	1	7	8	765
—	118	118	239	16	4	20	—	23	23	43	1	8	9	1,011
—	161	161	321	8	1	9	—	5	5	14	0	1	1	1,135
—	266	266	573	44	27	71	—	65	65	136	3	5	8	1,339
—	219	219	424	51	24	75	—	99	99	174	10	10	20	1,464
—	323	323	618	53	16	69	—	68	68	137	10	4	14	1,510
—	344	344	582	11	10	21	—	25	25	46	0	0	0	1,952
—	213	213	433	19	10	29	—	31	31	60	2	0	2	1,142
—	237	237	437	7	5	12	—	24	24	36	1	7	8	1,276
—	70	70	128	17	9	26	—	36	36	62	5	2	7	950
—	52	52	92	5	1	6	—	9	9	15	1	5	6	714
—	232	232	505	55	20	75	—	138	138	213	10	14	24	1,882
—	110	110	257	44	27	71	—	88	88	159	5	21	26	791

48.1%, in May 1978, and was slightly greater than the percentage of CV males in every month.

Among samples taken within 48 h, the percentage of males varied widely (Table 5), affecting the seasonal range of values. The median percentage of CVI males for all samples was 42.6% with a range of 70.5% to 26.1% for a sample each in April 1978 and May 1978. All months except August 1978 exhibited values differing by at least 15%. In 8 of 29 samples the percentage of CVI males was above 50%, with 3 occurrences in May 1978. For the percentage of CV males the median was 51.0% and overall monthly percentages were less extreme, reaching a maximum of 59.3% for a sample in October 1977 and a minimum of 40.6% for one in May 1978. The only monthly range to exceed 10% was October 1977. Seventeen of 29 samples were above 50%, with five months having more than one occurrence.

Figure 1 shows differences of the percentage of CVI males minus the percentage of CV males (from Table 5). Each value can be placed in one of five statistical categories: no difference [$\alpha > 0.05$] (6 samples); statistically significant increase (1 sample) or decrease (1 sample) [$\alpha \leq 0.05$] but low power [$\beta > 0.10$]; statistically significant decrease (15 samples) or increase (6 samples) [$\alpha \leq 0.05$] with high power [$\beta \leq 0.10$]. In total, 21 of 29 samples showed a statistically significant difference with high power between the percentages of CVI and CV males. Samples showing no difference or a decrease with high power were found throughout the year; three of six showing an increase with high power were found in May 1978.

The range of the percentage of CIV males was wide with a maximum of 66.7% and minimum of 35.7% for a sample each in August 1978 and May 1978. This result may be a consequence of the small numbers of

Table 4. Average percentages for eight months; four samples comprise the first six months (Aug 1977 to July 1978); three comprise Aug 1978, two comprise Sep 1978. F no mass refers to CVI females without a dark mass in the genital opening; M sper refers to males with a spermatophore in the spermatophore sac.

	Aug 1977	Oct 1977	Feb 1978	Apr 1978	May 1978	Jul 1978	Aug 1978	Sep 1978
F no mass	7.6	2.7	10.5	5.5	22.1	4.5	6.1	7.0
M sper	43.3	9.1	76.2	59.5	55.7	45.7	61.7	46.7
Male								
CVI	34.6	42.1	35.7	45.2	48.8	47.3	44.4	34.4
CV	47.1	51.5	53.7	50.1	47.1	53.4	54.6	44.9
CVI–CV	−12.5	−9.4	−17.9	−4.9	1.7	−6.2	−10.2	−10.5
CIV	55.3	56.2	54.0	53.1	48.1	53.5	61.1	60.8
CV–CIV	−8.1	−4.7	−0.3	−3.1	−1.0	−0.1	−6.4	−15.9
Left female								
CVI	34.3	33.6	38.0	34.7	36.2	36.7	34.9	34.9
CV	34.9	39.4	38.0	37.1	34.5	38.0	39.9	36.7
CVI–CV	−0.6	−5.8	−0.1	−2.3	1.6	−1.3	−5.0	−1.8
CIV	28.6	30.9	33.2	33.2	31.1	30.9	34.1	32.2

this stage. For example, in the five samples with more than 100 males this range was reduced to a maximum of 58.1% and a minimum of 53.5%.

Among all 29 samples, CVI left females (Table 6) varied from 39.2% for a sample in July 1978 to 26.2% for one in October 1977 with a median of 35.5%. The median of CV left females was 37.9% with a maximum of 47.5% and a minimum of 31.3% for a sample each in September 1978 and August 1977. The percentage of left females was relatively constant by month for each stage (CVI—33.6–38.0% = 4.4%, CV—34.5–39.9% = 5.0%, CIV—28.6–34.1% = 5.5%), and by month always increased between CIV and CV and usually decreased slightly between CV and CVI (except May 1978).

In comparing the percentage of left females in CVI and CV (Table 6), differences always were small and not significant; CV values were usually larger than CVI. Adjusted sample sizes were approximately 100, with power of about 20% and small effect sizes of 0.10; a single exception occurred in October 1977. In contrast, values of the percentage of CIV left females were usually smaller than those of CV. Although differences were not significant, adjusted sample sizes were small, with 13 of 29 below 20, and power was low. However, there are some very large effect sizes, 11 above 20%. These results suggest that future studies with an increased sample size may detect statistically significant differences in the percentage of left females between CIV and CV, particularly in October and May.

Discussion

Our results for *P. xiphias* show monthly changes of varying magnitudes in four attributes. Frequency data suggest several cooccurrences in May 1978: highest percentage of CVI males, highest percentage of CVI females without a dark mass in the genital opening, lowest percentage of CIV males, positive difference between the percentage of CVI minus that of CV males, and positive difference between the percentage of CVI minus that of CV left females. Among two to four samples which comprise each monthly value, variability is high for the percentage of CVI males, the percentage of CVI males with a spermatophore in the spermatophore sac, and the percentage of CVI females without a dark mass in the genital opening.

Our choice of collecting gear and sampling protocol may have affected some of these results. The relatively coarse mesh of the sampling gear certainly affected absolute abundances of different copepodid stages in our study. Younger, and smaller, copepodids passed through the meshes more easily than older copepodids. Ambler and Miller (1987), using nets with 0.333 mm and 0.183 mm in December, found adult abundances comparable to ours (about 10 animals per 100 m^3) but higher abundances of CV and

Table 5. Percentage of CVI, CV, and CIV males for all samples; *z* value, effect size, and power for tests of difference between percentage of males of succeeding stages. CVIM = percentage of CVI males, CVM = percentage of CV males, CIVM = percentage of CIV males, *z* = the *z* value for the test of equality, *ns* indicates a probability value greater than 0.05, * indicates a probability value equal to or less than 0.05 and greater than 0.01, ** indicates a probability value equal to or less than 0.01, harmonic mean is the average sample size adjusted for unequal numbers of animals in two samples.

Sample	CVIM	CVM	*z*	Harmonic mean	Observed effect size	Power	CVM	CIVM	*z*	Harmonic mean	Observed effect size	Power
770805	45.9	44.6	−0.47 *ns*	736.84	0.03	0.59	44.6	52.3	−1.23 *ns*	140.87	0.154	0.31
770806	33.2	49.7	5.76**	596.38	0.34	0.99	49.7	56.1	−1.12 *ns*	206.17	0.129	0.30
770811	29.6	50.5	7.90**	675.99	0.43	0.99	50.5	52.5	−0.24 *ns*	78.59	0.040	<0.16
770812	29.4	43.8	5.26**	612.12	0.30	0.99	43.8	56.9	−2.52*	252.10	0.262	0.90
771005	66.8	54.9	−2.00*	131.24	0.25	0.81	54.9	40.5	1.12 *ns*	29.14	0.289	0.31
771006	34.9	51.2	6.00**	655.09	0.33	0.99	51.2	55.0	−0.25 *ns*	21.57	0.079	0.09
771012	45.0	59.3	5.95**	866.75	0.29	0.99	59.3	63.3	−0.61 *ns*	111.84	0.082	0.17
771013	36.5	42.4	2.06*	591.50	0.12	0.65	42.4	56.0	−1.80 *ns*	92.73	0.274	0.65
780205	36.5	57.2	9.00**	941.47	0.42	0.99	57.2	58.1	−0.16 *ns*	174.34	0.018	<0.23
780206	34.9	52.4	6.70**	704.77	0.36	0.99	52.4	56.4	−0.64 *ns*	130.30	0.080	0.20
780213	48.2	52.3	1.52 *ns*	705.18	0.08	0.59	52.3	50.5	0.32 *ns*	176.69	0.035	<0.24
780214	29.7	51.0	9.06**	826.70	0.44	0.99	51.0	51.6	−0.09 *ns*	116.59	0.013	<0.19
780405	39.1	53.1	5.24**	695.18	0.28	0.99	53.1	61.4	−1.16 *ns*	97.28	0.169	0.37
780406	34.7	47.6	4.38**	555.80	0.26	0.99	47.6	55.8	−1.22 *ns*	115.90	0.165	0.19
780413	70.5	51.4	−6.82**	608.54	0.40	0.99	51.4	51.2	0.02 *ns*	42.58	0.003	0.00
780414	47.3	48.3	0.38 *ns*	637.37	0.02	0.54	48.3	50.4	−0.43 *ns*	283.25	0.041	<0.34
780505	58.0	40.6	−3.96**	257.89	0.35	0.97	40.6	47.8	−0.91 *ns*	70.32	0.146	0.24
780506	27.9	49.4	6.10**	358.87	0.45	0.99	49.4	53.5	−0.37 *ns*	41.96	0.083	<0.12
780513	57.3	50.2	−2.18*	458.00	0.14	0.91	50.2	35.7	0.64 *ns*	9.85	0.293	0.17
780514	54.8	46.4	−2.90**	596.50	0.17	0.97	46.4	47.8	−0.20 *ns*	116.76	0.028	<0.19
780705	47.5	51.7	1.39 *ns*	564.89	0.08	0.54	51.7	56.9	−0.94 *ns*	160.52	0.105	0.23
780706	47.4	52.3	1.80 *ns*	673.93	0.10	0.59	52.3	49.6	0.40 *ns*	122.52	0.053	<0.19
780713	37.3	59.1	8.83**	808.57	0.44	0.99	59.1	54.3	0.47 *ns*	47.94	0.097	0.13
780714	67.2	49.2	−5.93**	518.80	0.37	0.94	49.2	51.7	−0.27 *ns*	57.86	0.050	<0.14
780805	42.6	54.2	3.90**	563.99	0.23	0.97	54.2	66.7	−1.18 *ns*	45.50	0.256	0.38
780905	41.3	54.7	2.83**	218.81	0.27	0.91	54.7	58.1	−0.39 *ns*	56.20	0.069	<0.13
780906	50.7	56.5	1.03 *ns*	159.57	0.12	0.23	56.5	60.0	−0.21 *ns*	16.40	0.071	<0.09
781005	26.1	45.9	7.97**	699.94	0.42	0.98	45.9	64.8	−3.66**	216.77	0.382	0.89
781006	61.6	42.8	−4.59**	296.02	0.38	0.98	42.8	55.3	−1.99*	131.11	0.251	0.65

CIV; data from 0.320-mm mesh ncts of Ferrari (1985) in November are similar. However, we do not believe that the morphology of different categories of animals within the samc stage affected our findings about relativc abundances of the four attributes.

Incomplete sampling of vcrtically assorted copepodids may have affected at least one attribute that we examined, the percentage of CVI males. At night CV and CVI copepodids of *P. xiphias* exhibit a biomodal distribution (Ambler and Miller, 1987). Ferrari (1985) found that this distribution is similar for CV of both sexes; for CVI, the bimodal distribution is dissimilar for females and males with the percentage of males higher at the deep mode. Thus, CVI exhibits a degrce of vertical assortment by sex at night. Vertical assortment has been reported for other species of *Pleuromamma.* Nighttime assortment by male reproductive condition has been reported for a congcner, *P. piseki,* by Hayward (1981), and data of Beckmann (1984) for *P. indica* suggest daytime assortment by sex with the percentage of CVI males increasing with depth. If vertical assortment by sex occurs for *P. xiphias* in daytime distributions off Hawaii, failure to samplc deepest depths of its occurrence could explain our reduction in the pcrccntage of CVI males if similar assortment occurs during the day at all times of year.

To determinc the extent of this hypothesized effect, we examined unpublished data on daytimc vertical distributions of *P. xiphias* obtained during Loren Haury's study (Haury, 1988) of vcrtical distributions of

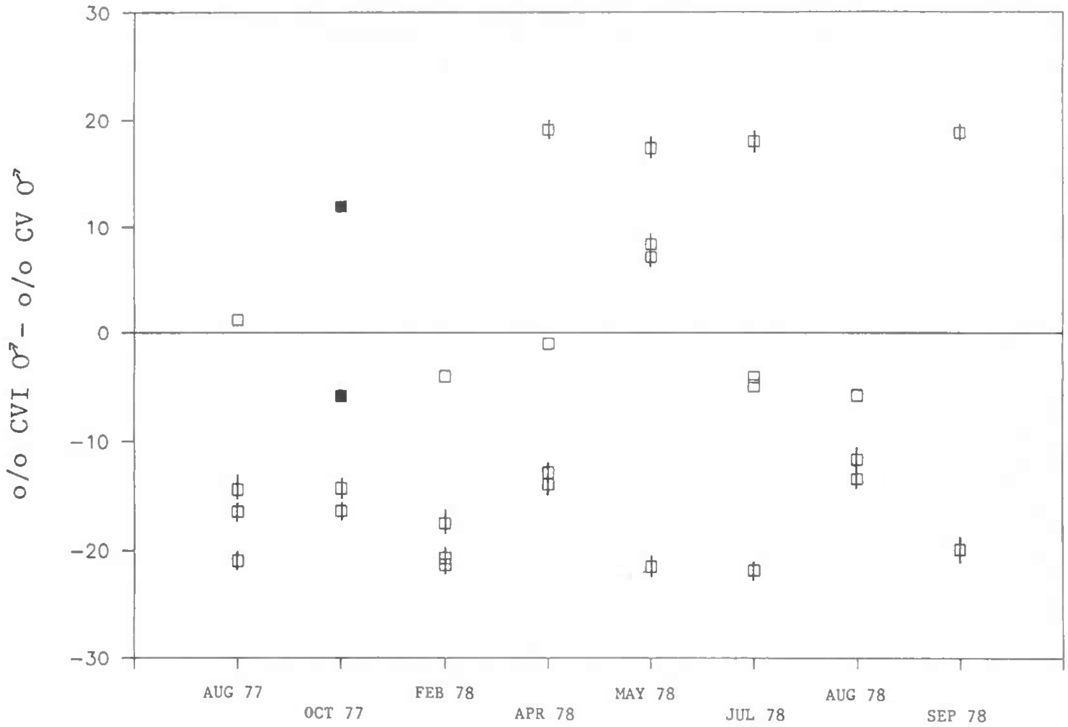

Fig. 1. Differences by month between percentage of CVI males minus CV males for each sample. Open squares signify no significant difference between the two percentages; closed squares signify a significant difference, but power for the test is low; squares with a vertical line signify a significant difference, power of the test is high.

species of *Pleuromamma* in the eastern North Pacific and Carin Ashjian's ongoing investigation of calanoid copepod distributions across the Gulf Stream in the western North Atlantic. Haury's day samples in the vicinity of Hawaii (2D, 3D, 6KD, 8D) in August 1982 covered the interval from 200–600 m in 20-m increments. From 47–554 specimens of CVI *P. xiphias* were collected, with males comprising 12.8, 13.7, 18.8, and 30.3% of CVI animals. These percentages are lower than ours. There was no direct indication of higher percentages of males at deeper depths sampled, but if collecting efficiency is similar to ours these data suggest that a greater percentage of CVI males may be expected below 600 m.

Ashjian's samples from September 1982 and May 1983 form three sets (North Wall, Central Stream, and Sargasso Sea) for each month. Each set consists of seven samples, four over 150-m intervals from 1,000–400 m, two over 100-m intervals from 400–200 m, and one at 0–200 m. Among the three sets for both months, males make up 26.0, 29.6, 31.3, 33.3, 36.9, and 47.0% of CVI *P. xiphias*. Specimens collected in the deepest interval, 1,000–850 m once and 850–700 m twice, were all males. Because small numbers of animals (1–37) were encountered in the deeper samples, deletion of animals from these depths would have affected calculations of the percentage of males in only one sample (from 26.0–14.9%).

If vertical assortment and incomplete sampling causes a lower percentage of CVI males of *P. xiphias* off Hawaii, its effect should be sharpest in our shallower samples and weakest in our deepest samples. There are 19 samples at 1,000 m or below; the percentage of CVI males ranges from 27.9–67.2% with an average of 45.1% and a median of 39.1%. Ten samples were fished above 1,000 m; these have a minimum value of 26.1% and a maximum of 70.5% with an average of 42.6% and median of 37.3%. A test of the two average percentages (z = 0.13) detected no significant difference. We also note that in 7 of our samples from below 1,000 m, the percentage of CVI males

Table 6. Percentage of CVI, CV, and CIV left females for all samples; *z* value, effect size, and power for tests of difference between percentage of left females of succeeding stages. CVIFL = percentage CVI left females, CVFL = percentage of CV left females, CIVFL = percentage of CIV left females; *z* = the *z* value for the test of equality, *ns* indicates a probability value greater than 0.05, * indicates a probability value equal to or less than 0.05 and greater than 0.01, harmonic mean is the average sample size adjusted for unequal numbers of females in two samples.

Sample	CVIFL	CVFL	*z*	Harmonic mean	Observed effect size	Power	CVFL	CIVFL	*z*	Harmonic mean	Observed effect size	Power
770805	36.5	31.3	0.90 *ns*	136.12	0.110	0.21	31.3	25.4	−0.51 *ns*	31.50	0.132	0.14
770806	31.7	38.5	−1.11 *ns*	120.60	0.140	0.30	38.5	29.6	−0.89 *ns*	46.24	0.188	0.25
770811	33.1	36.1	−0.51 *ns*	134.92	0.060	<0.21	36.1	26.3	−0.62 *ns*	18.32	0.212	0.15
770812	35.8	35.0	0.13 *ns*	132.90	0.020	<0.21	35.0	30.4	−0.51 *ns*	55.80	0.098	0.13
771005	26.2	32.6	−0.39 *ns*	15.48	0.140	0.11	32.6	32.0	−0.03 *ns*	10.43	0.013	<0.08
771006	33.6	32.8	0.13 *ns*	117.77	0.020	<0.19	32.8	55.6	1.04 *ns*	9.46	0.463	0.30
771012	35.1	41.8	−1.21 *ns*	151.81	0.140	0.33	41.8	30.6	−0.72 *ns*	19.76	0.234	0.19
771013	31.3	44.6	−2.25*	135.35	0.270	0.79	44.6	25.0	−1.20 *ns*	18.58	0.415	0.35
780205	38.5	38.9	−0.07 *ns*	182.98	0.010	<0.24	38.9	35.7	−0.30 *ns*	42.56	0.065	<0.12
780206	38.5	38.6	−0.01 *ns*	140.18	0.001	0.00	38.6	32.8	−0.47 *ns*	31.44	0.120	0.12
780213	37.2	38.4	−0.20 *ns*	132.33	0.020	<0.19	38.4	31.0	−0.76 *ns*	49.36	0.156	0.20
780214	37.6	36.1	0.27 *ns*	160.55	0.031	<0.20	36.1	34.4	−0.15 *ns*	34.71	0.036	<0.11
780405	34.5	32.6	0.30 *ns*	115.49	0.040	<0.23	32.6	38.2	0.39 *ns*	22.16	0.117	0.12
780406	34.6	39.6	−0.80 *ns*	118.67	0.103	<0.18	39.6	32.1	−0.58 *ns*	28.55	0.156	0.17
780413	37.1	38.8	−0.21 *ns*	82.67	0.033	0.19	38.8	28.6	−0.50 *ns*	11.45	0.215	0.13
780414	34.4	36.9	−0.40 *ns*	118.19	0.052	<0.16	36.9	33.1	−0.50 *ns*	80.59	0.079	<0.16
780505	36.4	41.3	−0.53 *ns*	54.66	0.101	<0.16	41.3	29.2	−0.81 *ns*	21.12	0.255	0.20
780506	37.4	36.4	0.13 *ns*	71.73	0.021	0.13	36.4	20.0	−0.66 *ns*	7.33	0.367	<0.22
780513	33.1	34.4	−0.16 *ns*	73.99	0.026	<0.15	34.4	11.1	−0.49 *ns*	1.96	0.574	<0.36
780514	37.4	31.6	0.86 *ns*	100.84	0.122	<0.15	31.6	38.0	0.63 *ns*	42.24	0.135	0.19
780705	39.2	40.0	−0.12 *ns*	111.47	0.017	0.20	40.0	32.0	−0.71 *ns*	37.13	0.167	0.16
780706	38.2	36.9	0.21 *ns*	125.90	0.026	<0.18	36.9	23.2	−1.08 *ns*	27.90	0.302	0.30
780713	35.8	36.1	−0.06 *ns*	133.38	0.007	<0.20	36.1	47.6	0.71 *ns*	17.92	0.233	0.18
780714	32.1	39.5	−0.96 *ns*	76.34	0.156	0.28	39.5	34.5	−0.31 *ns*	17.94	0.105	0.09
780805	35.5	39.0	−0.52 *ns*	105.30	0.072	<0.17	39.0	41.7	0.12 *ns*	9.40	0.055	<0.08
780905	33.7	37.9	−0.39 *ns*	38.34	0.088	<0.11	37.9	34.6	−0.17 *ns*	12.77	0.069	<0.08
780906	35.8	47.5	−0.97 *ns*	32.22	0.238	0.23	47.5	16.7	−0.60 *ns*	1.90	0.679	<0.47
781005	35.8	38.1	−0.42 *ns*	154.72	0.047	<0.20	38.1	26.7	−0.97 *ns*	33.55	0.244	0.28
781006	29.1	34.0	−0.49 *ns*	43.82	0.106	0.12	34.0	38.0	0.35 *ns*	35.06	0.083	<0.11

was low (770806, 780205, 780206, 780214, 780405, 780406, 780506), and in two of our shallower samples the percentage of CVI males was high (780413, 780514), the reverse of expectation if incomplete sampling of an assorted group of animals was a problem. We believe that vertical assortment by sex is an important but poorly understood phenomenon for this calanoid. Based on the above findings and correspondences among monthly patterns of percentages of CVI, CV, and CIV males, percentages of CVI females with dark masses, and differences between CVI and CV left females discussed below, we conclude that incomplete sampling of an assorted group of animals cannot alone explain the variation exhibited in our samples.

There is very little information about variability of sex-limited dimorphisms among calanoid copepods. Fleminger (1985) described seasonal frequencies of trithek and quadrithek females (a sex-limited, antenna 1 dimorphism) among *Calanus pacificus californiensis,* while examining a hypothesis of phenotypic sex change by genotypic males. He showed that the percentage of quadrithek CVI females (his switched genotypic males) decreased from above 12% in January, during the onset of copulatory activity when phenotypic switching among early maturing males would seem most favorably selected, to below 5% in later summer, when the presumed switching and resulting quadrithek morph would have less selective advantage. Frequency data for the male sex-limited dimorphism of spermatophore size in *Euchaeta antarctica* (Ferrari and Dojiri, 1987) were too sparse to discover a seasonal pattern or to relate variations to the percentage of CVI males.

Our data on the percentage of left females of *P. xiphias* from individual samples or grouped by month indicate that within stages this is a relatively stable, sex-limited dimorphism. Our calculations of the percentages of left animals extend this stability to CIII. Comparisons by month between stages suggest that there may be some selection for left females between CIV and CV, and for right females between CV and CVI. Generally, ranges of variation among the asymmetrical morphs of CV or CVI *P. xiphias* are comparable to those encountered by Fleminger for trithek and quadrithek morphs. Ferrari (1985) did not report vertical assortment by asymmetry during day or night for *P. xiphias,* and we do not believe vertical assortment and incomplete sampling have affected our conclusions about this attribute.

We believe that differential recruitment is a simple explanation for correlated changes in the percentages of morphs, such as males and females or left and right females, in succeeding stages of development of *P. xiphias.* May 1978 was the only month in which there was no significant difference between the percentage of CV and CVI males; the difference between the percentage of CIV and CV males also was low. In the remaining seven months, the percentage of CV males was significantly greater than the percentage of CVI males (z values range from -2.47 to -9.92). May 1978 also was the only month in which the difference between the percentage of CV and CVI left females was positive and the difference between the percentage of CIV and CV left females was lowest. We interpret this increase in the percentage of CVI males with corresponding decreases in the percentage of CV and CIV males and the increase in the percentage of CVI left females with corresponding decreases in the percentage of CV and CIV left females as indicating differential recruitment of CVI males and left females in May 1978. Abundances of all copepodids also are low in May 1978; this is not the month of highest percentage males with spermatophores, which reached its maximum earlier, in February 1978.

Several authors have used a sex ratio, with other attributes similar to those we studied, to describe calanoid reproductive cycles. Hopkins (1982) included spermatophore attachment and egg sac production, along with a sex ratio, in defining breeding intensity of *Euchaeta norvegica.* These attributes could not be used for *P. xiphias* because egg sacs were not found and attached spermatophores were rare, in only 3 of 13,922 CVI females in this study. Tande and Grønvik (1983) analyzed sex ratio, presumptive spermatophore presence in the genital duct of CV males, transparent spermatophore sac in CVI males, and stage of maturity of CVI female genital system in their study of *Metridia longa.* These authors interpreted higher percentage of CVI males with a transparent spermatophore sac, the spermatophore presumably having been ejaculated, as indicating more intense copulatory activity. Males of *P. xiphias* recently molted (with undeveloped internal tissues and soft, thin exoskeleton), as well as older males (those with a hard, rigid exoskeleton and well-developed internal tissues), were included among our counts of males without a spermatophore in the spermatophore sac. Thus, absence of a spermatophore in the spermatophore sac of *P. xiphias* may be ambiguously interpreted, because it may indicate either the animal has recently molted and the first spermatophore has not had time to form or that the animal has recently copulated and another spermatophore has not had time to form (no information is available about multiple spermatophore production for *P. xiphias*). We chose presence of a spermatophore in the spermatophore sac as an attribute more usefully interpreted. This attribute may be considered the inverse of Tande and Grønvik's percentage of CVI males with a transparent spermatophore sac. Hayward (1981) also used the presence of a spermatophore in the CVI male spermatophore sac of *P. piseki,* interpreting it as indicating a male in immediate precopulatory condition. Here we interpreted higher percentage males with a spermatophore in the spermatophore sac of *P. xiphias* as indicating an increased copulatory potential for adults. Although on the average half of males of *P. xiphias* have a spermatophore, the maximum of 76.7% in February 1978 contrasts sharply with a minimum of 9.1% in October 1977.

Presence of a dark mass in the genital opening or analogous conditions of the genital opening in other calanoids have not been studied seasonally. This dark mass usually occurred in adult females of *P. xiphias* with a hard, rigid exoskeleton and well-developed internal tissues (gut, oviducts, musculature). Absence of the dark mass always occurred in females with undeveloped internal tissues and soft, thin exoskeleton. We assume that these latter females without a dark mass were recently molted, and a greater percentage of them among CVI females indicates a period of more active recruitment to CVI. In our samples this percentage reached its maximum, 22.1%, in May 1978 when CVI females were relatively low, and CV and CIV females were relatively high [that is, the percentage of CVI males was highest (48.8%), the percentage of CV males was low (47.1%), and the percentage of CIV males was lowest (48.1%) in the study period].

Comparison of our data for *P. xiphias* with reports about the distribution of sex among other calanoid species (Table 1) indicates that in slightly more cases (26), males are present throughout the year, and in most of those cases (17), males constitute less than 50% of the adults sampled. Seasonal distribution of sex in CVI and CV *P. xiphias* is most similar to that of *Acartia longiremis* as reported by Lee and McAlice (1979). Males of both stages reported by them are present throughout the year and there is a monthly decrease in the percentage of males from CV (at about 50%) to CVI. *Pleuromamma xiphias* showed a unimodal maximum in the percentage of CVI males (a trait shared with 10 other calanoids) in May 1978, the only month in which the percentage of CV males was not significantly greater than the percentage of CVI males. *Pleuromamma xiphias* is also the only calanoid reported to date which exhibits statistically significant differences between the percentage of CV and CVI males in samples collected within 36 h.

Seasonal distribution of the percentage of CIV males of *P. xiphias* differs from three other calanoid species in which this attribute has been studied. In *Metridia longa* and *Senecella calanoides* CIV males are present during only part of the year. The percentage of CIV males of *Euchaeta norvegica* shows a sharp decrease to 25% from a maximum of over 90% during months of maximum percentage CVI males (31%). In contrast, the percentage of CIV males of *P. xiphias* is slightly above 50% and higher than the percentage of CV throughout the year; this latter difference is smallest in July.

Authors of studies of copepod population ecology often have suggested causes which explain adult sex ratios differing from 50%. Among sexually reproducing animals there are reasonable theoretical considerations for assuming this to be an important question based on selection for allocation of reproductive effort (Charnov, 1982; Leigh *et al.*, 1985), as well as considerations which predate selection theory (Arbuthnot, 1710). Authors of works on calanoids usually explain lower percentage of males as an intrinsic consequence of several effects: low adult densities (Bayly, 1965); genotypic males changing sex to become phenotypic females (Fleminger, 1985); differential development of immature males slower (Gurney, 1940) or faster (Tande and Grønvik, 1983) than females; differential mortality during molting (Comita, 1956; Lee and McAlice, 1979); or adult females being longer-lived (Marshall, 1949; Chapman, 1969; Hopkins, 1982; Uye *et al.*, 1982; Tande and Grønvik, 1983; Bayly, 1986). Goswami (1978) suggested that inefficient feeding by males resulted in their relatively shorter life, while Gibbons (1936) considered multiple copulations by males as an adaptation for this consequence. Landry (1978) referred to an extrinsic cause, predation by stickleback fishes, as contributing to higher percentages of CVI males of *Acartia clausii*. Hairston *et al.* (1983), in a compelling field and laboratory study, showed that sunfish fed preferentially on females of *Diaptomus sanguineus*, particularly those carrying egg sacs, and thus increased the percentage of CVI males significantly.

Our data for multiple samples taken within 36 h exhibit a wide range of values for the percentage of CVI males if sample sizes are selected to detect a minimum difference of 10% between stages with a 90% degree of confidence that this difference can be correctly identified if it exists. It is apparent from Fig. 1 that, had our study been limited to a single sample each month, our interpretation of the percentage of males may have changed and we may easily have missed recruitment of CVI males and left females in May 1978. This variability and the absence of knowledge about assortment by sex among calanoids suggest to us that changes in sampling design will be essential to future studies of this and similar attributes. Because selection can affect the distribution of sex among adult copepods, we believe that careful determination of the continued co-occurrence of males with females, the upper and lower limits of the percentage of CVI males, as well as the percentage of CV and CIV males, may be more useful values in comparisons among species.

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