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Comparative Fecundity and Reproductive Strategies in Seventeen Species of the Cumacea (Crustacea: Peracarida)

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Abstract

The fecundity of 17 species of cumaceans belonging to 5 families from the eastern and western temperate regions of the Atlantic and the Canadian Arctic and Subarctic Oceans are discussed separately and then compared. The species range from 0.78 to 10.11 mm (mean carapace length) with fecundities ranging from 15.1 to 168.9 (mean number of eggs brood^{-1} female^{-1}). Interspecific comparisons show that carapace volume versus volume of brood yields a very strong relationship (r = 0.99). Therefore, it is a combination of carapace volume plus egg volume which determines the fecundity in the Cumacea. A discussion of the various life-history and reproductive strategies employed by the Cumacea is included.

Introduction

The Cumacea form an important component of benthic infauna inhabiting soft substrates from the littoral to abyssal depths and from the Arctic to the tropics. The developing young are carried in a ventral brood pouch (marsupium) and are released at an advanced stage - the manca stage. Of the more than 900 known species the life history and fecundity have been studied in 7 species: *Diastylis rathkei* by Krüger (1940); *Iphinoe trispinosa, Cumopsis goodsiri, Pseudocuma longicornis, P. longicornis* by Corey (1969);*Manocuma stellifera* by Gnewuch and Croker (1973);*Diastylis sculpta* by Corey (1976a,b). Fecundity is defined as the number of young per brood per female.

Seventeen species, representing 5 families inhabiting both sides of the north Atlantic, the Canadian Arctic and Subarctic Oceans were collected. Depths ranged from littoral to 200 m. Because of the wide distribution and varied habitats of the Cumacea, comparative studies of spawning seasons and fecundities were undertaken in order to achieve a better understanding of the ecology of this taxon.

Materials and Methods

Shallow-water (0 to 20 m) species were collected from the Clyde Sea (UK) and Passamaquoddy Bay (Canada) by means of a small D-net as described by Corey (1969, 1979a). Deeper water (20 to 200 m) specimens were obtained from the Clyde Sea with a beam trawl (11.8 mesh per cm) with a 0.5 m townet (23.6 mesh per cm) mounted on top of the trawl. Deeper samples from Passamaquoddy Bay were obtained with an Issacs-Kidd trawl (Amaratunga and Corey, 1975).

Samples were fixed in 10% formalin in sea water. Carapace lengths (± 0.025 mm) were measured from the tip of the pseudorostrum to the mid-dorsal posterior edge of the carapace. The greatest depth and width of each species was also measured to obtain carapace volume.

The developing stages within the brood pouch were removed, counted and categorized after Corey (1969) into the following: Stage I, free round eggs; Stage II, young larvae; Stage III, well developed larvae; Stage IV, larvae ready to be released - manca stage. The volume of Stage I was calculated for each species. After Stage II, differential growth of the larvae occurs. Also, the manca stage are released over an extended period of time (up to 1 wk, Corey 1976 b). For this reason, fecundity was based mainly on Stages I and II larvae.

Regression lines and correlation coefficients were determined for the carapace length versus egg number; carapace length versus volume of brood; and carapace volume versus volume of brood.

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Table 1. Distribution (X, present; –, absent), breeding seasons and fecundity of 17 cumaceans studied. Code numbers of species are used in Fig. 1. *n* = actual number of specimens analyzed per species

Species and (Code No.)		Distribution		Depth range (m) collected	Breeding season(s)	Mean carapace length (mm) + (SD)	Mean no. of eggs + (SD)	*n*	Volume of 1 egg (mm^3)
		Clyde Sea	Coast of North America						
Family Bodotriidae									
Iphinoe trispinosa	(10)	X	X	0–20	Apr-June:Aug[b]	2.00 (0.15)	77.1 (22.6)	56	0.014
I. serrata	(11)	X	–	30–180	Dec-Mar	2.16 (0.21)	44.7 (14.9)	20	0.014
Cumopsis goodsiri	(1)	X	–	Littoral	Mar-June:July[b]	1.01 (0.11)	32.2 (11.0)	110	0.009
Family Lampropodae									
Lamprops fuscata	(2)	–	X[a]	3–10	July-Sept	1.04 (0.08)	15.1 (05.9)	16	0.027
L. fasciata	(8)	X	–	Littoral	Spring	1.24 (0.09)	23.5 (06.1)	44	0.024
L. quadriplicata	(15)	–	X	5–10	Apr-July	1.90 (0.16)	168.9 (20.1)	10	0.018
Hemilamprops rosea	(3)	X	–	40–200	Nov-Jan:June-Aug[c]	0.98 (0.07)	24.6 (05.3)	10	0.018
Family Leuconidae									
Leucon nasica	(12)	X	X	25–200	Nov-Mar	1.85 (0.14)	19.3 (09.9)	93	0.047
Eudorella pusilla	(4)	–	X	2–20	May-July	0.78 (0.11)	18.1 (04.3)	49	0.018
Family Diastylidae									
Diastylis lucifera	(7)	X	X	40–160	May-July	1.38 (0.08)	40.3 (10.4)	127	0.018
D. quadrispinosa	(17)	–	X	30–200	Feb-Mar	2.54 (0.28)	67.2 (32.8)	39	0.018
D. polita	(16)	–	X	2–18	May-June	2.80 (0.21)	162.1 (43.8)	14	0.018
D. goodsiri	(18)	–	X[a]	20–200	July-Sept	10.11 (0.39)	159.9 (17.1)	39	0.347
D. sculpta (fall)	(6)	–	X	10–20	May-Aug[b]	1.39 (0.10)	20.6 (04.6)	55	0.018
D. sculpta (spring)	(13)	–	X	10–20	Oct-Nov	1.71 (0.20)	65.4 (14.7)	101	0.018
Diastyloides biplicata	(14)	X	–	40–140	Nov-Feb	1.54 (0.11)	33.5 (07.5)	66	0.014
Leptostylis longimana	(9)	–	X	50–200	July-Aug:Dec[c]	1.27 (0.08)	26.3 (06.4)	32	0.018
Family Pseudocumidae									
Pseudocuma longicornis	(5)	–	X	0–20	Continuous	0.85/(0.07)	20.9/(05.6)	102	0.009

[a] Arctic - Subarctic

[b] Two generations per year

[c] Two breeding seasons per year (same female?)

Results

Of the 17 species examined, 3 occur on both sides of the North Atlantic Ocean: *Iphinoe trispinosa, Leucon nasica* and *Diastylis lucifera*. *D. goodsiri* was the only truly Arctic species. The remaining species are either subarctic or temperate, inhabiting either the eastern or western waters of the North Atlantic, respectively (Table 1).

The breeding seasons were estimated from the presence of gravid females in the population. In the majority of species, the duration of the breeding season was from 3 to 4 months. Two main exceptions occurred: *Pseudocuma longicornis* which breeds continuously through the year, and species producing two generations per year. In the latter case, the overwintering generation bred for 3 to 4 months and the summer generation for 1 to 1½ months (*Cumopsis goodsiri, Iphinoe trispinosa* and *Diastylis sculpta*) (Table 1).

Only rarely does a given female produce more than one brood, and generally dies after breeding once (Corey, 1969, 1976b). Thus, fecundity is expressed as the number of eggs per brood per female. Fecundity varies greatly intra- and interspecifically (Fig. 1, Tables 1-3). The average fecundity per species varied from 15.1 to 168.9; mean carapace lengths ranged from 0.78 to 10.11 mm (Table 1). Although fecundity varies intra- and interspecifically, there is a general trend of larger females carrying a larger number of young. A correlation coefficient of 0.65 was obtained for all data for all species (Table 5). The rate of increase of egg number per brood relative to increase in size of female was greatest in *Diastylis polita* and least in *D. goodsiri* (see Fig. 1).

The volume of one egg was consistent within a species, but varied between species from 0.009 to 0.347 mm^3. The smallest and largest species, *Eudorella pusilla* and *Diastylis goodsiri*, had individual egg volumes of 0.009 and 0.347 mm^3, respectively. However, there was no strong relationship between size of female and egg volume within species of intermediate size (average carapace lengths of 0.85 to 2.80 mm). The volume of brood per given female was analyzed because of this interspecific variability in egg volume (Table 4). The rate of increase in brood volume was greatest in *Lamprops fuscata* and

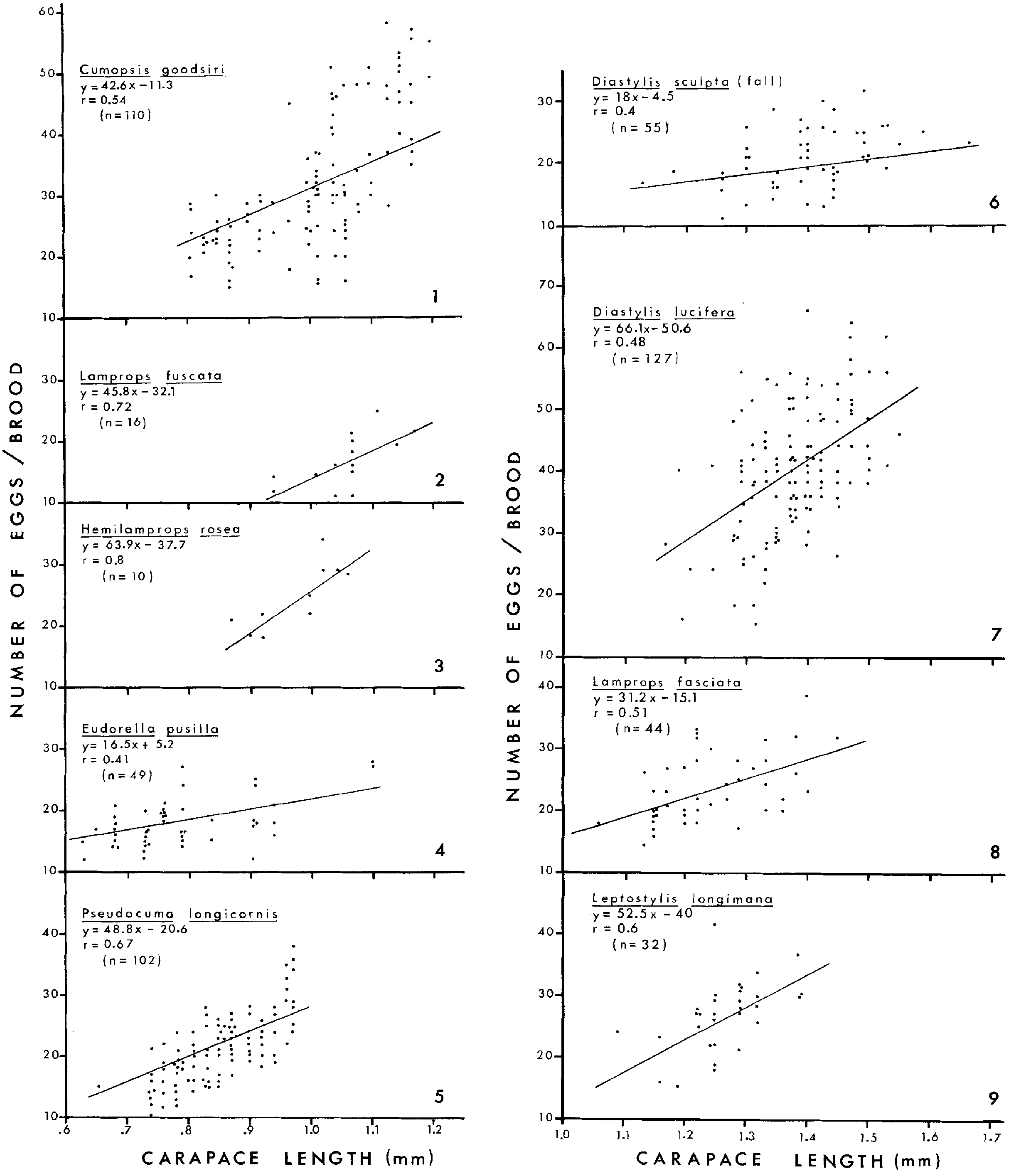

Fig. 1. Number of eggs per brood per female as a function of carapace length in 17 species of Cumacea. Code numbers used in Tables 1, 3 and 4 are given

(Fig. 1. continued on next page) ▶

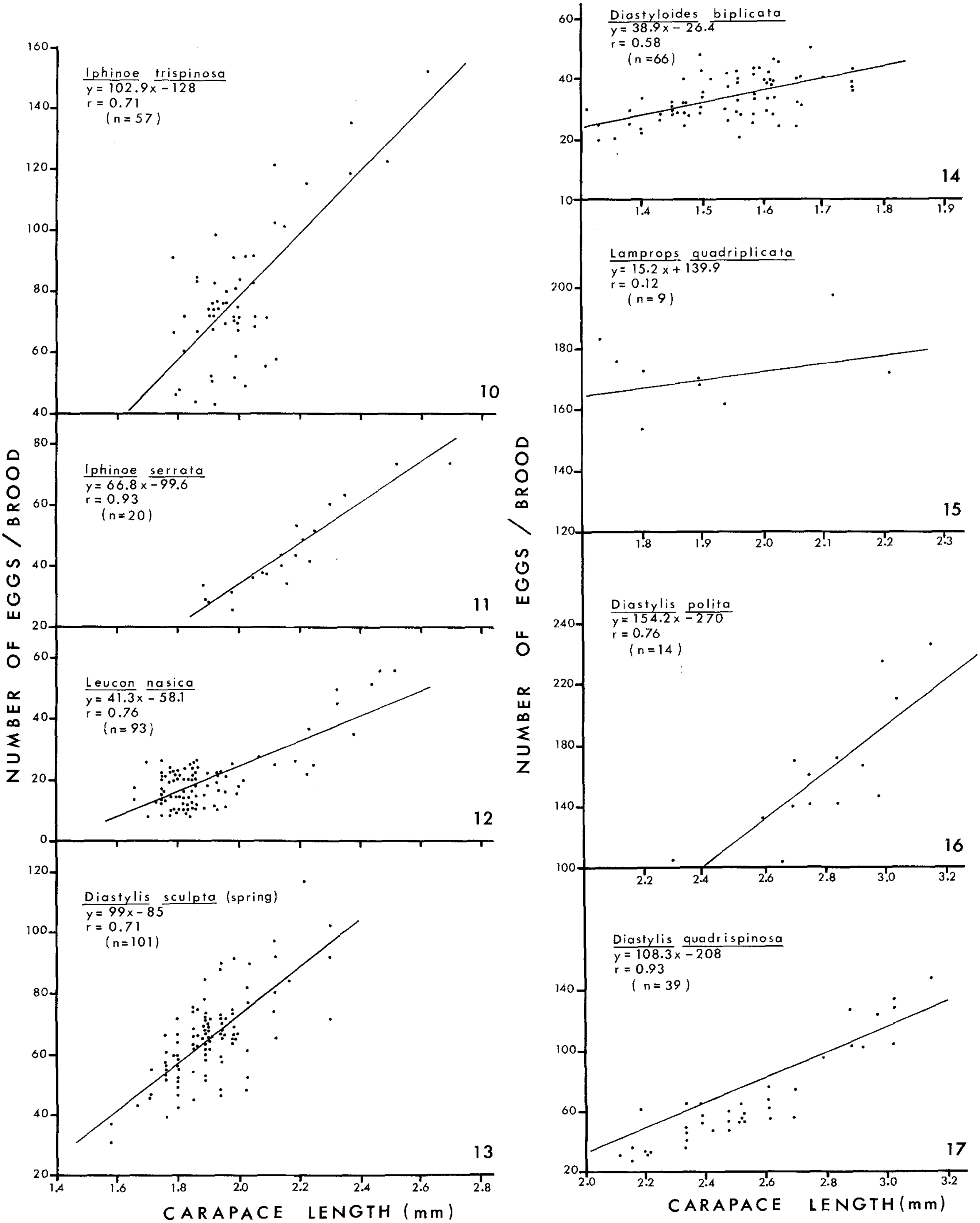

Fig. 1. (continued)

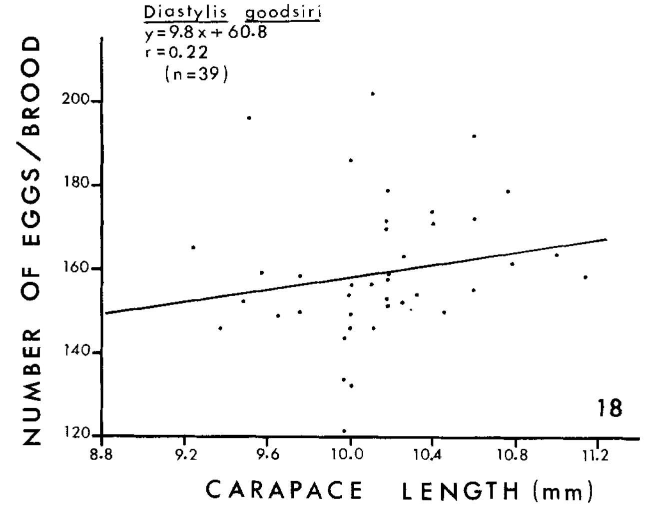

Fig. 1. (continued)

Table 2. Range of fecundity of Cumacea for which insufficient numbers (< 10) did not allow regression analysis

Species	Fecundity range[a]
Eudorella emarginata	30-50
Eudorella truncatula	20-42
Diastylis laevis	64-140
Diastylis tumida	56-70
Brachidiastylis resima	9-29
Oxurostylis smithi	32-74
Campylaspis rubicunda	6

[a] Actual egg counts

least in *L. quadriplicata*. Interspecific comparisons were analyzed in two ways: (1) excluding *D. goodsiri* because of the very large difference in both size of females and size of eggs from the rest of the species; (2) including *D. goodsiri* (Table 5, Fig. 2). The overall correlation coefficients (0.74 to 0.99) were stronger than for egg number per brood per female.

The shape of the carapace varies greatly interspecifically from a long tubular-shape in *Iphinoe* spp. to an almost square-shape in *Eudorella* spp. As a result, the carapace volume was compared to the volume of brood and yielded an extremely strong interspecific relationship of $r = 0.99$ (Table 5). This relationship was also the only one in which the slope did not change significantly (0.18 and 0.14), whether or not *Diastylis goodsiri* was included.

Discussion

Although the carapace volume plus the volume of the individual egg determines the overall fecundity in all the Cumacea studied; there are many aspects of the life histories and reproduction which vary interspecifically: shape of carapace, life span, age at maturity, breeding season, number of eggs per brood, and egg volume.

Most species studied (Krüger, 1940; Corey, 1969, 1976a,b) have a life span of approximately 1 yr or less and breed only once, e.g. *Iphinoe trispinosa, Cumopsis goodsiri, Diastylis sculpta* and *D. rathkei*. All but the last of these Cumacea produce 2 generations per year, an overwintering and a summer generation, with the summer females being smaller and producing fewer eggs than

Table 3. Regression equations and correlation coefficients for various fecundity relationships in 17 cumacean species. ns: not significant

Species and (Code No.)		Carapace length (x) versus no. of eggs brood^{-1} female^{-1} (y)			Carapace length (x) versus volume of brood (y)		
		Equation	r	Level of significance	Equation	r	Level of significance
Iphinoe trispinosa	(10)	$y = 102.9x - 128.0$	0.715	0.01	$y = 1.44x - 1.79$	0.714	0.01
I. serrata	(11)	$y = 66.8x - 99.6$	0.933	0.01	$y = 0.93x - 1.39$	0.933	0.01
Cumopsis goodsiri	(1)	$y = 42.6x - 11.3$	0.538	0.01	$y = 0.38x - 0.10$	0.538	0.01
Lamprops fuscata	(2)	$y = 45.8x - 32.1$	0.718	0.01	$y = 1.24x - 0.87$	0.718	0.01
L. fasciata	(8)	$y = 31.2x - 15.1$	0.511	0.01	$y = 0.75x - 0.36$	0.511	0.01
L. quadriplicata	(15)	$y = 15.2x + 139.9$	0.124	ns	$y = 0.27x + 2.52$	0.124	ns
Hemilamprops rosea	(3)	$y = 63.9x - 37.7$	0.789	0.01	$y = 1.15x - 0.68$	0.789	0.01
Leucon nasica	(12)	$y = 41.3x - 58.1$	0.759	0.01	$y = 1.94x - 2.73$	0.759	0.01
Eudorella pusilla	(4)	$y = 16.5x + 5.2$	0.412	0.01	$y = 0.30x + 0.09$	0.412	0.01
Diastylis lucifera	(7)	$y = 66.1x - 50.6$	0.479	0.01	$y = 1.19x - 0.91$	0.479	0.01
D. quadrispinosa	(17)	$y = 108.3x - 208.0$	0.926	0.01	$y = 1.95x - 3.74$	0.926	0.01
D. polita	(16)	$y = 154.2x - 270.0$	0.755	0.01	$y = 2.78x - 4.86$	0.755	0.01
D. goodsiri	(18)	$y = 9.8x + 60.8$	0.224	ns	$y = 3.40x + 21.09$	0.224	ns
D. sculpta (fall)	(6)	$y = 18.0x - 4.5$	0.708	0.01	$y = 0.32x - 0.80$	0.708	0.01
D. sculpta (spring)	(13)	$y = 79.0x - 85.0$	0.397	0.01	$y = 1.42x - 1.53$	0.397	0.01
Diastyloides biplicata	(14)	$y = 38.9x - 26.4$	0.578	0.01	$y = 0.54x - 0.37$	0.578	0.01
Leptostylis longimana	(9)	$y = 52.5x - 40.0$	0.596	0.01	$y = 0.95x - 0.72$	0.596	0.01
Pseudocuma longicornis	(5)	$y = 48.8x - 20.6$	0.665	0.01	$y = 0.44x - 0.18$	0.665	0.01

Table 4. Mean carapace and brood volumes of 17 cumaceans. n = actual number of specimens analyzed per species; ns: not significant

Species and (Code No.)		Mean carapace volume (mm^3) + (SD)	Mean brood volume (mm^3) + (SD)	n	Equation[a]	r	Level of significance
Iphinoe trispinosa	(10)	2.429 (0.640)	1.084 (0.315)	56	$y = 0.36x + 0.21$	0.734	0.01
I. serrata	(11)	3.630 (1.127)	0.626 (0.208)	20	$y = 0.17x + 0.01$	0.924	0.01
Cumopsis goodsiri	(1)	0.617 (0.363)	0.289 (0.099)	110	$y = 0.10x + 0.23$	0.351	0.01
Lamprops fuscata	(2)	0.923 (0.190)	0.425 (0.129)	16	$y = 0.50x - 0.03$	0.730	0.01
L. fasciata	(8)	2.138 (0.479)	0.568 (0.178)	44	$y = 0.14x + 0.27$	0.508	0.01
L.quadriplicata	(15)	5.637 (1.534)	3.040 (0.363)	10	$y = 0.04x + 2.83$	0.154	ns
Hemilamprops rosea	(3)	1.314 (0.260)	0.443 (0.095)	10	$y = 0.29x + 0.06$	0.803	0.01
Leucon nasica	(12)	3.096 (1.040)	0.923 (0.463)	93	$y = 0.35x - 0.16$	0.790	0.01
Eudorella pusilla	(4)	0.486 (0.226)	0.325 (0.078)	49	$y = 0.15x + 0.25$	0.429	0.01
Diastylis lucifera	(7)	1.705 (0.278)	0.725 (0.188)	127	$y = 0.32x + 0.18$	0.475	0.01
D. Quadrispinosa	(17)	9.347 (3.187)	1.210 (0.590)	39	$y = 0.17x - 0.42$	0.942	0.01
D. polita	(16)	13.861 (3.043)	2.917 (0.788)	14	$y = 0.20x + 0.11$	0.782	0.01
D. goodsiri	(18)	394.903 (45.681)	55.484 (5.937)	39	$y = 0.03x + 43.58$	0.232	ns
D. sculpta (fall)	(6)	1.135 (0.245)	0.371 (0.083)	55	$y = 0.13x + 0.22$	0.393	0.01
D. sculpta (spring)	(13)	2.687 (0.626)	1.177 (0.265)	101	$y = 0.30x + 0.33$	0.698	0.01
Diastyloides biplicata	(14)	0.925 (0.196)	0.468 (0.104)	66	$y = 0.30x + 0.19$	0.561	0.01
Leptostylis longimana	(9)	1.069 (0.179)	0.474 (0.114)	32	$y = 0.37x + 0.07$	0.587	0.01
Pseudocuma longicornis	(5)	0.407 (0.109)	0.188 (0.050)	102	$y = 0.31x + 0.06$	0.670	0.01

[a] x = carapace volume; y = brood volume

Table 5. Regression equations and correlation coefficients of combined data of Cumacea studied. All r values are significant at 0.01 level

Parameter			A*		B*	
			Equation	r	Equation	r
Carapace length	(x) versus egg No. per brood	(y)	$y = 38.7x - 17.2$	0.65	$y = 15.9\ x + 15.7$	0.74
Carapace length	(x) versus brood volume	(y)	$y = 0.84x - 0.54$	0.77	$y = 5.9\ x - 7.84$	0.96
Carapace volume	(x) versus brood volume	(y)	$y = 0.18x + 0.32$	0.79	$y = 0.14x + 0.42$	0.99

*A = all species excluding *Diastylis goodsiri*; B = all species including *D. goodsiri* (see text for explanation)

the overwintering generation (Corey, 1969, 1976b). From the distinct trimodal size-structure of the samples of *D. goodsiri* from the Arctic, it is apparent that this species lives for about 3 yr and breeds in its third year.

The timing of the breeding seasons varied interspecifically, with the littoral and shallow-water (< 20 m) species tending to breed during the spring, spring-summer, spring and fall or continuously. The continuous breeding of *Pseudocuma longicornis*, with relatively low fecundity (average 20.9 eggs) has also been noted for another shallow-water species, *Manocuma stelliferi*, which breeds more or less continuously with a fecundity ranging from 4 to 11.4 (Gnewuch and Croker, 1973).

Generally, the deeper-water species (> 20 m) bred during the winter or, if two breeding seasons occurred, one of these occured in the winter. The two exceptions noted during the present study were *Diastylis lucifera* (temperate) and *D. goodsiri* (Arctic). In both cases, breeding occurred during the summer months.

It has been shown many times that breeding is controlled by temperature and is species-specific, and usually occurs after an annual minimum or maximum in temperature. It would thus appear that the shallower-water species are triggered by a species-specific response to an increase in temperature after an annual minimum, whereas most deeper-water species respond to a decrease after an annual maximum. *Diastylis rathkei* in depths of 13 to 20 m breeds during October to February but in depths of 30 to 180 m breeds from May to April; *D. rathkei* will not breed in temperatures > 10 °C (Forsman, 1938; Krüger, 1940). A variable intraspecific breeding season related to depth and temperature was not noted for any of the species in the present study.

The number of eggs per brood tended to be greater in the littoral and shallow-water (< 20 m) species. This is probably due to the relatively unstable conditions of seasonal, daily and annual temperatures and salinities occurring in such environments. Also, predation on juvenile forms may be high, since many of the areas sampled were also known nursery grounds for fish. In deeper water areas (> 20 m), such unpredictable

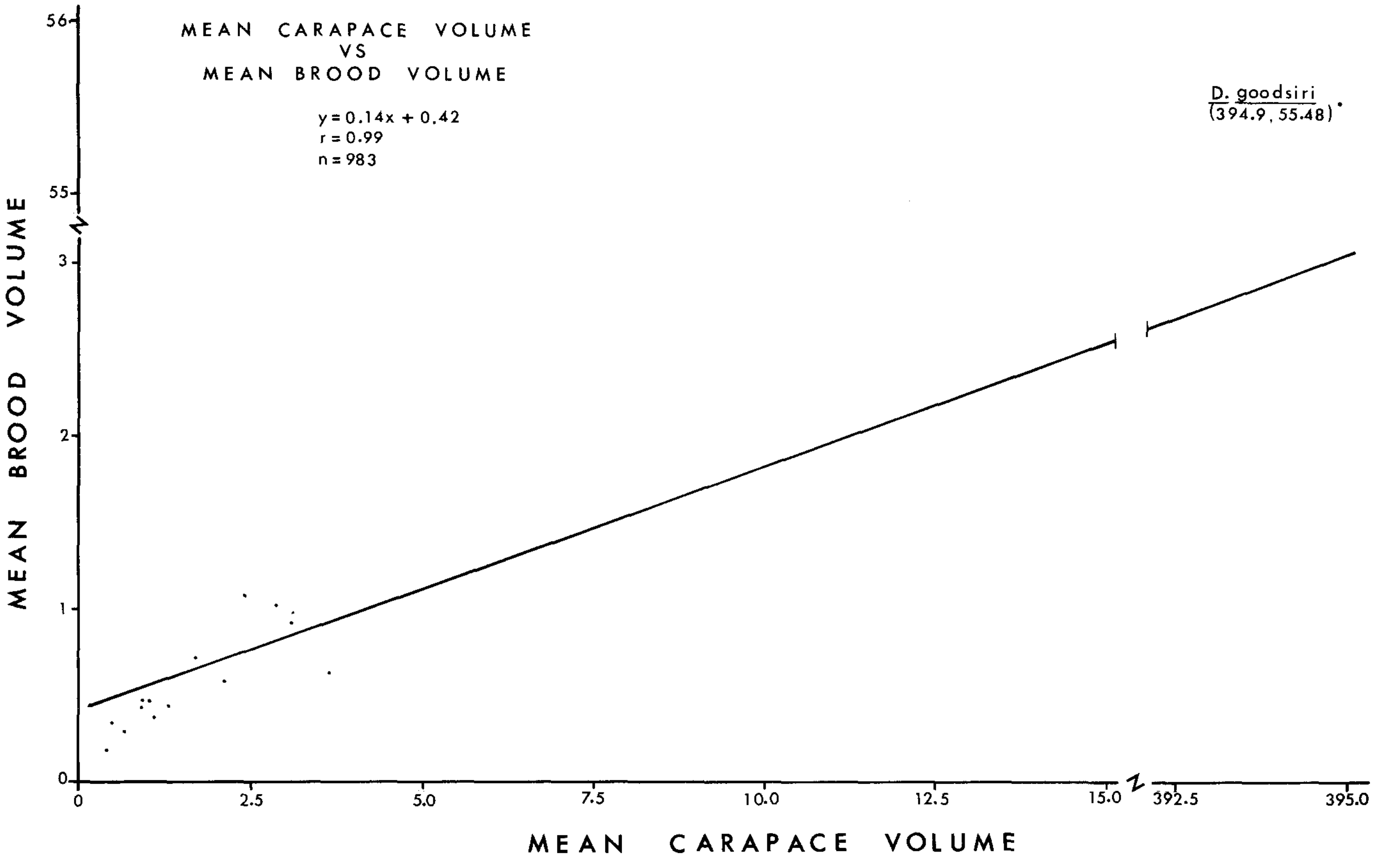

Fig. 2. Mean brood volume versus mean carapace volume for 17 species of Cumacea. Data for *Diastylis goodsiri* are given separately because of very large difference in both size of females and size of eggs from rest of the species

thermal and salinity fluctuations are less; also predation may not be as great and fecundity is generally less.

In the one Arctic species, *Diastylis goodsiri*, the volume of individual eggs was ≈6 to 38 times greater than for all other species studied. It appears that *D. goodsiri* combines increased size at maturity, increased life span, delay of sexual maturity and large eggs. A similar situation is found in deep-sea mysids where low temperatures and/or poor food supply exists (Mauchline, 1972). Mauchline suggests that an increased size of the female, combined with fewer and larger eggs and thus juveniles may allow such species to utilize a wider range of food size than smaller individuals.

In another order within the Peracarida, the Mysidacea, Mauchline (1973) showed that the volume of individual egg and volume of brood increased with an increase in size of female throughout all epipelagic and bathypelagic mysids studied. The number of eggs increased with an increase of size of female only in epipelagic species. The major differences between the Cumacea and Mysidacea is that the egg volume in the former does not increase with size of female, and also that the overall relationship in Cumacea between number per brood compared to size of species is relatively weak.

If all the above aspects of life cycles and reproduction are combined for the various Cumacea, a series of variable strategies emerges:

Arctic

Large females, long life span, delayed maturity, large eggs, e.g. *Diastylis goodsiri*.

Temperate

Strategies are variable:

Littoral to < 20 m

(1) Life span < 1 yr, 2 generations produced per year, large fecundity relative to size of female, small egg volume, e.g. *Iphinoe trispinosa, Cumopsis goodsiri, Diastylis sculpta*.

(2) Life span < 1 yr, continuous breeding, low fecundity, small eggs, e.g. *Pseudocuma longicornis*.

(3) Life span < 1 yr, 1 breeding season per year, very high fecundity, small eggs, e.g. *Lamprops quadriplicata, Diastylis polita*.

Deeper Water (> 20 m)

(1) Life span < 1 yr, 2 breeding seasons per year (same female?), relatively low fecundity, small eggs, e.g. *Hemilamprops rosea, Leptostylis longimana.*

(2) One breeding season per year: (1) Two types of winter breeders, the first type with a life span < 1 yr, low fecundity, small eggs, e.g. *Iphinoe serrata, Diastylis quadrispinosa, Diastyloides biplicata*; the second type the same except for lower fecundity and larger eggs, e.g. *Leucon nasica.* (ii) Spring-summer breeders, life span < 1 yr, relatively high fecundity, small eggs, e.g. *Diastylis lucifera.*

Although fecundity in the Cumacea is controlled chiefly by the carapace volume and the brood volume, many intricate combinations of life history and reproductive strategies are utilized interspecifically. As more data become available from the Cumacea inhabiting Arctic, tropical and deep-sea waters, a clearer picture of the reproductive aspects and hence ecology will evolve.

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