Composition and seasonality of nocturnal peracarid zooplankton from coastal New Hampshire (USA) waters, 1978–1980

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Abstract. Seasonal changes in the nocturnal peracarid zooplankton from a nearshore area of the Gulf of Maine were studied from January 1978 through December 1980 as a requirement of an ecological monitoring program for the Public Service Company of New Hampshire's Seabrook Generating Staton. Numerically dominant species included the mysids *Michteunysis mixta* and *Neomysis americana*, the amphipods *Pontogeneia inermis*. *Themisto gaudichaudi* and *Monoculodes edwardsi*, and the cumaceans *Diastylis polita* and *Lamprops quadriplicata*. A general seasonal cycle was documented with a more abundant and speciose assemblage during fall and winter than summer. Peak abundance occurred during spring months prior to emigration of juvenile *M.mixta* from the study area. Abiotic and biotic factors which may affect the structure and composition of this assemblage are discussed.

Introduction

Over the past 15–20 years, the importance of peracarid crustaceans as a component of the 'demersal zooplankton' (or 'hyper-' and 'suprabenthos') and their role in the trophodynamics of coastal, estuarine and reef systems have been recognized (Hesthagen, 1973; Brunel, 1979; Buhl-Jensen and Fossa, 1991). Their contribution to the plankton community is most apparent during night-time hours when a number of species migrate from the benthos into the water column (Brunel, 1979; Sainte-Marie and Brunel, 1985). Some peracarids, such as hyperiids and idoteid isopods, may be holoplanktonic, neustonic or associated with floating macroalgae (Grabe *et al.*, 1983; Locke and Corey, 1989), and are not necessarily demersal.

Despite the contribution of peracarids to the nocturnal zooplankton, ecological investigations have generally treated them as infauna and epifauna (Watling and Maurer, 1972; Dickinson *et al.*, 1980; Parker, 1984; Robertson *et al.*, 1989). Notable exceptions include the works of Whiteley (1948) on Georges Bank, Williams and Bynum (1972) in North Carolina, Tully and Ceidigh (1987) in Ireland, and an increasing number of investigations in Canada (Brunel, 1979; Sainte-Marie and Brunel, 1985; Locke and Corey, 1989; Corey, 1990). Within the Gulf of Maine, zooplankton have been the subject of a number of descriptive studies (Bigelow, 1926; Fish and Johnson, 1937; Jermolajev, 1958; Legare and Macclellan, 1960; Sherman, 1968), although peracarids have only been incidentally considered.

Economically, peracarids function as detritivores (Robertson and Mann, 1980; Hessler and Stromberg, 1989), microbial consumers (Bousfield, 1973), primary consumers (Hudon, 1983), predators (Sheader and Evans, 1975; DeBlois and Legett, 1991), parasites (Laval, 1980) and scavengers (Sainte-Marie, 1984). Their role as prey for fishes has long been recognized, particularly in the northwest Atlantic (Bigelow and Schroeder, 1953; Bowman, 1981; Hacunda, 1981; Langton and Bowman, 1981). The purpose of this article is to describe, from a nearshore area of the Gulf of Maine, qualitative and quantitative seasonal changes in a segment of the zooplankton frequently ignored: the Peracarida. This study was part of a more comprehensive biological monitoring program conducted by Normandeau Associates, Inc., for the Public Service Company of New Hampshire's Seabrook Generating Station.

Method

Field methods

Twice-monthly night-time plankton collections were made at three stations located offshore of Seabrook, New Hampshire (Figure 1). These stations represented the intake (Station 2) and discharge (Station 5) of the Seabrook Generating Station, and a reference station south of the generating station (Station 6). Four oblique tows were made with a 1 m diameter 0.505 mm mesh plankton net; sample volumes averaged 520 m³. The net was towed in a 'zig-zag' fashion, from surface to near-bottom and back to the surface; sample depth was determined by measuring the wire angle and length of cable deployed. Although samples were collected twice monthly, contractural requirements stipulated that only one series per month was to be analyzed at each of the three stations.

Within the study area, most of the peracarid species are concentrated below mid-depth (~ 10 m) at night (Grabe, 1980). Such a pattern has been observed by other investigators as well (Herman, 1963; Sainte-Marie and Brunel, 1985). Notable exceptions include *Calliopius laeviusculus* (Gammaridea), *Idotea balthica* (Isopoda), which are associated with floating and attached macroalgae, and *Themisto gaudichaudi* (Hyperiidea), which is common in the neuston (Grabe *et al.*, 1983; Locke and Corey, 1989; Corey, 1990).

Water column densities of vertically stratified zooplankton are underestimated by oblique tow paths (Peterson and Miller, 1977; Judkins *et al.*, 1980). Several studies (Kaartvedt, 1985; Sainte-Marie and Brunel, 1985; Rudstam *et al.*, 1989) have shown that the extent of the vertical migrations of peracarids can vary considerably between species. Therefore, as in other zooplankton studies using an oblique tow path, some interspecific relationships are likely to be misrepresented.

Laboratory analyses

Three of the four replicates per station were randomly selected for processing. Each sample was serially subsampled $(1/2, 1/4, 1/8 \dots 1/512 + 1/512)$ with a Folsom Plankton Splitter (McEwen *et al.*, 1954). Successive aliquots were analyzed until at least 30 individuals of a species were counted; once at least 30 individuals were counted, that species could be ignored in subsequent aliquots. Larger numbers of mysids were counted because they were the object of additional studies (e.g. Grabe and Hatch, 1982). Counting and identifications continued until at least 25% of each sample was analyzed.

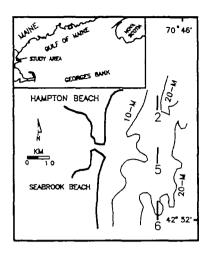


Fig. 1. Location of zooplankton sampling transects (2, 5 and 6) offshore of Seabrook, New Hampshire: 10 and 20 m depth contours are indicated. The inset shows the general location of the study area.

Data analyses

Seasonal changes in composition and abundance were evaluated via numerical classification. Bray–Curtis similarity was calculated for the seasonal analysis and percent similarity for the species analysis (Boesch, 1977); group average clustering was used in both analyses. The data base for these analyses were the $\log_{10} n + 1$ transformed monthly mean concentrations (3 replicates × 3 stations = 9 samples) of the 25 most abundant species. For this report, differences between stations were not of interest.

Month-year and species 'groups' were subjectively identified from the cluster analyses. To clarify these relationships, a nodal analysis (Boesch, 1977) was constructed, with an 'Importance Index' (Windell, 1971) calculated for each speciesseason 'group' identified (loss of the original data precludes any additional analyses, including presentation of the dendrograms). This Importance Index is calculated as:

[(% composition)(% occurrence)]^{0.5}

Polynomial regression (Neter *et al.*, 1985) was used to model monthly changes in species richness (i.e. numbers of species; Pielou, 1975). A fourth-degree polynomial provided the best fit.

Study area

Stations 2 (depth 18–21 m) and 6 (21–24 m) were located over areas of coarse sand. Station 5 (12–20 m) was located over an area of ledges and boulders; several species of macroalgae were present at around 12 m.

Bottom water temperatures (Figure 2) ranged from 0.7 to 14.8°C over the 3 year period. The annual averages were 6.6 (1978), 7.2 (1979) and 7.7°C (1980). Bottom salinities ranged from 30.5 to 33.8 p.p.t. (mean = 32.3). Salinities tended to be higher during late fall and winter than during spring and summer. Relatively low salinities (31.0–32.6 p.p.t.) were recorded from January through March 1978.

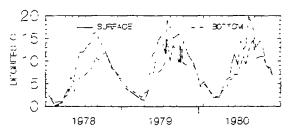


Fig. 2. Average monthly water temperatures in the vicinity of Seabrook, New Hampshire, 1978-1980.

Results

Species composition

At least 90 species of peracarids were identified (Table I) and gammarid amphipods (59 species) were the most speciose taxocene. Within each of the 3 years studied, five species constituted at least 90% of the total abundance (Table II), and the mysids *Michteimysis mixta* and *Neomysis americana* together composed almost 80% of the assemblage.

Seasonality

Species richness was cyclical, with a summer minimum and a fall/winter maximum (Figure 3). The generally greater numbers of species during winter 1980 versus winter 1978 possibly reflects more thorough analyses during 1980.

Reproductive activity, based on the numbers of taxa brooding, peaked during spring months and displayed a summer minimum (Figure 4). This cycle was primarily influenced by the numbers of gammarid amphipod species brooding; cumaceans appeared to brood during both late fall and late winter through spring. Species which had the most protracted brooding periods included *C.laeviusculus* (10 months), *Pseudoleptocuma minor* (9), *N.americana* (8) and *Pontogeneia inermis* (8).

Four primary seasonal groups (A-D) and 10 species groups (1-10) (Figure 5) were identified in the dendrograms (not shown). The seasons generally corresponded to fall-winter (A), spring (B and D) and summer (C). Species groups included an association which was numerically dominant and present throughout the year (1), two groups (3 and 4) which included common inshore species, which are either tubiculous or associated with macroalgae, and two groups of essentially boreal species (5 and 7).

The nocturnal plankton assemblage during the fall and winter months (Group A) was numerically dominated by *N.americana*, *P.inermis* and *T.gaudichaudi* (Figure 4)—species which were common throughout the year and among the overall numerical dominants (Table I). Subdominants, which had relatively high Importance values during this season, included *Erythrops erythropthalma*, *Syrrhoe crenulata* and *Eudorella pusilla*.

Among the rarer taxa, Eudorellopsis deformis, Lembos websteri, Diastylis quadrispinosa and Photis macrocoxa occurred in at least 40% of the fall/winter samples, but in none of the summer samples. These four species occur over a wide
 Table I. Inventory of peracarid crustaceans identified in night-time zooplankton collections from New Hampshire coastal waters, 1978–1980

MYSIDACEA				
Mysidae	Erythrops erythropthalma (Goes)			
	Heteromysis formosa Smith			
	Michtemysis mixta Lilljeborg			
	Neomysis americana (Smith)			
CUMACEA				
Bodotriidae	Mancocuma stellifera Zimmer			
	Pseudoleptocuma minor Calman			
Leuconidae	Eudorella pusilla Sars			
	Eudorellopsis deformis (Kroyer)			
	Leucon americanus Zimmer			
Nannastacidae	Campylampsis rubicunda (Lilljeborg)			
Lampropidae	Lamprops quadriplicata Smith			
Pseudocumatidae	Petalosarsia declivis (Sars)			
Diastylidae	Diastylis polita Smith			
	D.quadrispinosa Sars D.sculpta Sars			
TANAIDACEA				
Paratanaidae	Leptochelia sp.			
ISOPODA Cirolanidae	Circlana sp			
Epicarida—undet. gen.	Cirolana sp.			
Gnathiidae	Gnathia cerina (Harger)			
Idoteidae	Chiridotea arenicola (Wigley)			
	C.coeca (Say)			
	C.tuftsi (Stimpson)			
	Edotea triloba (Say)			
	Idotea balthica (Pallas)			
	I.metallica Bosc			
	I.phosphorea Harger			
Janiridae	Jaera marina (Fabricius)			
Munnidae	Munna (Neomunna) fabricii (Kroyer)			
AMPHIPODA				
CAPRELLIDEA				
Caprellidae	Aeginina longicornis Kroyer			
	Caprella septentrionalis Kroyer			
CANO A DIRE :				
GAMMARIDEA				
Acanthonotozomatidae	Acanthonotozoma serratum (Fabricius)			
Ampeliscidae	Ampelisca agassizi (Judd) A.macrocephala Lilljeborg			
Amphilocidae	Gitanopsis arctica Sars ^a			
Ampithoidae	Ampithoe longimana Smith			
Amphinoidae	Cymadusa compta (Smith) ^b			
Argissidae	Argissa hamatipes (Norman)			
Corophiidae	Corophium acherusicum Costa			
	C.bonelli (Milne Edwards)			
	C.crassicorne Bruzelius			
	C.insidiosum Crawford			
	Lembos websteri Bate			
	Leptocheirus pinguis (Stimpson)			

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	Phous macrocoxa Shoemaker			
	Unciola irrorata Say			
Dexaminidae	Dexamine thea Boeck			
Eusiridae	Calliopius laeviusculus (Kroyer)			
	Pontogeneia inermis (Kroyer)			
	Rhachotropis oculata (Hansen)			
Gammarıdae	Gammarellus angulosus (Rathke)			
	Gammarus duebeni Lilljeborg			
	G.lawrencianus Bousfield			
	G.oceanicus Segerstrale			
	Mucrogammarus mucronatus Say			
	Maera danae Stimpson			
	Maeta danae Stimpson Melita dentata (Kroyer)			
Haustoriidae	Acanthohaustorius millsi Bousfield			
Trausionnuae	Amphiporeia virginia Shoemaker			
I Issalida a	Bathyporeta quoddyensis Shoemaker			
Hyalidae	Hyale nilssoni (Rathke)			
Ischyroceridae	Erichthonius fasciatus Smith			
	Ischyrocerus anguipes Kroyer			
	Jassa marmorata Holmes			
Lafystiidae	Lafystius sturionis Kroyer			
Lysianassidae	Anonyx sarsi Steele & Brunel			
	Hippomedon serratus Holmes			
	Orchomenella pinguis (Boeck)			
	Psammonyx nobilis (Stimpson)			
	P terranovae Steele			
Melphidippidae	Melphidippa goesi Stebbing			
Oedicerotidae	Monoculodes edwardsi Holmes			
	M.longirostris (Goes) ^a			
	M.tuberculatus Boeck*			
	Paraoediceros lynceus Sars			
	Synchelidium americanum Bousfield			
	Westwoodilla brevicalcar Bate			
Phoxocephalidae	Phoxocephalus holbolli (Kroyer)			
Pleustidae	Pleustes panoplus Kroyer			
	Pleusymtes glaber (Boeck)			
	Stenopleustes gracilis (Holmes)"			
Podoceridae	Dulichia falcata Bate			
Stenothoidae	Metopa borealis Sars			
	M.propingua Sars			
	M.solsbergi Schneider			
	Metopella carinata (Hansen) ^a			
	Proboloides holmesi Bousfield			
	Stenula nordmanni (Stephensen) ^a			
Synopiidae	Syrrhoe crenulata (Goes)			
eynophule	Tiron spiniferum (Stimpson)			
HYPERIIDEA				
Hyperiidae	Hyperia galba (Montagu)			
, spendee	H.medusarum (Muller)			
	Hyperoche medusarum Kroyer			
	Themisto gaudichaudi (Guerin-Meneville)			

[•]Extends range south from Gulf of St Lawrence (Bousfield, 1973). •Extends range north from Cape Cod, Massachusetts (Bousfield, 1973).

Rank	Species	Annual mean density (% composition)			
		1978	1979	1980	
1.	Michteimysis mixta	536 (34.6)	1075 (56.0)	2890 (61.8)	
2.	Neomysis americana	365 (23.5)	531 (27.6)	1037 (22.2)	
3.	Pontogeneia inermis	104 (6.7)	51 (2.6)	374 (8.0)	
4.	Themisto gaudichaudi	173 (11.2)	63 (3.3)	37 (0.8)	
5.	Monoculodes edwardsi	140 (9.0)	88 (4.6)	30 (0.6)	
6.	Diastylis polita	29 (1.9)	16 (0.8)	92 (2.0)	
7.	Lamprops quadriplicata	47 (3.0)	31 (1.6)	33 (0.7)	
8.	D.sculpta	18 (1.1)	7 (0.4)	39 (0.8)	
9.	Monoculodes tuberculatus	39 (2.5)	8 (0.4)	15 (0.3)	
0.	Psudoleptocuma minor	32 (2.1)	8 (0.4)	18 (0.4)	
1.	Erythrops erythropthalma	12 (0.8)	2 (0.1)	10 (0.2)	
12.	Unciola irrorata	3 (0.2)	4 (0.2)	11 (0.2)	
13.	Hyperoche medusarum	3 (0.2)	12 (0.6)	2 (<0.1)	
4.	Ischyrocerus anguipes	1 (<0.1)	5 (0.3)	11 (0.2)	
15.	Gammarus lawrencianus	11 (0.7)	1 (<0.1)	2 (<0.1)	
l 6 .	Calliopius laeviusculus	5 (0.3)	2 (<0.1)	6 (0.1)	
17.	Anonyx sarsı	2 (0.1)	3 (0.2)	7 (0.2)	
8.	Syrrhoe crenulata	6 (0.4)	<1 (<0.1)	4 (<0.1)	
19.	Idotea balthica	6 (0.4)	1 (<0.1)	3 (<0.1)	
20.	Dulichia falcata	1 (<0.1)	2 (0.1)	6 (0.1)	
21	Jassa marmorata	2 (0.1)	1 (<0.1)	5 (0.1)	
22.	Corophium crassicorne	0 (0)	0 (0)	4 (<0.1)	
23a.	Mancocuma stellifera	<1 (<0.1)	1 (<0.1)	3 (<0.1)	
23b.	Stenula nordmannı	2 (0.1)	1 (<0.1)	1 (<0.1)	
24.	Eudorella pusilla	1 (<0.1)	<1 (<0.1)	2 (<0.1)	
	Others	11 (0.7)	9 (0.5)	21 (0.4)	
fotal (i	number per 1000 m ³)	1550	1922	4663	

 Table II. Annual mean density (number per 1000 m') and percent composition of the 25 most abundant peracarids in night-time zooplankton collections from New Hampshire coastal waters, 1978–1980

geographic range and the latter two are common on sandy bottoms (Bousfield, 1973; Watling, 1979a), such as occur in the study area. A plot of temperaturesalinity combinations (by station and month) indicated that this fall-winter 'season' was characterized by a wide range of temperatures and high salinities (Figure 5).

The two spring groups (B and D) were primarily differentiated by the presence (B) or absence (D) of *M.mixta* (Figure 4). *Ischyrocerus anguipes*, *Dulichia falcata* (Group 3 species) and, to a lesser extent, Group 1 species were also abundant during spring. Overall mean plankton densities were highest in spring 'B' (8400 per 100 m³), when *M.mixta* was numerically dominant, and lowest (180 per 100 m³) in spring 'D', where *M.mixta* were virtually absent (cf. Grabe and Hatch, 1982). Water temperatures were somewhat higher during spring 'B' (range 7.1–14.8; mean 10.3) than during spring 'D' (range 6.0–8.1; mean 7.1) and salinities were generally similar (31.3–33.7 versus 31.0–32.1 p.p.t.) (Figure 5). *Neomysis americana*, *P.inermis*, *T.gaudichaudi* and their associated species (Figure 4) also had somewhat higher Importance values in spring 'B' than 'D'.

The summer assemblage (Group C) was also dominated by Group 1 species (Figure 4), with *I.anguipes* and *D.falcata* relatively important. Both overall mean density (400 per 100 m³) and species richness (Figure 2) were low. Among the rarer

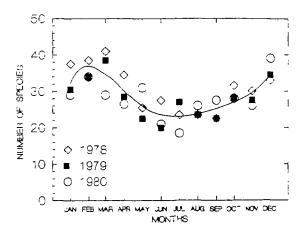


Fig. 3. Monthly changes in the species richness of peracarid zooplankton in night-time collections in New Hampshire coastal waters, 1978–1980. Seasonal cycle fitted by polynomial regression.

species, only *Dexamine thea* and *Corophium bonelli* were collected more frequently during the summer season than during any other. Water temperatures were at their highest during summer and salinities were below average (Figure 5).

Discussion

With the exception of *M.mixta*, the most abundant nocturnally planktonic peracarids in this area were also the dominants on Georges Bank (Whiteley, 1948): *Monoculodes edwardsi*, *N.americana*, *T.gaudichaudi* (= *Themisto compressa*) and *P.inermis. Michteimysis mixta* has not been reported from Georges Bank (Whiteley, 1948; Wigley and Burns, 1971). *Themisto gaudichaudi* and *M.edwardsi*, predominant in Corey's (1990) neuston collections, were also among the most abundant species in this study.

The majority of the peracarids in the study area are boreal species, although some range as far south as Chesapeake Bay (Gosner, 1971; Bousfield, 1973; Watling, 1979a,b). Few were found throughout the year in these waters, suggesting that they are either absolutely rare, not resident in nearshore waters or, that whether by habitat (e.g. intertidal) or activity, they are less susceptible to capture by plankton nets.

If these are transient species, they must originate either outside of the Gulf of Maine proper or in deeper, generally colder waters. For example, the cumaceans *Lamprops quadriplicata*, *D.quadrispinosa*, *E.deformis* and *Petalosarsia declivis*, the mysid *E.erythropthalma* and the gammarid *S.crenulata* are considered to be mid to outer continental shelf species, not nearshore species (Wigley and Burns, 1971; Barnard, 1972; Watling, 1979a). Each of these species was most abundant during winter and spring months.

Vertical mixing events in the area may be an important mechanism for transporting these organisms inshore. Three types of mixing events can be identified: the winter formation of Gulf of Maine Intermediate Water (MIW) (Hopkins and

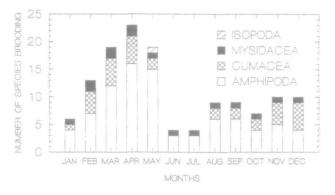


Fig. 4. Numbers of peracarid species brooding in New Hampshire coastal waters, 1979-1980.

Garfield, 1977; Brown and Beardsley, 1978), storms and tidal mixing (Hartwell, 1977).

Although the formation of MIW may not penetrate any further inshore than the 50 m isobath (Brown and Beardsley, 1978), this is a regular occurrence and involves the mixing of colder, less saline inshore surface waters with warmer, more saline offshore bottom waters. The result is a water mass more saline (\sim 32.8 p.p.t.) and slightly warmer (\sim 4.5°C) (Hopkins and Garfield, 1977) than that normally characteristic of inshore surface waters at this time of year. These characteristics approximate the salinity regime of the fall-winter species assemblage, although water temperatures are often lower than those of MIW. The timing of the formation of this water mass is in concurrence with the presence of the fall-winter assemblage.

Butman (1987) has observed that major storms in the area of Georges Bank and the Gulf of Maine may affect the biological communities associated with sediments. During severe storms, sediments may be reworked and resuspended up to 10 m from the bottom and may disturb the infauna. Such a mechanism may contribute to the dispersal of infaunal and epifaunal peracarids.

Other species may originate from inshore and estuarine environs. Examples include Gammarellus angulosus, Gammarus lawrencianus, Corophium acherusicum and Heteromysis formosa (Wigley and Burns, 1971; Bousfield, 1973). Their appearance in coastal waters may be due to storm events and the spring thaw flushing them from local estuaries (e.g. the Hampton River). Other species, such as N.americana (Hulburt, 1957) and M.mixta (Grabe and Hatch, 1982) may undergo seasonal migrations from the study area.

Locke and Corey (1989) discuss the putative role of surface currents in the distribution of some peracarids, particularly those associated with floating macroalgae (e.g. *I.balthica* and *C.laeviusculus*). These otherwise littoral species may become associated with offshore rafts of macroalgae either by active swimming (Highsmith, 1985) or as a consequence of storm events sweeping them offshore.

In addition to the abiotic factors discussed above, biotic factors will also influence when a species, and which individuals of a species, will be pelagic. These include age (Herman, 1963), reproductive status (Fincham, 1970), sex (Tully and

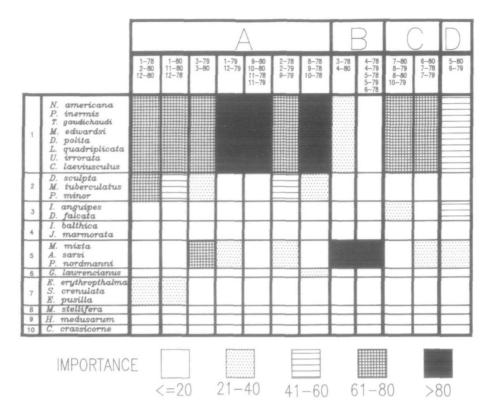


Fig. 5. Nodal diagram showing the Importance of peracarid species groups within seasonal groups from New Hampshire coastal waters, 1978–1980.

Ceidigh, 1987) and ecdysis (Valentin and Anger, 1977). A more thorough review of vertical migrations in peracarids can be found in Tully and Ceidigh (1987).

'Regular' seasonal cycles of abundance were observed for only three of the more abundant species: *M.mixta*, *N.americana* and *P.inermis*. All are free-living species which spend more time in the plankton then do infaunal species. This is consistent with Williams and Bynum's (1972) observations of planktonic amphipods in North Carolina estuaries. The presence of hyperiids which are commensal or parasitic on hydrozoan medusae (Evans and Sheader, 1972; Williams and Robins, 1981) can be influenced by those factors which affect the distribution of the host species. The number of individuals of a species present in any locale is also affected by reproductive cycles. In this assemblage, reproductive activity, based on numbers of species brooding, was greatest during the spring, generally corresponding with the occurrence of the spring diatom bloom in the Gulf of Maine (Sherman *et al.*, 1988) and least during the summer. The presence of a more speciose and reproductively active assemblage in the plankton, at the same general time of the year as a suitable source of nutrition is most available, may be significant in enhancing dispersal of juvenile peracarids (cf. Tully and Ceidigh, 1987).

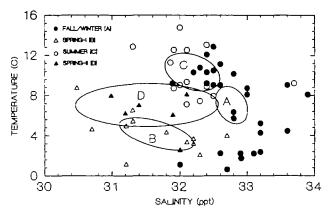


Fig. 6. Relationship between seasonal peracarid assemblages (identified by cluster analysis; cf. Figure 4) and bottom water temperature and salinity in New Hampshire coastal waters, 1978–1980. Ellipses are 95% confidence intervals of the mean temperature and salinity within each seasonal group.

Conclusions

The nocturnal peracarid plankton assemblage in New Hampshire coastal waters is subject to marked seasonal fluctuations in abundance and species richness. Numerically dominant species included two mysids (*M.mixta*, *N.americana*), three amphipods (*P.inermis*, *T.gaudichaudi* and *M.edwardsi*) and two cumaceans (*D.polita* and *L.quadriplicata*).

Both abiotic and biotic factors may interact to affect the structure of this assemblage. Abiotic factors include large-scale cyclic phenomena (e.g. circulation patterns and thermal cycles) and vertical and horizontal water column-mixing events (e.g. storms). Biotic factors include natality and both species-specific and age-specific (vertical and inshore–offshore) migrations.

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