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

Stephen A. Grabe

Environmental Protection Commission of Hillsborough County, 1410 N. 21st Street, Tampa, FL 33605, USA

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 Station. Numerically dominant species included the mysids *Michtemysis 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, contractual 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* (Hyperiidia), 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 (Kaarvedt, 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 ... 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.

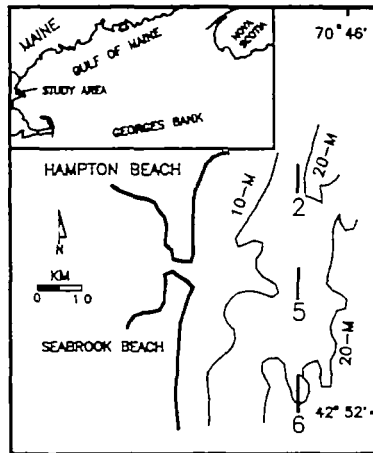


Fig. 1. Location of zooplankton sampling transects (2, 5 and 6) offshore of Seabrook, New Hampshire: 10 and 20 m depth contours are indicated. The inset shows the general location of the study area.

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 \times 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 species–season ‘group’ identified (loss of the original data precludes any additional analyses, including presentation of the dendrograms). This Importance Index is calculated as:

$$[(\% \text{ composition})(\% \text{ occurrence})]^{0.5}$$

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.

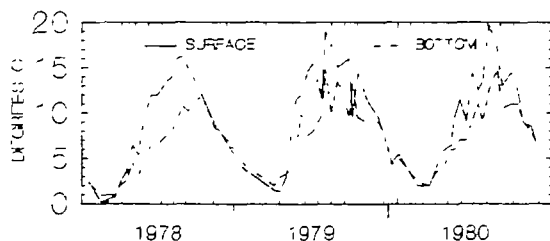


Fig. 2. Average monthly water temperatures in the vicinity of Seabrook, New Hampshire, 1978–1980.

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

Table I. Inventory of peracarid crustaceans identified in night-time zooplankton collections from New Hampshire coastal waters, 1978–1980

	<i>Phots macrocoxa</i> Shoemaker
	<i>Unciola irrorata</i> Say
Dexaminidae	<i>Dexamine thea</i> Boeck
Eusiridae	<i>Calliopius laeviusculus</i> (Kroyer)
	<i>Pontogeneia inermis</i> (Kroyer)
	<i>Rhachotropis oculata</i> (Hansen)
Gammaridae	<i>Gammarellus angulosus</i> (Rathke)
	<i>Gammarus duebeni</i> Lilljeborg
	<i>G.lawrencianus</i> Bousfield
	<i>G.oceanicus</i> Segerstrale
	<i>Mucrogammarus mucronatus</i> Say
	<i>Maera danae</i> Stimpson
	<i>Melita dentata</i> (Kroyer)
Haustoriidae	<i>Acanthohaustorius millsii</i> Bousfield
	<i>Amphiporeia virginia</i> Shoemaker
	<i>Bathyporeia quoddyensis</i> Shoemaker
Hyalidae	<i>Hyale nilssoni</i> (Rathke)
Ischyroceridae	<i>Erichthonius fasciatus</i> Smith
	<i>Ischyrocerus anguipes</i> Kroyer
	<i>Jassa marmorata</i> Holmes
Lafystiidae	<i>Lafystius sturionis</i> Kroyer
Lysianassidae	<i>Anonyx sarsi</i> Steele & Brunel
	<i>Hippomedon serratus</i> Holmes
	<i>Orchomenella pinguis</i> (Boeck)
	<i>Psammonyx nobilis</i> (Stimpson)
	<i>P.terranova</i> Steele
Melphidippidae	<i>Melphidippa goesi</i> Stebbing
Oedicerotidae	<i>Monoculodes edwardsi</i> Holmes
	<i>M.longirostris</i> (Goes)*
	<i>M.tuberculatus</i> Boeck*
	<i>Paraoedicerus lynceus</i> Sars
	<i>Synchelidium americanum</i> Bousfield
	<i>Westwoodilla brevicealcar</i> Bate
Phoxocephalidae	<i>Phoxocephalus holbolli</i> (Kroyer)
Pleustidae	<i>Pleustes panoplus</i> Kroyer
	<i>Pleusymtes glaber</i> (Boeck)
	<i>Stenopleustes gracilis</i> (Holmes) ^b
Podoceridae	<i>Dulichia falcata</i> Bate
Stenothoidae	<i>Metopa borealis</i> Sars*
	<i>M.propinqua</i> Sars*
	<i>M.solsbergi</i> Schneider
	<i>Metopella carinata</i> (Hansen)*
	<i>Proboloides holmesi</i> Bousfield
	<i>Stenula nordmanni</i> (Stephensen)*
Synopiidae	<i>Syrrhoë crenulata</i> (Goes)
	<i>Tiron spiniferum</i> (Stimpson)
HYPERIIDEA	
Hyperiidæ	<i>Hyperia galba</i> (Montagu)
	<i>H.medusarum</i> (Muller)
	<i>Hyperoche medusarum</i> Kroyer
	<i>Themisto gaudichaudi</i> (Guerin-Meneville)

*Extends range south from Gulf of St Lawrence (Bousfield, 1973).

^bExtends range north from Cape Cod, Massachusetts (Bousfield, 1973).

Table II. Annual mean density (number per 1000 m³) and percent composition of the 25 most abundant peracarids in night-time zooplankton collections from New Hampshire coastal waters, 1978–1980

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

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 temperature–salinity 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

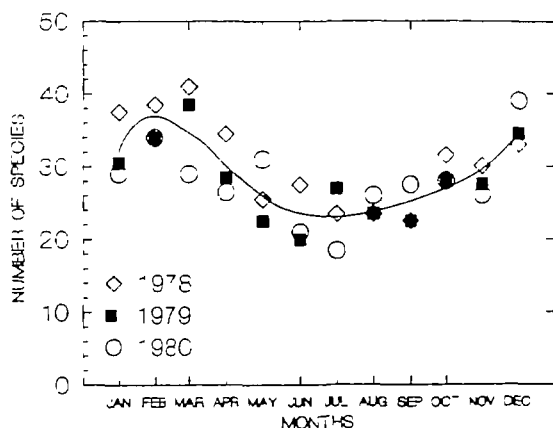


Fig. 3. Monthly changes in the species richness of peracarid zooplankton in night-time collections in New Hampshire coastal waters, 1978–1980. Seasonal cycle fitted by polynomial regression.

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. erythroptalma* 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

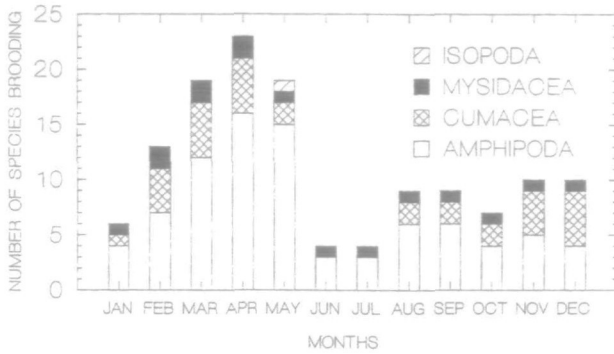


Fig. 4. Numbers of peracarid species brooding in New Hampshire coastal waters, 1979–1980.

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 (~ 32.8 p.p.t.) and slightly warmer ($\sim 4.5^\circ\text{C}$) (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.laevisculus*). 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

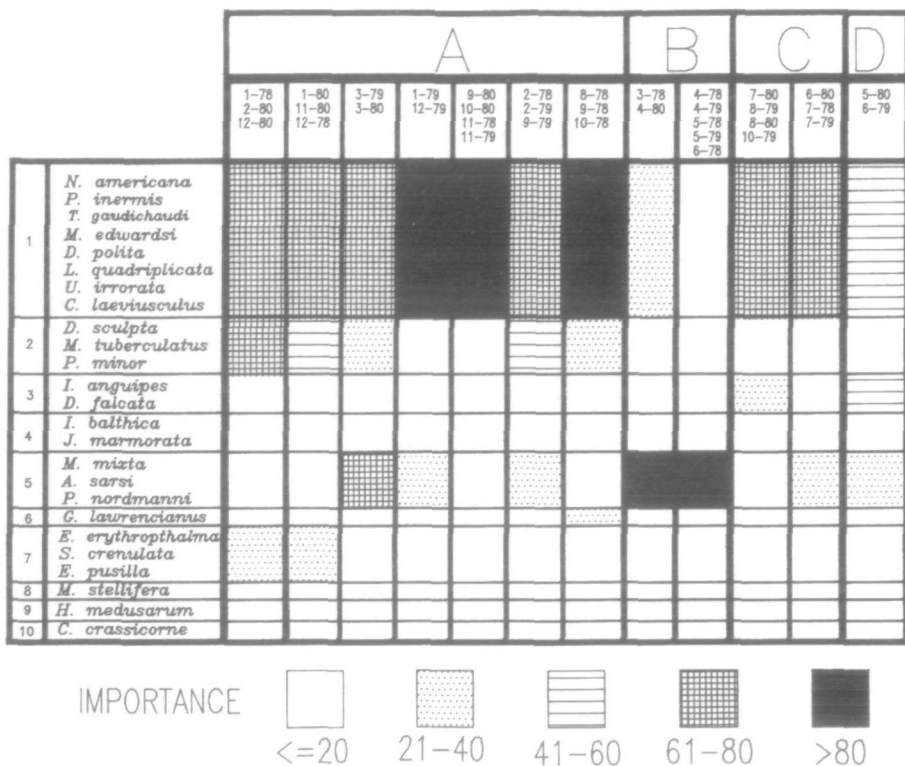


Fig. 5. Nodal diagram showing the Importance of peracarid species groups within seasonal groups from New Hampshire coastal waters, 1978-1980.

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 than 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 Shearer, 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).

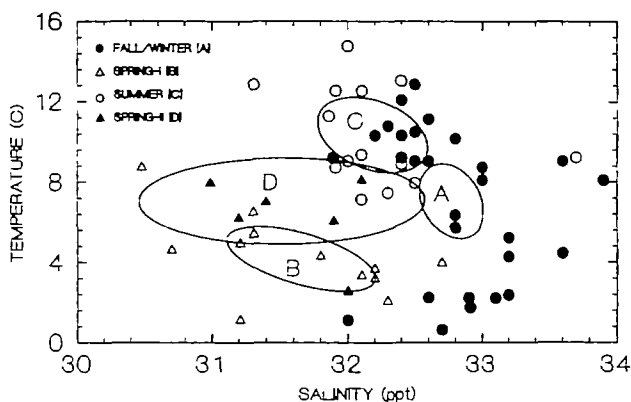


Fig. 6. Relationship between seasonal peracarid assemblages (identified by cluster analysis; cf. Figure 4) and bottom water temperature and salinity in New Hampshire coastal waters, 1978–1980. Ellipses are 95% confidence intervals of the mean temperature and salinity within each seasonal group.

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.

Acknowledgements

Appreciation is extended to the Public Service Company of New Hampshire and Normandeau Associates, Inc. (NAI) for permission to publish this material. M. Dadswell, B. Kensley, D. H. Steele, L. Watling and, most importantly, T. E. Bowman verified/corrected many of the species identifications. B. Smith, S. Santos and C. Owen reviewed earlier drafts. The efforts of the staff of NAI's Seabrook Field Station and the invaluable assistance of E. Hatch with the laboratory analyses are gratefully acknowledged. Finally, special appreciation is extended to E. L. Bousfield, not only for his guidebook, without which this work would have been considerably more difficult, but also his encouragement of my interest in peracarid ecology.

References

- Barnard, J. L. (1972) A review of the family Synopiidae (=Tironidae), mainly distributed in the deep sea (Crustacea: Amphipoda). *Smithson. Contrib. Zool.*, **124**, 94 pp.

- Bigelow, H.B. (1926) Plankton of the offshore waters of the Gulf of Maine. *Bull. US Bur. Fish.* **40**(Part 2), 1–509.
- Bigelow, H.B. and Schroeder, W.C. (1953) Fishes of the Gulf of Maine. *US Fish Wildl. Serv. Fish. Bull.*, **53**, 577 pp.
- Boesch, D.F. (1977) *Application of Numerical Classification in Ecological Investigations of Water Pollution*. EPA-600/3-77-033. United States Environmental Protection Agency, Corvallis, OR, 115 pp.
- Bousfield, E.L. (1973) *Shallow-Water Gammaridean Amphipoda of New England*. Cornell University Press, Ithaca, 312 pp.
- Bowman, R.E. (1981) Food of ten species of northwest Atlantic juvenile groundfish. *US Fish Wildl. Serv. Fish. Bull.*, **79**, 200–206.
- Brown, W.S. and Beardsley, R.C. (1978) Winter circulation in the western Gulf of Maine. Part 1: Cooling and water mass formation. *J. Phys. Oceanogr.*, **8**, 265–277.
- Brunel, P. (1979) Seasonal changes of daily vertical migrations in a suprabenthic cold-layer shelf community over mud in the Gulf of St. Lawrence. In Naylor, E. and Hartnoll, R.G. (eds), *Cyclic Phenomena in Marine Plants and Animals. Proceedings of the 13th European Marine Biology Symposium*, Isle of Man. Pergamon Press, Oxford, pp. 383–390.
- Buhl-Jensen, L. and Fossa, J.H. (1991) Hyperbenthic crustacean fauna of the Gullmarfjord area (western Sweden): species richness, seasonal variation and long-term changes. *Mar. Biol. (Berlin)*, **109**, 245–258.
- Butman, B. (1987) The effects of winter storms on the bottom. In Backus, R.H. and Bourne, D.W. (eds), *Georges Bank*. MIT Press, Cambridge, pp. 74–77.
- Corey, S. (1990) Distributional patterns of Amphipoda in the Bay of Fundy region, Canada. *Crustaceana*, **58**, 292–308.
- Deblois, E.M. and Leggett, W.C. (1991) Functional response and potential impact of invertebrate predators on benthic fish eggs: analysis of the *Callinectes laeviusculus*-capelin (*Mallotus villosus*) predator-prey system. *Mar. Ecol. Prog. Ser.*, **69**, 205–216.
- Dickinson, J.J., Wigley, R.L., Brodeur, L.D. and Brown-Leger, S. (1980) *Distribution of Gammaridean Amphipoda (Crustacea) in the Middle Atlantic Bight Region*. NOAA Tech. Rep. NMFS SSRF-741, 46 pp.
- Evans, F. and Shearer, M. (1972) Host species of the hyperiid amphipod *Hyperoche medusarum* (Kroyer) in the North Sea. *Crustaceana*, **Suppl. 3**, 275–276.
- Fincham, A.A. (1970) Amphipods in the surf plankton. *J. Mar. Biol. Assoc. UK*, **50**, 177–198.
- Fish, C.J. and Johnson, M.W. (1937) The biology of the zooplankton population in the Bay of Fundy and Gulf of Maine with special reference to production and distribution. *J. Biol. Board Can.*, **3**, 189–322.
- Gosner, K.L. (1971) *Guide to Identification of Marine and Estuarine Invertebrates*. Wiley-Interscience, New York, 693 pp.
- Grahe, S.A. (1980) Diel changes in the peracarid hyperbenthos from the nearshore Gulf of Maine. Paper presented at the Spring, 1980 New England Estuarine Research Society Meeting, Mystic, CT.
- Grahe, S.A. and Hatch, E.R. (1982) Aspects of the biology of *Mysis mixta* (Lilljeborg 1852) (Crustacea, Mysidacea) in New Hampshire coastal waters. *Can. J. Zool.*, **60**, 1275–1281.
- Grahe, S.A., Shipman, J.W. and Bosworth, W.S. (1983) New Hampshire lobster larvae studies. In Fogarty, M.J. (ed.), *Distribution and Relative Abundance of American Lobster, Homarus americanus Larvae: New England Investigations, 1974–1979*. NOAA Tech. Rep. NMFS SSRF-775, pp. 53–57.
- Hacunda, J.S. (1981) Trophic relationships among demersal fishes in a coastal area of the Gulf of Maine. *US Fish Wildl. Serv. Fish. Bull.*, **79**, 775–788.
- Hartwell, A.D. (1977) Nearshore circulation in the western Gulf of Maine. In *A Summary of an Informal Workshop of the Physical Oceanography of the Gulf of Maine and Adjacent Seas*. Woods Hole Oceanogr. Inst. Spec. Rep., 52 pp. (Abstract).
- Herman, S.S. (1963) Vertical migration of the opposum shrimp, *Neomysis americana* Smith. *Limnol. Oceanogr.*, **8**, 228–238.
- Hessler, R.R. and Stromberg, J.O. (1989) Behavior of janiroidean isopods (Asellota), with special reference to deep-sea genera. *Sarsia*, **74**, 145–160.
- Hesthagen, I.H. (1973) Diurnal and seasonal variations in the near-bottom fauna—the hyperbenthos—in one of the deeper channels of the Kieler Bucht (Western Baltic). *Kiel. Meeresforsch.*, **29**, 116–140.
- Highsmith, R.C. (1985) Floating and algal rafting as potential dispersal mechanisms in brooding invertebrates. *Mar. Ecol. Prog. Ser.*, **25**, 169–179.
- Hopkins, T.S. and Garfield, N. (1977) The existence of the Maine Intermediate Water. In *A Summary of an Informal Workshop of the Physical Oceanography of the Gulf of Maine and Adjacent Seas*. Woods Hole Oceanogr. Inst. Spec. Rep., 52 pp. (Abstract).
- Hudon, C. (1983) Selection of unicellular algae by the littoral amphipods *Gammarus oceanicus* and *Callinectes laeviusculus* (Crustacea). *Mar. Biol. (Berlin)*, **78**, 59–67.

- Hulburt, E.M. (1957) The distribution of *Neomysis americana* in the estuary of the Delaware River. *Limnol. Oceanogr.*, **2**, 1–11.
- Jermolajev, E.G. (1958) Zooplankton of the inner Bay of Fundy. *J. Fish. Res. Board Can.*, **15**, 1219–1228.
- Judkins, D.C., Wirick, C.D. and Esaias, W.E. (1980) Composition, abundance and distribution of zooplankton in the New York Bight, September 1974–September, 1975. *US Fish Wildl. Serv. Fish. Bull.*, **75**, 717–724.
- Kaartvedt, S. (1985) Diel changes in small-scale vertical distribution of hyperbenthic mysids. *Sarsia*, **70**, 287–295.
- Langton, R.W. and Bowman, R.E. (1981) Food of eight northwest Atlantic pleuronectiform fishes. *US Dep. Comm. NOAA Tech. Rep. NMFS SSRF-749*, 16 pp.
- Laval, P. (1980) Hyperiid amphipods as crustacean parasitoids associated with gelatinous zooplankton. *Oceanogr. Mar. Biol. Annu. Rev.*, **18**, 11–56.
- Legare, J.E.H. and Maccelean, D.C. (1960) A qualitative and quantitative study of the plankton of the Quoddy region in 1957 and 1958 with special reference to the food of the herring. *J. Fish. Res. Board Can.*, **17**, 409–448.
- Locke, A. and Corey, S. (1989) Amphipods, isopods and surface currents: a case for passive dispersal in the Bay of Fundy, Canada. *J. Plankton Res.*, **11**, 419–430.
- McEwen, G.F., Johnson, M.W. and Folsom, T.R. (1954) A statistical analysis of the performance of the Folsom Plankton Sample Splitter, based upon test observations. *Arch. Meteor. Geophys. Biokem. A*, **7**, 502–527.
- Neter, J., Wasserman, W. and Kutner, M.H. (1985) *Applied Linear Statistical Models. Regression, Analysis of Variance, and Experimental Designs*, 2nd edn. Irwin, Homewood, IL, 1127 pp.
- Parker, J.G. (1984) The distribution of the subtidal Amphipoda in Belfast Lough in relation to sediment types. *Ophelia*, **23**, 119–140.
- Peterson, W.T. and Miller, C.B. (1977) Seasonal cycle of zooplankton abundance and species composition along the central Oregon coast. *US Fish Wildl. Serv. Fish. Bull.*, **75**, 717–724.
- Pielou, E.C. (1975) *Ecological Diversity*. Wiley-Interscience, New York, 165 pp.
- Robertson, A.I. and Mann, K.H. (1980) The role of isopods and amphipods in the initial fragmentation of eelgrass detritus in Nova Scotia, Canada. *Mar. Biol. (Berlin)*, **59**, 63–69.
- Robertson, M.R., Hall, S.J. and Eleftheriou, A. (1989) Environmental correlates with amphipod distribution in a Scottish sea loch. *Cah. Biol. Mar.*, **30**, 243–258.
- Rudstam, L.G., Danielsson, K., Hansson, S. and Johansson, S. (1989) Diel vertical migration and feeding patterns of *Mysis mixta* (Crustacea, Mysidacea) in the Baltic Sea. *Mar. Biol. (Berlin)*, **101**, 43–52.
- Sainte-Marie, B. (1984) Morphological adaptations for carrion feeding in four species of littoral or circalittoral lysianassid amphipods. *Can. J. Zool.*, **62**, 1668–1674.
- Sainte-Marie, B. and Brunel, P. (1985) Suprabenthic gradients of swimming activity by cold-water gammaridean amphipod Crustacea over a muddy shelf in the Gulf of St. Lawrence. *Mar. Ecol. Prog. Ser.*, **23**, 57–69.
- Shedler, M. and Evans, F. (1975) Feeding and gut structure of *Parathemisto gaudichaudi* (Guern) (Amphipoda, Hyperiidea). *J. Mar. Biol. Assoc. UK*, **55**, 641–656.
- Sherman, K. (1968) Seasonal and areal distribution of zooplankton in coastal waters of the Gulf of Maine, 1965 and 1966. *US Fish Wildl. Serv. Spec. Sci. Rep. Fish.* **562**, 11 pp.
- Sherman, K., Grosslein, M., Mountain, D., Busch, D., O'Reilly, J. and Theroux, R. (1988) The continental shelf ecosystem off the northeast coast of the United States. In Postma, H. and Zijlstra, J.J. (eds), *Ecosystems of the World. 27. Continental Shelves*. Elsevier, Amsterdam, pp. 279–337.
- Tully, O. and Ceidigh, P.O. (1987) Investigations of the plankton of the west coast of Ireland—VIII. The neustonic phase and vertical migratory behaviour of benthic Peracaridea in Galway Bay. *Proc. R. Irish Acad. Sect. B*, **87**, 43–64.
- Valentin, C. and Anger, K. (1977) *In-situ* studies on the life cycle of *Diastylis rathkei* (Cumacea: Crustacea). *Mar. Biol. (Berlin)*, **39**, 71–76.
- Watling, L. (1979a) Marine flora and fauna of the northeastern U.S.: Crustacea: Cumacea. *NOAA Tech. Rep. NMFS Circ.* **423**. US Dep. Comm., NOAA, NMFS, 23 pp.
- Watling, L. (1979b) Zoogeographic affinities of northeastern North American gammaridean Amphipoda. *Bull. Biol. Soc. Wash.*, **3**, 256–282.
- Watling, L. and Maurer, D. (1972) Marine shallow water amphipods of the Delaware Bay area, U.S.A. *Crustaceana, Suppl.* **3**, 251–266.
- Whiteley, G.C. (1948) The distribution of large planktonic crustacea on Georges Bank. *Ecol. Monogr.*, **18**, 233–264.
- Wigley, R.L. and Burns, B.R. (1971) Distribution and biology of mysids (Crustacea, Mysidacea) from the Atlantic coast of the U.S. in the NMFS Woods Hole collection. *US Fish Wildl. Serv. Fish. Bull.*, **69**, 717–744.

- Williams,A.B. and Bynum,K.H (1972) A ten-year study of meroplankton in North Carolina estuaries: amphipods. *Chesapeake Sci.*, **13**, 175–192.
- Williams,R. and Robins,P. (1981) Seasonal variability in abundance and vertical distribution of *Parathemisto gaudichaudi* (Amphipoda: Hyperiiidea) in the northeast Atlantic Ocean. *Mar. Ecol. Prog. Ser.* **4**, 289–298.
- Windell,J.T. (1971) Food analysis and rate of digestion. In Ricker,W.E. (ed.), *Methods for Assessment of Fish Production in Fresh Waters*. 2nd edn. *IBP Handbook 3*. Blackwell Scientific, Oxford, pp. 215–226.

Received on June 7, 1995, accepted on January 15, 1996