

HYPERIID AMPHIPODS AS INDICATORS OF CLIMATE CHANGE IN THE CALIFORNIA CURRENT

BY

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ABSTRACT

We investigated long-term changes in the abundance and species composition of hyperiid amphipods in the Southern California Bight and nearby waters from twelve springtime CalCOFI cruises spanning the period 1951-1997. Sixty-two hyperiid species were detected in the study region. We found diminution in species diversity and in total hyperiid abundance during the studied period. Despite high interannual variability, there was higher species richness, evenness of species numbers, and abundances of hyperiids in an earlier time period (1951 to 1972) and generally lower species richness, evenness, and abundances in a more recent time period (1979 to 1997). Variations in abundance of total hyperiids were significantly correlated with variations in abundance of presumed gelatinous zooplankton hosts, especially salps, physonect siphonophores, and pyrosomes. Species-specific correlations showed significant associations between ten species of hyperiids and different species of salps, siphonophores, and medusae. Some amphipods were correlated with more than one host. Hyperiid amphipod assemblages appear to be sensitive to large-scale climate changes in the NE Pacific, through either direct responses or indirectly through their association as parasitoids on gelatinous hosts.

INTRODUCTION

Interdecadal-scale climate change in the North Pacific is receiving increasing attention. Shifts in atmospheric pressure patterns with periods of twenty or thirty years have produced changes in climatic regimes in the subarctic (Brodeur & Ware, 1992; Trenberth & Hurrell, 1994) and central Pacific (Venrick et al., 1987; Polovina et al., 1994) Ocean. In the California Current system, coastal sea level has risen in the last few decades (Roemmich, 1992) in conjunction with a warming of the surface layer and decline in total zooplankton biomass (Roemmich & McGowan, 1995a, b). Brodeur et al. (1996) found evidence for a negative correlation between zooplankton biomass in the Gulf of Alaska and in the California

Current system. Two states of atmospheric and oceanic circulation have been hypothesized to alternate in the eastern North Pacific on an interdecadal time scale (Hollowed & Wooster, 1992). One state involves a strong Aleutian low, strong circulation in the Alaska Gyre, and weak circulation in the California Current system. In the other state, the circulation pattern is reversed. Despite growing awareness of such changes in NE Pacific pelagic ecosystems, almost nothing is known about long-term changes in the species composition of the zooplankton. An exception is the study of Mullin (1998), who found no significant differences in numbers of *Calanus pacificus* Brodsky, 1948 per unit volume when comparing 1956-1959 with 1989-1993.

Enumeration of individual taxa is essential to understanding the responses of zooplankton to climatic forcing because organisms with different life histories, generation times, biogeographic affinities, and feeding habits may show markedly different responses to the same conditions. As part of an effort to understand long term changes in zooplankton abundance and community structure in the NE Pacific, the present study focuses on interdecadal changes in the hyperiid amphipod community and the gelatinous groups with which they are associated.

Amphipods of the suborder Hyperiidea are strictly marine and pelagic. Although they are not as abundant as copepods or euphausiids, they sometimes occur in huge swarms (Gray & McHardy, 1967; Vinogradov et al., 1996), which are consumed by oceanic fishes such as tuna (Iversen, 1962), salmon (LeBrasseur, 1966), and dolly varden (Volkov et al., 1996), as well as by baleen whales (Nemoto, 1959). Hyperiid amphipods, while pelagic, are not necessarily planktonic. Many species maintain particular associations with gelatinous zooplankton hosts (Harbison, 1998). This association has long been noted in diverse studies based on samples collected with nets. Subsequently, in situ behavioural observations presented direct proof for associations of hyperiids with salps (Madin & Harbison, 1977), and with cnidarians and ctenophores (Harbison et al., 1977, 1978). According to Laval (1980), perhaps all hyperiids are associated with gelatinous zooplankton at the onset of their existence, but the persistence of this relationship varies with different hyperiid species. Some, such as members of the genus *Parathemisto*, appear to leave their host at an early stage, and from then on to behave more like predators, with prey used as resting places (Madin & Harbison, 1977). *Phronima sedentaria* (see tables I and III for authors and dates of all species referred to herein) shows a singular behavior, fashioning barrels from the tunics of pelagic tunicates (Laval, 1978). Many hyperiids are known to deposit their embryos in or on their host.

METHODS

This analysis of hyperiid amphipods and their gelatinous hosts is based on samples collected by the California Cooperative Oceanic Fisheries Investigations (CalCOFI), in the Southern California Bight and region immediately offshore. The zooplankton samples used in this study were from twelve CalCOFI cruises (5104, 5304, 5604, 6604, 7203, 7402, 7904, 8004, 8605, 9103, 9504, and 9704, where the first two digits designate the year and the last two the month of the cruise). These cruises were selected to span the time period censused by CalCOFI, avoiding strong El Niño years since our focus was on interdecadal rather than interannual variations. Springtime samples were selected to obtain the largest number of years for this study. Sampling methods are described in detail in Ohman & Smith (1995). Briefly, a 1-m diameter ring net with 0.55 mm mesh was towed to a depth of 140 m from 1951-1968, a 1-m ring net with 0.505 mm mesh to 210 m from 1969-1977, and a 0.71-m diameter bongo net with 0.505 mm mesh was towed to 210 m from December 1977 to present. We analyzed only samples collected during night hours (before 05:00 and after 19:00) from the area between Point Conception (34°26'N 120°28'W) to the border between Mexico and the U.S.A., and a maximal distance approximately 300 km offshore. Eight to 19 zooplankton samples were analyzed per cruise, 158 in total. These include CalCOFI lines 80 through 93 and those stations extending from the coast offshore through station 70.

Hyperiid amphipods and gelatinous zooplankton groups (siphonophores, hydrozoan and small scyphozoan medusae, ctenophores, doliolids, salps, and pyrosomes) were counted from the complete sample when individual body size exceeded 25 mm in length. After removal of these large specimens, subsampling was done with a 5 ml Stempel pipette until 1/8 of the original sample had been enumerated. In cases where the resulting total number of hyperiids for a particular cruise was much less than 100 individuals, we counted a larger fraction of the samples. All hyperiid amphipods in this fraction were identified to species. For gelatinous groups, animals were identified to genus or species if the specimen permitted, otherwise to basic taxon. Hyperiids were identified with reference to Brusca (1981) and Vinogradov et al. (1996).

Counts were standardized to individuals $\cdot m^{-2}$ of sea surface. To estimate mean abundance and 95% confidence interval, data were first $\text{Ln}(x + 1)$ transformed. Diversity of hyperiid amphipods was estimated using modified rarefaction curves with the equation proposed by Hurlbert (1971):

$$E(S_n) = \sum_{i=1}^S \left[1 - \frac{\binom{N-N_i}{n}}{\binom{N}{n}} \right]$$

where $E(S_n)$ is the expected number of species in a sample of n individuals, N_i is the number of individuals of the i th species ($i = 1, 2, \dots, S$), and N is the total number of individuals enumerated in a sample.

Spearman rank order correlation analysis was carried out between abundance of total hyperiids and abundance of potential gelatinous hosts (calycophoran siphonophores, physonect siphonophores, medusae, ctenophores, doliolids, salps, and pyrosomes). Furthermore, correlation analysis was done between the common hyperiid species and individual potential host species. The Bonferroni criterion for significance level ($\alpha' = \alpha/k$) was used, where k is the number of possible correlations, to correct the α level for multiple testing.

RESULTS

Sixty-two species of hyperiid amphipods were found in the Southern California Bight region. In addition, *Cystisoma* sp. was detected in two years (1956 and 1995), although the species present could not be assigned definitively. *Primno brevidens* was the most frequently encountered species, observed in 78% of the samples. Eighteen other species may be considered common since they were present in 11 to 47% of the samples. The remaining 43 species were found in less than 10% of the samples, and 19 of them were very rare, occurring in only one sample (table I). *Primno brevidens* was the most abundant species in all the years under study excepting 1974 when it was surpassed by *Parathemisto pacifica* and *Scina tullbergi*. Though *P. brevidens* maintained its dominance during the period under study, most of the hyperiid species showed changes in abundance. Before describing temporal patterns by species, the hyperiid community as a whole will be considered.

A decrease in the number of individuals per species was observed when comparing the period from 1951 to 1974 with 1979 to 1997. These changes are evident when log-abundances of species are ranked in decreasing order (fig. 1a). In this type of graph, also called a dominance-density curve or a species importance curve, a community with a high degree of diversity will tend to have more species and more equitable abundances of each species than a community of low diversity (Brower et al., 1990). The initial slopes of the lines in 1951-1974 were lower than in 1979-1997 ($P < 0.05$, Mann-Whitney U test based on regression slopes fitted to the first three species from each year), reflecting greater evenness

TABLE I
Hyperiid amphipods from the extended Southern California Bight. Number of samples in which they were present (total = 158), and associations with gelatinous hosts (from the literature, supplemented by the present study). (Si, siphonophores; M, medusae; C, ctenophores; Sa, salps; D, doliolids; Py, pyrosomes; Pt, pteropods)

Hyperiid amphipods	Samples	Hosts
LANCEOLIDAE¹		
<i>Lanceola loveni</i> Bovallius, 1885	2	
<i>Scypholanceola aestiva</i> (Stebbing, 1888)	4	
SCINIDAE²		
<i>Scina borealis</i> (G. O. Sars, 1882)	24	
<i>Scina crassicornis</i> (Fabricius, 1775)	3	
<i>Scina curvidactyla</i> Chevreux, 1914	1	
<i>Scina damasi</i> Pirlot, 1929	2	
<i>Scina incerta</i> Chevreux, 1900	1	
<i>Scina inermis</i> Chevreux, 1919	1	
<i>Scina nana</i> Wagler, 1926	4	
<i>Scina tullbergi</i> (Bovallius, 1885)	65	<i>Sphaeronectes gracilis</i> (Claus, 1873) ¹⁰ (Si); <i>Salpa fusiformis</i> Cuvier, 1804 ¹⁴ (Sa)
VIBILIDAE		
<i>Vibilia armata</i> Bovallius, 1887	61	Salps ⁶ ; <i>Ihlea punctata</i> (Forskål, 1775), <i>Pegea confederata</i> (Forskål, 1775) <i>Salpa fusiformis</i> ³ , <i>Thalia democratica</i> (Forskål, 1775) ¹⁰ ; <i>Salpa aspera</i> Foxton, 1961 ¹⁴ (Sa); <i>Pyrosoma</i> Péron, 1804 ¹⁴ (Py)
<i>Vibilia australis</i> Stebbing, 1888	14	<i>Lenzia conoidea</i> (Keferstein & Ehlers, 1860) ¹⁴ (Si)
<i>Vibilia chuni</i> Behning & Woltereck, 1912	6	<i>Cyclosalpa polae</i> Sigl, 1912, <i>Salpa maxima</i> Forskål, 1775 ¹⁰ (Sa)
<i>Vibilia cultripes</i> Vosseler, 1901	2	
<i>Vibilia gibbosa</i> Bovallius, 1887	2	
<i>Vibilia propinqua</i> Stebbing, 1888	7	<i>Ihlea punctata</i> , <i>Pegea confederata</i> , <i>Salpa cylindrica</i> Cuvier, 1804, <i>S. fusiformis</i> ³ , <i>S. maxima</i> , <i>Thalia democratica</i> ¹⁰ ; <i>S. aspera</i> ¹⁴ (Sa)

TABLE I
(Continued)

Hyperiid amphipods	Samples	Hosts
<i>Vibilia pypipes</i> Bovallius, 1887	1	Salps, <i>Iasis zonaria</i> (Pallas, 1774) ¹⁰ (Sa)
<i>Vibilia stebbingi</i> Behning & Woltereck, 1912	3	<i>Cyclosalpa polae</i> , <i>Salpa fusiformis</i> ³ , <i>S. maxima</i> ¹⁰ (Sa)
<i>Vibilia viatrix</i> Bovallius, 1887	15	Salps, <i>Pegea confederata</i> , <i>Pegea socia</i> (Bosc, 1802), <i>Salpa cylindrica</i> , <i>S. maxima</i> ¹⁰ ; <i>Iasis zonaria</i> ¹⁴ (Sa)
CYSTISOMATIDAE		
<i>Cystisoma</i> sp.	2	
PARAPHRONIMIDAE		
<i>Paraphronima crassipes</i> Claus, 1879	22	<i>Rosacea cymbiformis</i> (Delle Chiaje, 1822) ^{6,10} ; <i>Diphyes</i> Cuvier, 1817, <i>Galeolaria</i> Blainville, 1830 ¹⁰ (Si)
<i>Paraphronima gracilis</i> Claus, 1879	74	<i>Sphaeronectes gracilis</i> ¹⁴ (Si); <i>Ritteriella picteti</i> (Apstein, 1904) ¹⁴ (Sa)
HYPERIIDAE		
<i>Hyperia medusarum</i> (O. F. Müller, 1776)	1	<i>Leucothea ochracea</i> Mayer, 1912 (= <i>Eucharis multicornis</i>) (C), medusae, <i>Aurelia aurita</i> Lamarck, 1816, <i>Cyanea capillata</i> Eschscholtz, 1829, <i>Rhizostoma octopus</i> Linné, 1788, "Thaumatias" (could be either <i>Chromatonema</i> Fewkes, 1882, <i>Cosmetira</i> Forbes, 1848, or <i>Gossea</i> L. Agassiz, 1862); <i>Aequorea</i> Péron & Lesueur, 1809, <i>Chrysaora melanaster</i> Brandt, 1835, <i>Pelagia noctiluca</i> (Forskål, 1775) ¹¹ ; <i>Chrysaora</i> Péron & Lesueur, 1809 ¹² (M)
<i>Hyperietta luzoni</i> (Stebbing, 1888)	1	
<i>Hyperietta parviceps</i> Bowman, 1973	1	
<i>Hyperietta stebbingi</i> Bowman, 1973 ⁴	2	
<i>Hyperietta stephensi</i> Bowman, 1973 ⁴	5	
<i>Hyperietta vosseleri</i> (Stebbing, 1904)	1	
<i>Hyperoche martinezii</i> (F. Müller, 1864)	1	<i>Beroe forskali</i> Milne-Edwards, 1841, <i>Beroe ovata</i> Bruguère, 1789 (= <i>Beroe gilva</i>), <i>Bolinopsis vitrea</i> (L. Agassiz, 1860) (= <i>Bolina hydantina</i>) ¹⁰ (C)

TABLE I
(Continued)

Hyperiid amphipods	Samples	Hosts
<i>Hyperoche mediterranea</i> Senna, 1908	9	<i>Leucothea ochracea</i> Mayer, 1912 (= <i>Leucothea multicornis</i>), <i>Ocyropsis maculata</i> (Rang, 1828) ⁹ ; <i>Beroe</i> sp., <i>B. forskali</i> , <i>Lampea pancarina</i> (Chun, 1880), <i>Pleurobrachia bachei</i> L. Agassiz, 1860 ¹⁰ (C); <i>Geryonia</i> Péron & Lesueur, 1809 (= <i>Carmarina</i>) ¹⁰ ; <i>Eutonina indicans</i> (Romanes, 1876), <i>Phialidium</i> Leuckart, 1856 ¹¹ (M); <i>Abyla</i> Quoy & Gaimard, 1827 ¹⁰ (Si); <i>Salpa</i> sp. ¹⁰ (Sa) <i>Beroe forskali</i> , <i>Pleurobrachia bachei</i> , <i>Pleurobrachia pileus</i> (O. F. Müller, 1776) ¹⁰ (C); medusae, <i>Aurelia aurita</i> , <i>Phialidium</i> , <i>Polyorchis</i> sp., <i>Sarsia</i> sp., <i>Thiaropsis</i> sp., <i>Tima formosa</i> L. Agassiz, 1862 ¹⁰ (M)
<i>Hyperoche medusarum</i> (Krøyer, 1838)	11	
<i>Iulopis mirabilis</i> Bovallius, 1887	5	
<i>Lestrigonus macrophthalmus</i> (Vosseler, 1901)	1	
<i>Lestrigonus schizogenetos</i> (Stebbing, 1888)	30	<i>Aequorea</i> , <i>Chrysaora hyoscella</i> Eschscholtz, 1829 ⁶ , <i>Leuckartiara nobilis</i> Hartlaub, 1914, <i>Liriope tetraphylla</i> (Chamisso & Eysenhardt, 1821), <i>Phialidium</i> sp. ¹⁰ (M); <i>Lampea pancarina</i> ¹⁰ (C); <i>Lenzia</i> sp. ¹³ (Si); <i>Doliolletta gegenbauri</i> Ulljanin, 1884 ¹⁴ (D)
<i>Lestrigonus shoemakeri</i> Bowman, 1973	24	<i>Calyropsis nematophora</i> Bigelow, 1913 ¹⁰ (M); salps ¹¹ (Sa)
<i>Parathemisto pacifica</i> Stebbing, 1888	47	
<i>Phronimopsis spinifera</i> Claus, 1879	41	
DAIRELLIDAE	11	
<i>Dairella californica</i> (Bovallius, 1885)		
PHRONIMIDAE	7	<i>Beroe</i> ⁹ (C); <i>Salpa fusiformis</i> ³ , <i>Thalia democratica</i> ¹⁰ (Sa)
<i>Phronima atlantica</i> Guérin-Ménéville, 1836	1	
<i>Phronima bucephala</i> Giles, 1887	4	<i>Abylopsis tetragona</i> (Otto, 1823) ¹⁰ (Si)
<i>Phronima curvipes</i> Vosseler, 1901	1	<i>Abylopsis tetragona</i> ⁶ , <i>Lenzia fowleri</i> (Bigelow, 1911) ¹⁰ (Si); <i>Salpa aspera</i> ⁶ (Sa) in barrel ⁶
<i>Phronima pacifica</i> Streets, 1877		
<i>Phronima sedentaria</i> (Forskål, 1775)	38	<i>Beroe</i> ⁶ (C); <i>Ihlea punctata</i> , <i>Salpa fusiformis</i> ³ , <i>Thalia democratica</i> ¹⁰ , <i>S. aspera</i> ¹⁴ (Sa); <i>Pyrosoma</i> ⁶ , <i>Pyrosoma atlanticum</i> (Péron, 1804) ¹⁰ (Py); in barrel ⁶
<i>Phronima stebbingi</i> Vosseler, 1901	6	In barrel ¹⁰

TABLE I
(Continued)

Hyperiid amphipods	Samples	Hosts
PHROSINIDAE		
<i>Phrosina semilunata</i> Risso, 1822	2	
<i>Primno brevidens</i> Bowman, 1978	123	<i>Ceratocymba sagittata</i> Quoy & Gaimard, 1827 ¹⁴ (Si)
<i>Primno latreillei</i> Stebbing, 1888	1	
<i>Primno macropa</i> Guérin-Méneville, 1836	2	<i>Abylopsis tetragona</i> , <i>Sulculeolaria chuni</i> (Lens & Van Riemsdijk, 1908) ⁸ (Si)
PRONOIDAE ⁵		
<i>Eupronoe minuta</i> Claus, 1879	56	<i>Agalma elegans</i> (M. Sars, 1846) ⁶ ; <i>Apolenia uvaria</i> Lesueur, 1811, <i>Sulculeolaria quadrivalvis</i> Blainville, 1834 ¹⁰ (Si)
LYCAEIDAE		
<i>Lycaea pachypoda</i> (Claus, 1879)	4	<i>Liriope tetraphylla</i> ⁶ (C); salps, <i>Salpa maxima</i> ¹⁰ (Sa); pyrosomes, <i>Pyrosoma atlanticum</i> ¹⁰ (Py)
<i>Lycaea pauli</i> Stebbing, 1888	1	
<i>Lycaea pulex</i> Marion, 1874	1	Salps ⁷ , <i>Cyclosalpa affinis</i> (Chamisso, 1819), <i>Cyclosalpa bakeri</i> (Ritter, 1905), <i>Cyclosalpa pinnata</i> (Forskål, 1775), <i>C. polae</i> , <i>Helicosalpa komaii</i> (Ihle & Ihle-Landenberg, 1936), <i>Ihlea punctata</i> , <i>Pegea bicaudata</i> (Quoy & Gaimard, 1826), <i>P. confederata</i> , <i>P. socia</i> , <i>Salpa cylindrica</i> , <i>S. maxima</i> , <i>Traustedia multitentaculata</i> (Quoy & Gaimard, 1834) ¹⁰ (Sa); pyrosomes, <i>Pyrosoma atlanticum</i> ¹⁰ (Py)
<i>Lycaea</i> sp.	3	
<i>Simorhynchotus antennarius</i> (Claus, 1871)	4	<i>Geryonia proboscidalis</i> (Forskål, 1775) ¹⁰ (M)
TRYPHANIDAE		
<i>Tryphana malmi</i> Boeck, 1870	28	<i>Ceratocymba sagittata</i> ¹⁰ (Si)
OXYCEPHALIDAE		
<i>Calamorrhynchus pellucidus</i> Streets, 1878	1	
<i>Leptocotis tenuirostris</i> (Claus, 1871)	1	
<i>Oxycephalus clausi</i> Bovallius, 1887	1	<i>Beroe</i> spp., <i>Cestum veneris</i> (Lesueur, 1813), <i>Mnemiopsis mccradyi</i> (Mayer, 1900), <i>Ocyropsis cristallina</i> (Rang, 1828), <i>O. maculata</i> ⁹ (C)
<i>Oxycephalus latirostris</i> Claus, 1889	1	<i>Cestum veneris</i> , <i>Eurhamphaea vexilligera</i> (Gegenbaur, 1856) ⁹ (C)

TABLE I
(Continued)

Hyperiid amphipods	Samples	Hosts
<i>Streetsia challengeri</i> Stebbing, 1888	13	
<i>Streetsia steenstrupi</i> (Bovallius, 1887)	22	<i>Corolla spectabilis</i> Dall, 1871 ¹⁴ (Pt)
PLATYSCELIDAE		
<i>Platyscelus ovooides</i> (Risso, 1816)	5	<i>Aequorea</i> ¹⁰ (M)
PARASCCELIDAE		
<i>Hemiscelus diplochelatus</i> Stewart, 1913	4	

¹ Lanceolids are parasitoids of deep water coelenterates.¹³

² *Scina* sp. was reported associated with *Sphaeronectes gracilis* and siphonophores in general.⁶

³ *Salpa fusiformis* may be *S. aspera*, which was considered a variety of *S. fusiformis* before Foxton (1961).

⁴ Associated with radiolarian colonies^{6,10}.

⁵ Juvenile Pronoioidea were found encysted in the physonect siphonophores *Agalma okeni* Eschscholtz, 1825, *Agalma clausi* Bedot, 1888, *Athorybia rosacea* (Forskål, 1775), *Forskalia edwardsi* Kölliker, 1853, and *Forskalia tholoides* Haeckel, 1888⁶.

⁶ Quoted in Harbison et al. (1977); ⁷ quoted in Thurston (1977); ⁸ Bowman (1978); ⁹ Harbison et al. (1978); ¹⁰ quoted in Laval (1980); ¹¹ Brusca (1981); ¹² Martin & Kuck (1991); ¹³ Vinogradov et al. (1996); ¹⁴ this study.

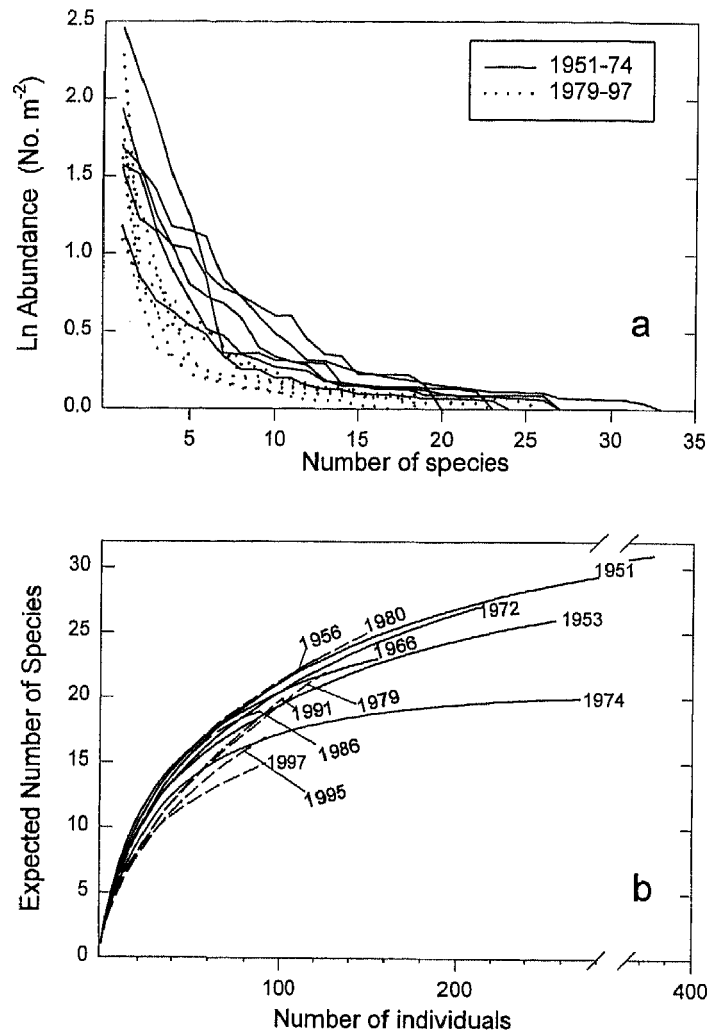


Fig. 1. a, Dominance-density curves based on logarithmic abundance as a function of number of species of hyperiid amphipods; and b, Hurlbert's modified rarefaction curves for hyperiid amphipods from twelve cruises in Southern California waters.

during the earlier time period (fig. 1a). However, 1974 showed a steep slope due to the dominance of *Parathemisto pacifica* in that year. A change in species diversity over time also appeared when plotted as Hurlbert's modified rarefaction curves (fig. 1b). The curves for the period 1951-1972 show higher species richness, while most of the curves for 1979-1997 have lower species richness. The curve for 1974 has a different behavior than the rest of the earlier period, with low species richness and elevated abundances of the two species mentioned

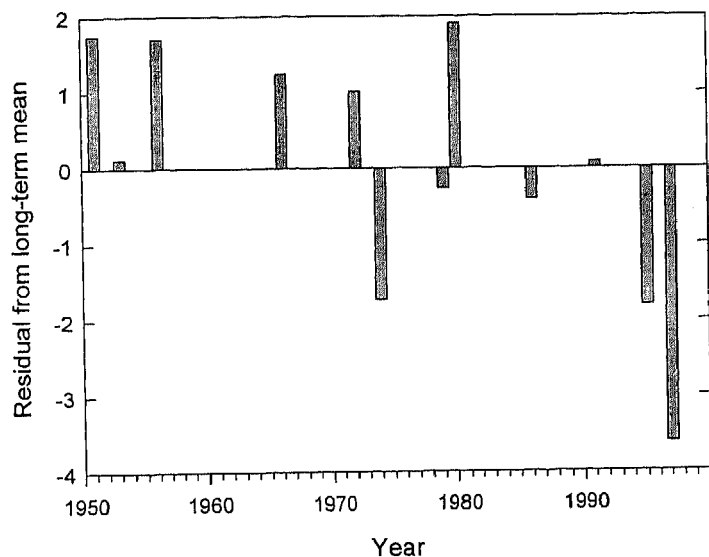


Fig. 2. Interannual variation in residual from the long-term mean of hyperiid species richness, based on Hurlbert's modified rarefaction estimated when the number of individuals enumerated is 88.

previously. The expected number of species at an abundance of 88 individuals ($E(S_{88})$, for which all years can be compared) was 18 to 21 species for 1951 to 1972, 17 in 1974, and 15 to 18 species for 1979-1997, excepting in 1980 when $E(S_{88})$ was 20. The trend of decrease in species richness during the recent years, especially 1995 and 1997, is most clearly observed when plotted as residuals from the long-term mean (fig. 2).

In addition to these changes in species richness, median abundances of hyperiids from 1951 to 1974 were almost twice hyperiid abundances from 1979-1997 ($P < 0.001$, Mann-Whitney U test, fig. 3a). To examine a possible diminution in gelatinous hosts, with which hyperiids are thought to be associated, correlations were explored between total abundance of hyperiids and abundances of different gelatinous taxa (table II). Total abundance of hyperiid amphipods was significantly correlated with salps, physonect siphonophores, pyrosomes, ctenophores, and doliolids. Total hyperiids was not significantly correlated with medusae or calyphoran siphonophores. Analysis of temporal trends in abundance of amphipods and possible hosts showed that in 1951, 1953, 1956, 1966, 1972, and 1974 mean hyperiid abundances were at or above the historic mean (dashed line in fig. 3a), shifting to lower values in the six more recent years. Some gelatinous taxa, particularly physonect siphonophores (fig. 3c) and ctenophores (fig. 3e) showed a similar trend, although some years between 1979-1997 did not agree

TABLE II

Spearman rank correlation coefficients (r) between the abundance of total hyperiid amphipods and various gelatinous taxa ($N = 158$ sample pairs); "ns" indicates $\alpha' > 0.05$

Taxa	r	α'
Salps	0.385	< 0.001
Physonect siphonophores	0.339	< 0.001
Pyrosomes	0.294	0.001
Ctenophores	0.239	< 0.05
Doliolids	0.218	< 0.05
Medusae	0.162	ns
Calycophoran siphonophores	-0.010	ns

with this trend (e.g., 1980 and 1986). The abundance of salps (fig. 3b) and doliolids (fig. 3f) showed a tendency toward lower values in the most recent years. The temporal pattern of pyrosomes (fig. 3d) was less clear, with values generally low and a distinctive high mean abundance only in spring of 1956. Medusae (fig. 3g) and calycophoran siphonophores (fig. 3h) tended to increase over the recent time period.

Previous authors (table I) have extensively documented the associations between hyperiid species and hosts. Most of this information comes from Atlantic and Mediterranean areas. In our samples, some hyperiid specimens were found embedded in the tissues of gelatinous specimens, particularly in salps (table I), a situation that is easily distinguished from artifacts of association in the cod end of a net. Some of these associations have been reported in earlier studies, including the association of *Salpa aspera* (= *Salpa fusiformis aspera*) with *Vibilia armata* or *V. propinqua*. Detection of *Streetsia steenstrupi* inside the thecosome "pteropod" *Corolla spectabilis*, and *Lestrignonus schizogeneios* in *Doliolletta gegenbauri*, must be considered tentative, requiring confirmation through in situ observations, as there are no previous records for these hosts. Also, the relation of *Vibilia australis* and *Primno brevidens* with siphonophores could be questionable since the amphipods could be prey of these carnivorous animals. However, many amphipods in our samples likely separated from the host at the moment of capture. It is well known that turbulence and abrasion during net collections can result in escape of the hyperiid from its host (Laval, 1980). It is also possible that the destruction of soft tissues by formalin contributes to the release of parasitoids in old preserved samples.

To explore associations between specific parasitoids and hosts, we tested correlations among the 15 most common species of hyperiids and 10 siphonophore species, 9 medusae species (or genera), 5 salp species, one doliolid species, one pyrosome genus, and total ctenophores. From 405 Spearman correlation coefficients only twelve were significant at $\alpha' < 0.05$ (when corrected for multiple

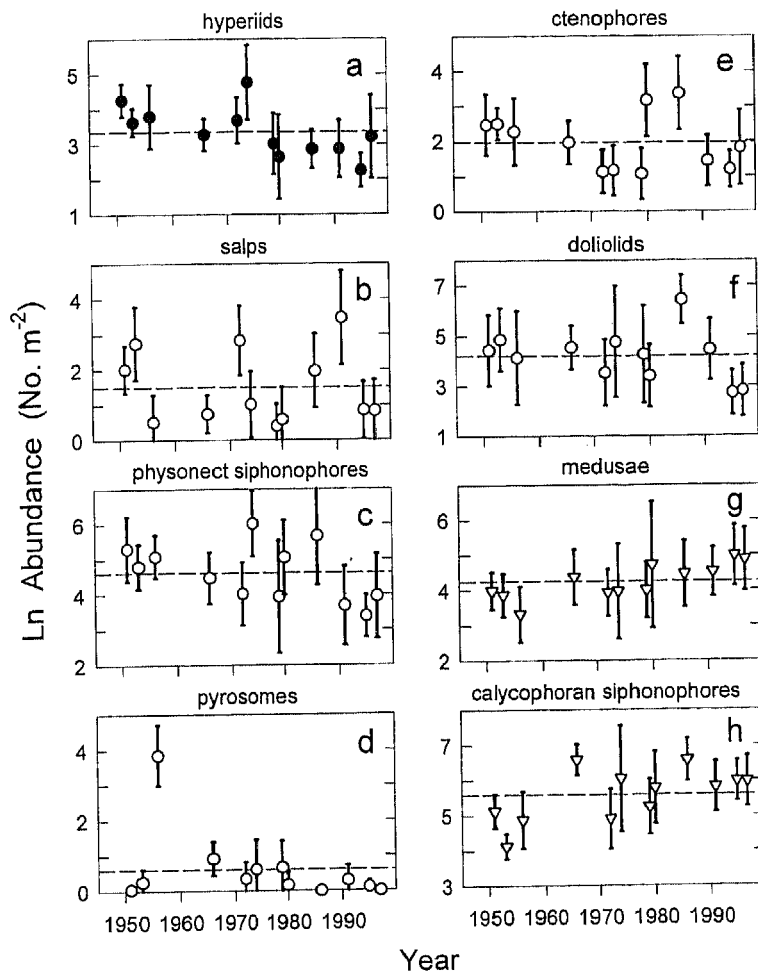


Fig. 3. Interannual variation in mean abundance ($\pm 95\%$ confidence interval) of a, hyperiid amphipods; b, salps; c, physonect siphonophores; d, pyrosomes; e, ctenophores; f, doliolids; g, medusae; and h, calycophoran siphonophores. Dashed line is the long-term mean for each taxon. Open circles indicate taxa that were significantly correlated with hyperiid amphipods; open triangles indicate taxa that were not correlated.

testing) and one more may be included if the rejection level is taken as 0.1 (table III). Forty-six percent of these correlations involved a salp as host. The correlation coefficients with the highest significance ($\alpha' < 0.001$) were between the salp *Pegea confoederata* and the hyperiids *Vibilia viatrix*, *Streetsia steenstrupi*, and *Phronimopsis spinifera*. The salp was found only in the 1950s and in 1974. In the years when *P. confoederata* was absent, the amphipods *V. viatrix*, *S. steenstrupi*, and *P. spinifera* were also absent or limited in abundance

TABLE III

Correlations between common hyperiid amphipods and potential gelatinous hosts. Solid arrows indicate Spearman rank correlation coefficients with α' level ≤ 0.05 , dotted arrows indicate $0.05 < \alpha' < 0.10$, and no arrows indicate $\alpha' > 0.10$ ($N = 158$). (Si, siphonophores; M, medusae; Sa, salps; D, doliolids; P, pyrosomes)

Hyperiids	Hosts
<i>Vibilia viatrix</i>	→ <i>Pegea confoederata</i> (Sa)
<i>Streetsia steenstrupi</i>	→ <i>Liriope tetraphylla</i> (M)
<i>Phronimopsis spinifera</i>	→ <i>Salpa fusiformis</i> (Sa)
<i>Eupronoe minuta</i>	→ <i>Diphyes dispar</i> Chamisso & Eysenhardt, 1821 (Si)
<i>Scina tullbergi</i>	→ <i>Lensia conoidea</i> (Si)
<i>Vibilia armata</i>	→ <i>Chelophyes appendiculata</i> (Eschscholtz, 1829) (Si)
<i>Parathemisto pacifica</i>	→ <i>Iasis zonaria</i> (Sa)
<i>Lestrignonus shoemakeri</i>	→ <i>Salpa aspera</i> (Sa)
<i>Lestrignonus schizogeneios</i>	→ <i>Salpa aspera</i> (Sa)
<i>Paraphronima gracilis</i>	→ <i>Ceratocymba sagittata</i> (Si)
	→ <i>Chuniphyes multidentata</i> Lens & Van Riemsdijk, 1908 (Si)
<i>Paraphronima crassipes</i>	→ <i>Eudoxides spiralis</i> (Bigelow, 1911) (Si)
<i>Phronima sedentaria</i>	→ <i>Muggiaea atlantica</i> Cunningham, 1892 (Si)
<i>Prinno brevidens</i>	→ <i>Nanomia bijuga</i> (Chiaje, 1841) (Si)
<i>Scina borealis</i>	→ <i>Praya dubia</i> (Quoy & Gaimard, 1833) (Si)
<i>Tryphana malmi</i>	→ <i>Sphaeronectes gracilis</i> (Si)
	→ <i>Aegina citrea</i> Eschscholtz, 1829 (M)
	→ <i>Aglaura hemistoma</i> Péron & Lesueur, 1809 (M)
	→ <i>Obelia</i> Péron & Lesueur, 1809 (M)
	→ <i>Periphylla</i> Haeckel, 1880 (M)
	→ <i>Phialopsis diegensis</i> Torrey, 1909 (M)
	→ <i>Solmundella bitentaculata</i> (Quoy & Gaimard, 1833) (M)
	→ <i>Velella</i> Linnaeus, 1775 (M)
	Ctenophores
	→ <i>Thalia democratica</i> (Sa)
	→ <i>Dolioletta gegenbauri</i> (D)
	→ <i>Pyrosoma</i> (P)

(fig. 4c, g, h). Some hyperiids may be associated with more than one host, since they showed more than one significant correlation.

Other common hyperiid species, though not significantly correlated with a particular host, showed varying tendencies toward lower abundances in recent years (fig. 4d-f, i), although large confidence intervals were associated with each mean. *Phronima sedentaria*, whose behavior of digging barrels from gelatinous hosts is well known, showed mean abundances below the historic mean in the last six years studied (fig. 4d). It is interesting to note that in spring 1972 the highest number of gelatinous barrels was found in the samples, just the year of highest abundance for both *P. sedentaria* and *Salpa aspera*. The correlation between the abundances of barrels and *P. sedentaria* was significant ($\alpha < 0.01$). *Parathemisto*

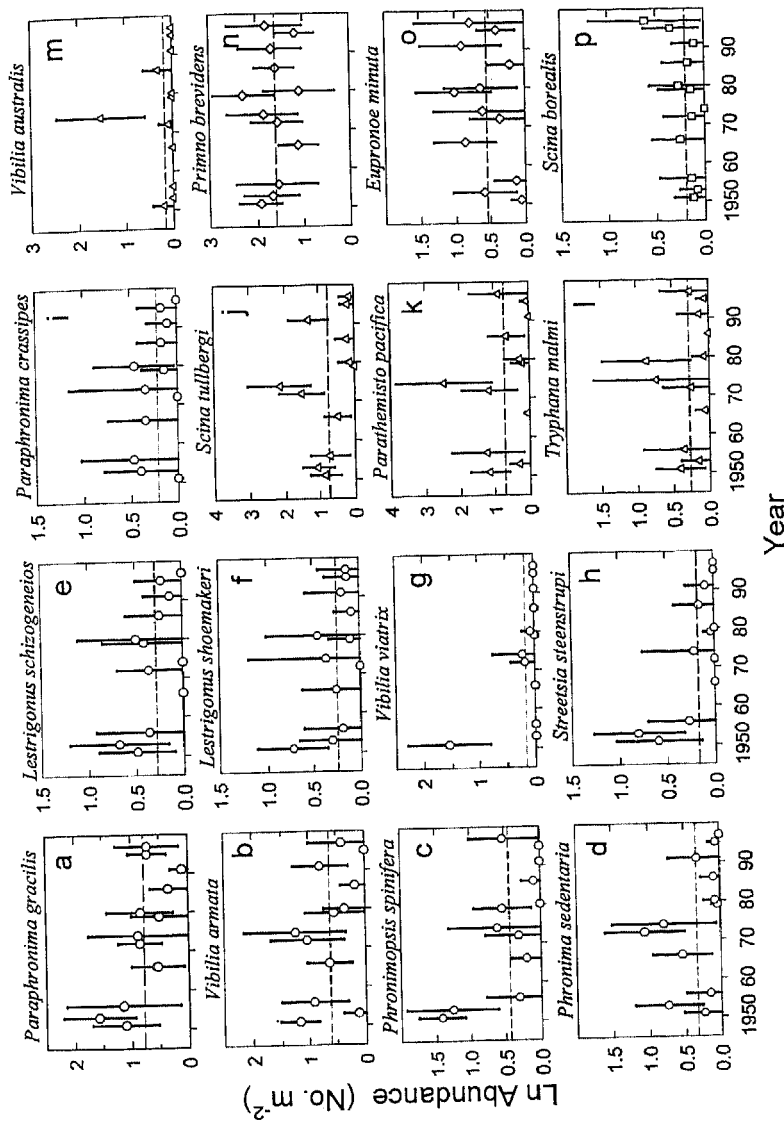


Fig. 4. Interannual variation in mean abundance ($\pm 95\%$ confidence interval) of the most common hyperiid species: a, *Paraphronima gracilis*; b, *Vibilia armata*; c, *Phronimopsis spinifera*; d, *Phronima sedentaria*; e, *Lestrigonus schizogeneios*; f, *Lestrigonus shoemakeri*; g, *Vibilia viatrix*; h, *Sireetsia steenstrupi*; i, *Paraphronima crassipes*; j, *Scina tullbergi*; k, *Parathemisto pacifica*; l, *Tryphana malmi*; m, *Vibilia australis*; n, *Primno brevidens*; o, *Eupronoe minuta*; and p, *Scina borealis*. Dashed line is the long-term mean. Symbols indicate trends in abundance (circles, decline; triangles, peak in 1974; diamonds, no clear trend; squares, possible increase). (See table I for authors and dates of all species.)

pacifica showed a different pattern of variability, decreasing in 1953 and 1966, with high values in the seventies, and then sharply declining, being virtually absent in 1980, 1991 and 1995, and reappearing in 1997 (fig. 4k). A similar pattern was observed in *Tryphana malmi* and *Vibilia australis* (fig. 4l, m).

DISCUSSION

The smallest number of species of hyperiid amphipods observed over the 47-year span of this study was found in the most recent years analyzed, 1995 and 1997. However, the transition to lower hyperiid species richness probably occurred before the 1990's. At present the timing of this transition is difficult to resolve because we do not yet have annual level resolution of hyperiid diversity trends. Furthermore, interdecadal trends can be obscured by interannual variations. For example, the years 1974 and 1980 had anomalously low and anomalously high numbers of hyperiid species, respectively. Apart from these years, which may reflect the effects of unusual circulation, the rarefaction results suggested that all other years between 1951 to 1972 had anomalously high numbers of species, while the years from 1979 to 1997 showed lower numbers of hyperiid species. In addition, the evenness of hyperiid species abundances was higher in the period 1951-1974 than in 1979-1997, reflecting more equitable distributions of individuals among species in the earlier time period.

These changes in hyperiid diversity and abundance recall the large-scale climate transition in the North Pacific, which has been placed in the winter of 1976-1977 (Ebbesmeyer et al., 1991; Miller et al., 1994; Polovina et al., 1994; Trenberth & Hurrell, 1994). Examination of 40 time series of environmental variables, including atmospheric, oceanographic and biological factors, consistently showed a step-like change in 1976 (Ebbesmeyer et al., 1991). A southward shift and intensification of the Aleutian Low atmospheric pressure system (Graham, 1994; Trenberth & Hurrell, 1994) marked the change in climate regime.

In the central North Pacific Ocean, a doubling of chlorophyll occurred after the mid 1970s, associated with cooling of surface waters and increase in winter winds (Venrick et al., 1987). The elevated phytoplankton biomass in the area has been linked to a substantial increase of calanoid copepods and sablefish after 1976 (McFarlane & Beamish, 1992). In contrast, the Southern California Bight and region offshore showed a decrease in macrozooplankton biomass (Roemmich & McGowan, 1995a, b) and in the abundance of pelagic seabirds (Veit et al., 1996), associated with a warming of the surface layer and increased stratification. The reduced abundance of hyperiids agrees with the decline in zooplankton biomass in Southern California Bight (Roemmich & McGowan, 1995a, b). The decrease of

hyperiid amphipods as a whole (fig. 3a) and of many individual species (fig. 4a-i) during the warm climate regime in the California Current, is further biological evidence of a shift in climate regime. The present study indicates that abundance as well as species richness of some zooplankton taxa has declined in recent decades.

Neither the long-term decline in zooplankton biomass (Roemmich & McGowan, 1995a, b), nor the richness of the hyperiid community observed in the present study, can be attributed to changes in sampling methods over the course of the CalCOFI time series. Ohman & Smith (1995) compared how changes in sampling depth (from 140 to 210 m in 1969) and in type of net (from 1-m diameter ring net to a 0.71 m bongo net in 1977) affected the efficiency of collecting zooplankton biomass. They found that biomass in samples collected to 210 m compared with samples collected to 140 m was 27% lower when biomass is expressed per unit volume filtered, while samples collected with the bongo net contained 37% more biomass than those collected with the 1-m bridled ring net (Ohman & Smith, 1995). Therefore, biomass values pre-1969 and post-1977 were quite comparable. Hewitt (1980) found that the bongo net collected more large larvae of the northern anchovy, and Brinton & Townsend (1981) observed that catch efficiency of the bongo net design was better for juvenile and adults of most euphausiid species. Therefore, the decrease in hyperiid abundance and hosts observed in the last two decades does not appear to be due to changes in sampling techniques. In fact, these changes suggest a possible underestimation of the magnitude of that decrease.

The Southern California Bight region showed strong dominance of *Primno brevidens* through the period under study. This species, described by Bowman (1978), must have been confused in early studies with *Primno macropa* (cf. Hurley, 1956; Brusca, 1967). Both species coexist in the California Current, but *P. brevidens* is more abundant in adjacent waters of California, while *P. macropa* is associated with subarctic water (Bowman, 1978). Though *Primno* was mentioned as a common genus in the region during 1948-1955, it was not the most important (Hurley, 1956; Brusca, 1967). Since the abundance of *P. brevidens* was relatively stable through the period 1951-1997, the increased relative abundance of this species was due to a decrease of other co-dominant amphipods, such as *Vibilia armata*, *V. viatrix*, *Paraphronima crassipes*, *P. gracilis*, and *Phronima sedentaria* (fig. 4). Three of these hyperiids showed significant correlations with gelatinous organisms, suggesting that the decline in total zooplankton biomass observed by Roemmich & McGowan (1995a, b) could be due to a decrease in gelatinous organisms necessary for hyperiids to survive. This decline is particu-

larly true for *Pegea confoederata* and *Salpa aspera*, which showed high pulses of abundance in the period previous to the 1976-1977 climate shift, but not after.

Along with the numerous reports of hyperiids found in the tissues of inferred gelatinous hosts (table I), direct evidence of the association hyperiid-host has been provided by behavioral studies (Harbison et al., 1977, 1978; Madin & Harbison, 1977). Multivariate analysis of zooplankton groups also pointed to the close relation between hyperiids and gelatinous groups in the California Current system (Colebrook, 1977). The nature of the association is still not clear. Laval (1980) suggested that all hyperiids are associated with gelatinous zooplankton early in their development. The relation previously had been described as commensalism but because some of the amphipods eventually destroy their host, they are more appropriately called parasitoids (Laval, 1980). Undischarged nematocysts have been frequently observed in fecal pellets of hyperiids but it is difficult to prove that they originated from the host (Thurston, 1977). Further research emphasizing in situ behavioral approaches is clearly needed to understand the hyperiid-host association. Whatever the exact details of these associations, our results are in agreement with the dependence of hyperiids on host organisms and suggest that hyperiids have been influenced by decreased availability of gelatinous hosts, thus reducing the diversity of this planktonic group.

Prior to the warm climate regime, a strong influence of Subarctic water in the Southern California Bight appears to have occurred, since *Parathemisto pacifica* dominated the hyperiid community in 1974 (fig. 4k). This species overwhelmingly dominates the cool-water epipelagic hyperiid amphipod fauna, as has been observed in northern regions of the California Current and other regions of the North Pacific (Bowman, 1960; Sanger, 1973; Lorz & Percy, 1975). Although Bowman (1960) considered *P. pacifica* to be free living, later studies reported this species inside the medusa *Calycopsis nematophora* (cf. Renshaw, 1965) or in association with salps (Brusca, 1981). In the present study it was positively correlated with the calycophoran *Lensia conoidea* (table III). Another hyperiid with high abundance in 1974 was *Vibilia australis*, which apart from that year was only found in low numbers during the colder climate regime (fig. 4m). This species is the most northerly recorded species of *Vibilia* occurring in our study region (cf. Sanger, 1973).

This study found differences in the rank order of importance of some species in comparison with reports from previous studies in the Southern California Bight (Hurley, 1956; Brusca, 1967, 1981). The abundance of *Scina tullbergi*, *Phronimopsis spinifera*, and *Tryphana malmi* was relatively higher in the present research compared to that of those authors. The probable reason for this is the coverage of the sampling area. Our working area extended further offshore.

In contrast, *Scina borealis*, *S. crassicornis*, and *Cystisoma fabricii* were less abundant in our samples, perhaps due to the wide vertical range of these species compared to *S. tullbergi*, which lives in the upper 500 m (Thurston, 1976).

In conclusion, we have found changes in the biodiversity of zooplankton from the Southern California region that may be related to long-term warming in the California Current System. Analysis of plankton samples from intervening years is needed to understand the precise timing of the changes and the underlying mechanisms. Further studies in other regions of the California Current are required to estimate the extent of the affected area. Comparative studies with other North Pacific regions are also important in order to assess the large-scale spatial coherence of trends in the diversity and abundance of hyperiids and the gelatinous groups with which they are associated.

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