



Distribution and relative importance of jellyfish in a region of hydrothermal venting

Brenda J. Burd*, Richard E. Thomson

*Department of Fisheries & Oceans, Institute of Ocean Sciences, 9860 West Saanich Rd. P.O. Box 6000,
Sidney, BC, Canada V8L 4B2*

Received 19 August 1998; received in revised form 11 August 1999; accepted 15 November 1999

Abstract

Net sampling to 3000 m depth at Endeavour Ridge in the northeast Pacific in July 1991–1994 shows that medusae in the immediate vicinity of the hydrothermal vent fields often make up a larger proportion of the total zooplankton abundance and biomass from mesopelagic to bathypelagic depths than in the surrounding waters. This was particularly evident in the dominant Trachymedusae, and least evident in the siphonophores. In addition, the large red Scyphomedusa *Stygiomedusa gigantea* was a major biomass component in the region of the deep (1000–1800 m depth) migrating scattering layers at the vent field, but was not found in any net tows greater than 10 km away from vents. There is no concurrent increase in relative or percent biomass of fish or chaetognaths, which are the other major predators in the community. We hypothesize that predaceous medusae respond opportunistically to the enhanced zooplankton biomass throughout the water column around vents in spring to early summer, in a way that other predators do not. © 2000 Elsevier Science Ltd. All rights reserved.

Keywords: Hydrothermal vents; Zooplankton; Jellyfish; Migration

1. Introduction

Net sampling to 3000 m depth over the active hydrothermal vent sites at Endeavour Ridge in the northeast Pacific suggests that mesopelagic zooplankton migrate throughout the water column, aggregating in layers down to depths of 2000 m (Burd and Thomson, 1994, 1995). Enhanced zooplankton biomass is evident throughout the

* Corresponding author. Tel.: + 1-250-363-6345; fax: + 1-250-363-6310.

E-mail address: burdb@dfo-mpo.gc.ca (B.J. Burd).

water column compared with off-vent sites. During our trophic studies of the enhanced biomass region in spring and early summer around the Endeavour Ridge venting region (Burd and Thomson, 1994), we noted unusually high abundances of jellyfish in nets towed through deep water near vents (Thomson et al., 1992a, b; Burd and Thomson, 1994, 1995). This observation, coupled with the occurrence of large amounts of gelatinous material from the giant medusa *Stygiomedusa gigantea* covering our instrument package on several survey tows in 1994, triggered a closer examination of the composition and relative importance of gelatinous zooplankton around the vents.

Several researchers (e.g. Greve and Parsons, 1977; Parsons, 1979) have speculated that predaceous jellyfish are most likely to be the dominant predators in low productivity systems dominated by smaller zooplankton and nanoplankton, whereas fish are considered more important predators in higher productivity systems such as coastal upwelling zones. However, a review by Mills (1995) indicates that jellyfish can be important predators in both low and high productivity (cf. Mackie, 1985) systems. For example, jellyfish often make up 50–80% of the live biomass in coastal plankton ecosystems, consuming copious quantities of zooplankton (Moeller, 1979, 1984; Shushkina and Musayeva, 1983) and larval fish (Moeller, 1980). Mills (1995) indicates that species diversity is similar in both low and high productivity ecosystems and describes blooms of shallow and mesopelagic jellyfish in high productivity zones.

The misconception about jellyfish importance in both low and high productivity systems is related, in part, to the inadequacy of traditional zooplankton net sampling methods for capturing these fragile fauna. SCUBA and submersible studies have indicated that there can be three times as many jellyfish in the water column as are estimated by plankton net sampling (Hamner et al., 1975; Vinogradov and Shushkina, 1982; Vinogradov et al., 1994; Laval et al., 1989). Although researchers have specifically sampled for gelatinous forms in the ocean to depths of 1000 m or more (C.E. Mills, Friday Harbor Marine Laboratory, Washington, pers. comm.), little is known about these important predators in pelagic ecosystems. Vereshchaka and Vinogradov (1999) show that gelatinous animals and radiolarians can dominate plankton biomass throughout the water column at the Broken Spur vent field, mid-Atlantic ridge.

Declines in fisheries due to habitat degradation and over-fishing may provide an opportunity for gelatinous fauna to become the dominant predators in systems previously dominated by fish (Parsons, 1979; Mills, 1995). Furthermore, Mills (1995) suggests that, because of their rapid sexual and asexual reproduction potential, resident jellyfish the world over are in a position to take advantage of changes in local ecology.

Pelagic regions of the northeast Pacific are generally considered to be low productivity environments in which fish and jellyfish can make up a considerable percentage of the normally low biomass deep-sea fauna (Angel and Baker, 1982; Longhurst, 1985; Vinogradov et al., 1994). However, venting regions such as Endeavour Ridge have seasonally enhanced zooplankton biomass compared with surrounding areas of the northeast Pacific (Burd and Thomson, 1994).

In this paper, we utilize the distinct spatial dichotomy in deep-water Zooplankton standing stock between the Endeavour Ridge venting region and the surrounding

oligotrophic ocean to compare the relative importance of jellyfish in low and higher productivity regions of an ecosystem for which there is no anthropogenic disruption of existing fish populations.

2. Survey area and deep scattering layers

Endeavour Ridge is an active mid-ocean ridge venting region rising to about 2000 m depth off the coast of British Columbia and Washington State (Fig. 1). Detailed water property sampling in the vicinity of the ridge (Lupton et al., 1985; Feely et al., 1990, 1992; Thomson et al., 1992a, b) has revealed a well-defined plume

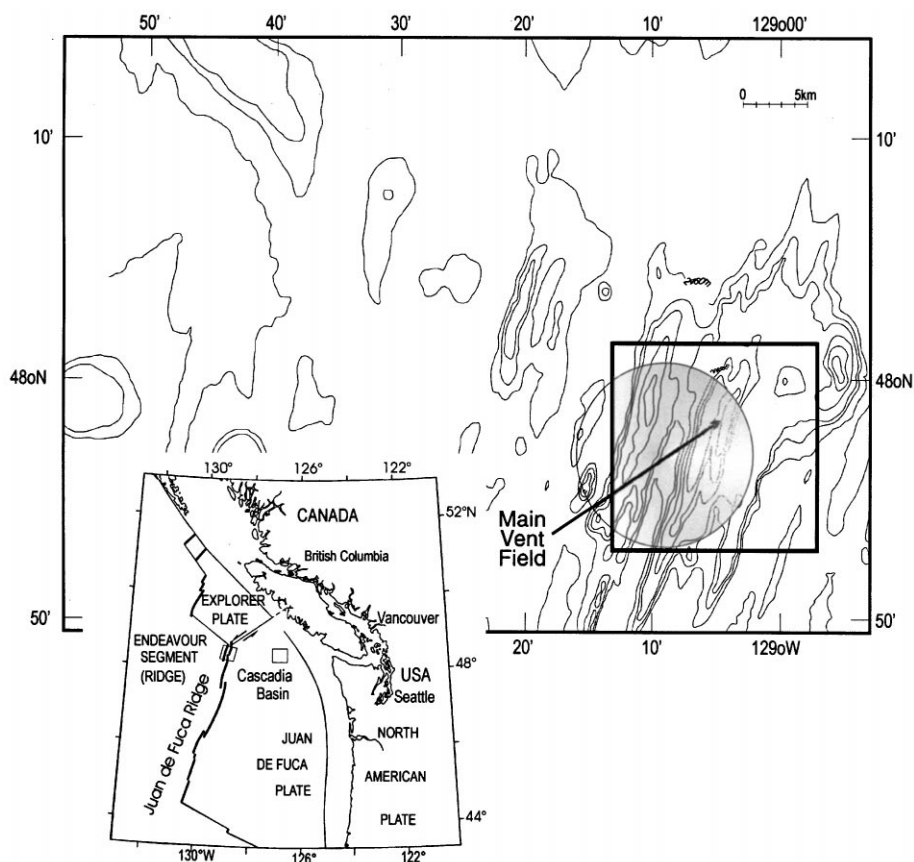


Fig. 1. Location of sampling regions in the northeast Pacific. The 10 km zone is shown around the main vent field at Endeavour Ridge, along with a shaded ellipse estimating the general extent and area of the particle plume (however, this varies depending on currents). The inset shows the location of Endeavour Ridge and the Cascadia Basin area 100 km to the east of the Endeavour Ridge zone. Tow locations are listed in Table 1.

with enhanced organic material and bacterial biomass (Baker et al., 1987; Cann and Strens, 1987; Cowen et al., 1986, 1990; Dymond and Roth, 1988; Karl and Knauer, 1984). Dissolved and particulate organic matter are rapidly recycled in the vicinity of the plume (Roth and Dymond, 1989), and bacteria-rich bottom material near the vent fields is entrained in the rising plume (Lupton et al., 1985). As a consequence, the Endeavour Ridge plume is a rich source of reduced inorganic and organic material for primary producers and consumers. Therefore, hydrothermal venting has the potential to affect productivity in the water column near actively venting orifices. This is supported by the finding that there is an increased upward particulate flux of organic material at vents compared with off-axis sites at Endeavour Ridge (Cowen et al., 2000).

Using a deep-towed sampling package including a 150 kHz acoustic Doppler current profiler (ADCP) and multiple opening/closing trawl nets (Burd and Thomson, 1993, 1994), we discovered a deep scattering layer consisting of macro-zooplankton and micro-nekton situated at about 1900 m depth, just above the laterally spreading hydrothermal plume at Endeavour Ridge (Burd et al., 1992; Thomson et al., 1992a, b).

Inferential multivariate analyses of fauna from net samples taken in 1991 and 1992 revealed that the typical mesopelagic fauna normally located between about 400 and 800 m depth (Miller et al., 1984; Burd and Thomson, 1995), above the oxygen minimum layer in the northeast Pacific, are also the main organisms constituting the acoustic scattering layer observed at 1900 m depth above the hydrothermal plume at Endeavour Ridge (Burd and Thomson, 1994, 1995). This epiplume community is also sometimes found in transit between these two depth layers. The epiplume fauna are dominated by filter-feeding copepods and typical mesopelagic chaetognath, fish and gelatinous predators (Burd and Thomson, 1995). A simple migratory model showed that the mesopelagic fauna with a sustained swimming speed of 1 cm/s or greater could readily migrate from the mid-depth scattering layer (400 and 800 m depth) to the region just above the vent plume (1900 m depth) and back to the mid-depth layer without being advected from the 10 km zone around the venting region (Burd and Thomson, 1994). As extensive ontogenetic migrators, the major copepod species (*Neocalanus* spp.) and their associated predators are capable of travelling the vertical distances required. At the present time, it is not clear how and when they migrate or what cues cause them to migrate, but the patterns do not suggest diurnal movements. It is probable that the mesopelagic zooplankton are present at bathypelagic depths in order to feed upon the upward flux of vent-derived and bottom organic material, mucous aggregates and microorganisms entrained in the rising plume, or bacteria living in the plume (Cowen et al., 1990; Burd et al., 1992; Burd and Thomson, 1994, 1995). Isotopic analyses of the zooplankton at the vent plume area indicate that they consume a mixture of vent-derived and surface-derived particulate material (Burd and Thomson, in prep.).

In addition to the unusual distribution of mesopelagic fauna, total water column biomass of zooplankton in spring and early summer has been found to be two to three times higher over the main vent field than 15–50 km away (Burd and Thomson, 1994). This biomass enhancement occurred not only in the deep water due to the presence of mesopelagic fauna above the spreading plume, but also in the upper 800 m of the

water column in the immediate vicinity of the hydrothermal vents. Enhancement of shallow-water biomass appears to result from the transport of vent-derived organic material to surface waters in the vicinity of the ridge by (a) upwardly migrating zooplankton (Burd and Thomson, 1994) and (b) the upward flux of organic material shown to occur in the region of the vents (Cowen et al., 2000). Acoustic profiles in September do not show an obvious deep scattering layer, although an acoustic or zooplankton depletion (backscatter from zooplankton less than background levels) is evident within the toxic plume (Thomson et al., 1989, 1990, 1991), suggesting that deep biomass enhancement may be a seasonal phenomenon related to the spring reproductive bloom of mesopelagic zooplankton in the upper ocean.

3. Methods

In July of 1991–1994, bioacoustic tows were conducted in the vicinity of the hydrothermal vent fields at Endeavour Ridge and at sites 10–100 km off-axis (Table 1, Fig. 1). The towed body consisted of a rigid aluminum frame supporting a modified Tucker trawl with seven, 1.4 m² opening-and-closing, 0.33 mm mesh nets for sampling discrete depth intervals. The tow frame also supported a Guildline digital conductivity–temperature–depth (CTD) probe and a Sea Tech 25 cm path-length transmissometer. Acoustic backscatter, net orientation and flow volume relative to the towed body were measured with a downward-looking RD Instruments 150 kHz acoustic Doppler current profiler (ADCP). Net volumes were calculated with precision ($SD \pm 0.9$ –3% total volume) using attitude and current data from the ADCP (Burd and Thomson, 1993). Nets were triggered electronically to capture animals in the acoustic scattering layers observed in the real-time read-out from the ADCP. Normally, one net was open on descent, and six nets were opened progressively on the ascent. Processing of faunal samples is described in detail in Burd et al. (1992). Fauna were identified to species whenever possible, sized, sexed and dry-weighed. Each tow spanned the entire water column except for the bottom 100 m, which was considered to encompass the benthic boundary layer. Table 1 includes net sample numbers, abundance, biomass, depth ranges and locations. Nets were towed slowly (1–2 knots), so that we often captured jellyfish intact, or complete but broken into distinct pieces. Because of the difficulties sampling these animals, it is impossible from our data to quantify the abundance of jellyfish in the deep layers. However, sampling procedures were consistent throughout the four years, so that relative abundances are assumed to be comparable. Considerable variation in shallow water tow catches may reflect time of day or night. However, there was no overall pattern in faunal abundance in nets related to time of day (Fig. 2). Time of day was not considered a factor in faunal catches below 1000 m depth.

Siphonophore abundance was estimated by counting nectophores and dividing by the estimated size of the colony, which was based on taxonomic expertise (see acknowledgements). Methods of estimation were consistent for a given species for all samples. Biomass estimates, however, were based on weights of the sum of all nectophores found in each net.

Table 1
Sample summary values, depths and times. Samples marked with an asterisk * were considered off-vent(> 10 km from vent sites). Sample numbers include year (1991–1994) followed by tow number (1–7) and net number (1–6)

Net sample	Abundance No/m ³	Biomass mg/m ³	Max depth (m)	Min depth (m)	Start and end	
					Latitude	Longitude
9112	3.8	1.7	1888	1848	47°57.925	129°05.550
9113	1.5	0.9	1848	1796		
9114	4.4	1.7	1796	1706	48°02.127	129°03.630
9115	15.3	7.8	1706	704		
9116	50.2	29.3	704	455		
9117	67.6	50.0	455	0		
*9121	10.5	11.3	1900	0	48°05.975	129°58.037
*9122	15.2	7.0	1915	1900		
*9123	9.8	5.0	2025	1915	48°05.941	129°04.422
*9124	6.2	2.9	2200	2025		
*9125	12.8	5.6	2261	2200		
*9126	5.2	2.4	2078	2255		
9132	4.3	1.8	2036	1985	47°53.193	129°08.031
9133	66.3	65.7	1985	1787		
9134	2.5	2.5	1787	1730	48°01.51	129°03.56
9135	4.0	3.5	1730	700		
9136	52.5	55.0	693	470		
9137	19.3	20.8	470	0		
*9142	5.0	1.2	2323	2306	47°48.418	129°11.288
*9143	4.6	2.3	2306	1925		
*9144	7.3	3.3	1925	1875	47°54.454	129°07.309
*9145	8.3	6.0	1865	713		
*9146	16.7	14.7	713	560		
*9147	19.4	18.4	560	0		
*9212	6.6	2.9	2457	2450	48°11.51	129°49.96
*9213	3.6	0.8	2500	2369		
*9214	7.5	2.1	2369	1700	48°13.21	129°51.34
*9215	8.9	5.4	1700	901		
*9216	53.0	24.0	901	390		
*9217	94.8	18.9	390	0		
*9222	3.3	0.9	2607	2500	47°57.01	129°07.00
*9223	5.9	1.0	2500	2364		
*9224	9.1	1.4	2364	1700	48°04.11	129°03.85
*9225	4.8	2.7	1700	900		
*9226	50.6	25.3	900	390		
*9227	26.9	11.8	390	0		
9232	4.3	1.2	2015	1800	47°58.45	129°04.26
9233	10.7	3.8	1800	1600		
9234	8.7	7.7	1600	1398	48°00.30	129°02.76
9235	3.9	8.6	1398	800		
9236	106.5	47.0	800	398		
9237	74.2	17.4	398	0		
9242	27.9	6.7	1961	1907	48°07.90	129°52.66

Table 1 (continued)

Net sample	Abundance No/m ³	Biomass mg/m ³	Max depth (m)	Min depth (m)	Start and end	
					Latitude	Longitude
9243	16.0	4.3	1907	1796		
9244	17.8	4.8	1796	1730		
9245	29.3	15.7	1800	1700		
9246	17.3	11.5	1700	800		
9247	96.1	72.1	800	0	48°08.99	129°54.44
9252	5.9	4.8	2045	1977	47°58.88	129°04.42
9253	8.3	2.7	1977	1903		
9254	13.6	4.1	1903	1550		
9255	22.3	13.4	1550	1330		
9256	129.4	60.1	1330	798		
9257	67.5	35.4	798	0	48°56.37	129°06.21
9312	3.7	2.2	2000	2032	48°02.51	129°02.87
9313	3.9	1.7	1900	2016		
9314	2.9	1.5	1700	1900		
9315	11.4	10.8	1200	1700		
9316	11.6	7.3	800	1200		
9317	37.5	10.8	0	800	47°53.81	129°07.81
9322	10.0	3.9	2000	2036	48°02.48	129°03.02
9323	4.7	1.7	1900	2000		
9324	17.6	14.5	1675	1900		
9325	2.8	2.4	1200	1675		
9326	19.7	11.4	800	1200		
9327	48.4	26.4	0	800	47°50.39	129°05.88
*9412	1.9	1.8	2200	2540	48°00.229	128°20.713
*9413	3.7	1.8	1990	2200		
*9414	5.1	3.7	1700	1990		
*9415	4.8	4.1	787	1700		
*9416	11.3	10.8	400	787		
*9417	20.8	18.6	0	400	48°11.727	128°23.931
*9422	0.6	0.5	2200	2562	47°59.433	128°19.889
*9423	4.7	2.0	1998	2200		
*9424	17.5	12.5	1701	1998		
*9425	7.9	6.3	803	1701		
*9426	0.6	0.6	400	803		
*9427	28.6	14.5	0	400	48°02.216	128°22.241
9432	0.7	0.6	1888	2152	47°55.265	129°05.963
9433	26.2	11.3	1750	2000		
9434	5.2	1.9	1200	1751		
9435	3.5	3.9	800	1200		
9436	16.3	6.1	402	800		
9437	47.3	78.3	0	402	47°58.416	129°08.289
9442	11.2	6.2	2037	2111	47°56.886	129°06.552
9443	9.2	3.3	1799	2037		
9444	4.3	2.6	1200	1799		
9445	6.7	4.2	800	1200		

(continued on next page)

Table 1 (continued)

Net sample	Abundance No/m ³	Biomass mg/m ³	Max depth (m)	Min depth (m)	Start and end	
					Latitude	Longitude
9446	1.0	0.7	400	800		
9447	59.6	30.0	0	400	47°54.478	129°00.165
9462	5.6	2.4	1933	2120	47°57.708	129°06.531
9463	8.4	5.4	1801	1933		
9464	9.9	5.7	1602	1801		
9465	3.6	2.5	1204	1602		
9466	1.5	2.0	800	1204		
9467	40.5	23.7	0	822	47°51.010	129°09.923
9472	4.1	3.1	1940	2380	47°53.203	129°09.555
9473	47.0	28.6	1799	1940		
9474	6.2	4.2	1200	1799		
9475	9.6	4.9	796	1200		
9476	51.0	24.5	389	796		
9477	14.2	10.2	0	389	47°58.0	129°05.0

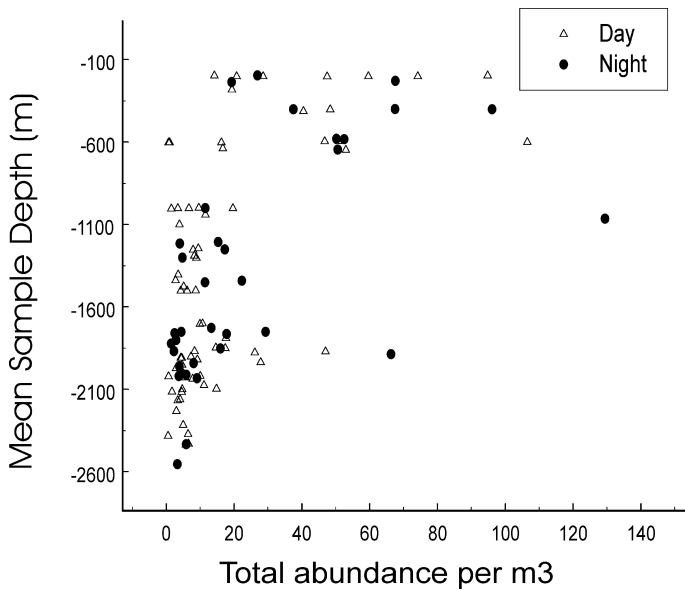


Fig. 2. Total faunal abundance (all zooplankton and micronekton) of nets towed by day (800–2000 h Pacific Daylight Time) and night for all samples.

For all years, off-vent samples were arbitrarily designated as those taken at greater than 10 km from the main vent field. Tow 914 was just at this boundary, and had water properties similar to those for tows taken nearer vents (Burd and Thomson, 1994).

4. Results

Fig. 3 provides examples of acoustic profiles and coincident light attenuation profiles for July 1993. Profiles were similar for July 1994. Examples of 1991 and 1992 profiles are given in Burd and Thomson (1994). In all years, distinct deep scattering layers were evident either just above the neutrally buoyant particle plume, or in a transit layer between the plume and 1200 m depth.

Approximately 30 medusae and 16 siphonophore taxa were identified from our samples over the 4 year survey (see Table 2). There were relatively few salps and ctenophores in the net samples. The surface-dwelling anthomedusa *Velevella velevella* were so thick in surface waters in some surveys that they filled nets and had to be discarded. In addition, *V. velevella* were sometimes found contaminating deeper nets when there was a surface bloom. For these reasons, *V. velevella* were not included in estimates of jellyfish abundance.

Fig. 4 shows that relative abundance and biomass (percent of total fauna) contributed by medusae (see Table 2) were sometimes considerably elevated in deep water

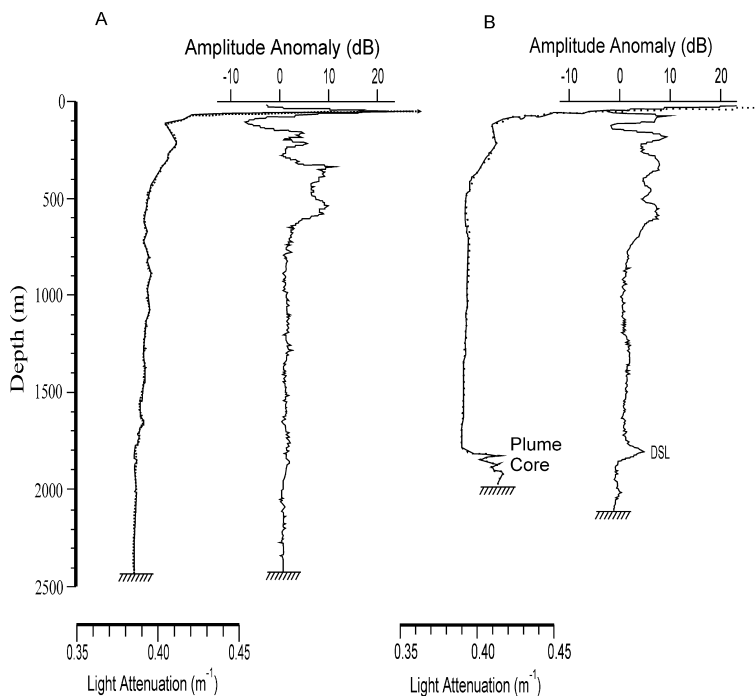


Fig. 3. (a) Off-vent acoustic and light attenuation profiles for Cascadia Basin 100 km to the east of Endeavour Ridge in July 1993; and (b) Typical acoustic profile of the vent-related deep scattering layer at Endeavour Ridge vent field relative to the distribution of particles from the plume (light attenuation signal) for July 1993. In July of 1992, a migrating scattering layer was observed moving between 1200 m and 2000 m depth, and weak scattering layers composed of typical deep-sea fauna were noted at plume depth up to 50 km downstream from the main vent field (Burd and Thomson, 1994). No scattering layers have been found at depth outside the near-vent area.

Table 2

List of gelatinous taxa identified in net samples from 1991 to 1994

Phylum	Class	Order	Family	Species
Cnidaria	Hydrozoa	Anthomedusae	Calyropsidae	<i>Bythotiara</i> sp.
		Anthomedusae	Calyropsidae	<i>Calyropsidae</i> indet.
		Anthomedusae	Calyropsidae	<i>Calyropsis nematophora</i>
		Anthomedusae	Calyropsidae	<i>Sibogita geometrica</i>
		Anthomedusae	Corymorphidae	<i>Euphysa</i> sp.
		Anthomedusae	Rathkeidae	<i>Rathkea</i> sp.
		Anthomedusae	Veellidae	<i>Veella veella</i>
		Leptomedusae	Campanulariidae	<i>Phialidium</i> sp.
		Leptomedusae	Eirenidae	<i>Phialopsis</i> sp.
		Leptomedusae	Mitrocomidae	<i>Mitrocomidae</i> indet.
		Leptomedusae	Aequoridae	<i>Aequorea</i> sp.
		Hydromedusae		Hydromedusae indet.
		Limnomedusae		Limnomedusae indet.
		Narcomedusae	Aeginidae	<i>Aegina citrea</i>
		Narcomedusae	Aeginidae	<i>Aeginura grimaldii</i>
		Narcomedusae	Cuninidae	<i>Cunina</i> sp.
		Narcomedusae	Cuninidae	<i>Solmissus</i> sp.
		Narcomedusae	Cuninidae	<i>Solmundella bitentaculata</i>
		Siphonophora	Abylidae	<i>Abyla</i> sp.
		Siphonophora	Abylidae	<i>Bassia</i> sp.
		Siphonophora	Abylidae	<i>Ceratocymba</i> sp.
		Siphonophora	Agalmidae	<i>Agalma</i> sp.
		Siphonophora	Agalmidae	<i>Nanomia</i>
		Siphonophora	Diphyidae	<i>Dimoyphes</i> sp.
		Siphonophora	Diphyidae	<i>Diphyes</i> sp.
		Siphonophora	Diphyidae	<i>Lensia</i> sp.
		Siphonophora	Diphyidae	<i>Muggiaea</i>
		Siphonophora	Diphyinae	<i>Chelophyes</i> sp.
		Siphonophora	Hippopodiidae	<i>Vogtia</i> sp.
		Siphonophora	Hippopodiidae	<i>Vogtia serrata</i>
		Siphonophora	Nectopyramidinae	<i>Nectopyramis</i> sp.
		Siphonophora	Prayidae	<i>Praya</i> sp.
		Siphonophora	Pyrostephidae	<i>Bargmannia</i> sp.
		Siphonophora	Rhizophysidae	<i>Bathyphysa</i> sp.
		Trachymedusae	Rhopalonematidae	<i>Aglantha digitale</i>
		Trachymedusae	Rhopalonematidae	<i>Crossota rufobrunnea</i>
		Trachymedusae	Rhopalonematidae	<i>Halicreas minimum</i>
		Trachymedusae	Rhopalonematidae	<i>Haliscera conica</i>
		Trachymedusae	Rhopalonematidae	<i>Pantachogon</i> sp.
		Trachymedusae	Rhopalonematidae	Rhopalonematidae
		Trachymedusae	Rhopalonematidae	<i>Sminthea</i> sp.
		Trachymedusae		Trachymedusae indet.
				Medusa indet.
				Medusa sp. J
Scyphozoa	Coronatae	Coronatae	Atollidae	<i>Atolla</i> sp.
		Coronatae	Atollidae	<i>Atolla wyvillei</i>
		Coronatae	Periphyllidae	<i>Periphylla periphylla</i>
		Coronatae	Periphyllidae	<i>Periphyllopsis galathea</i>

Table 2 (continued)

Phylum	Class	Order	Family	Species
Other		Semaestomae	Pelagiidae	<i>Pelagia</i> sp.
		Semaestomae	Ulmaridae	<i>Stygiomedusa gigantea</i>
		Semaestomae		<i>Semaestomae</i> indet.
Ctenophora		Cydidippida	Pleurobrachiidae	<i>Hormiphora cucumis</i> (<i>ctenophore</i>)
Chordata – subph. Tunicata	Thaliacea	Salpida		<i>Iasis zonaria</i>

(mean depth 600–2000 m) over the Endeavour Ridge vent field compared with off-vent samples. A simple ANOVA comparing vent and off-axis percentages of total fauna contributed by medusae shows that the differences were significant for biomass but not for abundance (Table 3). Following are relative abundance or biomass versus depth distributions for several dominant medusae taxa.

Trachymedusae of the family Rhopalonematidae were the most common jellyfish. *Aglantha digitale* was visibly abundant in surface waters throughout the study area during several of the surveys and was collected in high numbers in some upper ocean nets. *Aglantha digitale* accounted for up to 4% of total faunal abundance (Fig. 5a) and 6% of total faunal biomass and dominated medusa abundance and total biomass (up to 40%) in the upper 600 m. The ecology of this species suggests that it is found in the northeast Pacific from the surface (Zelickmann, 1972; Arai and Fulton, 1973) in tight depth bands to depths of at least 700 m (Arai and Brinkman Voss, 1980; Mackie and Mills, 1983; Mackie, 1985; Arai et al., 1993) and has sometimes been found at depths > 1000 m (Angel and Baker, 1982). We found *A. digitale* to depths over 2000 m. The distribution patterns for this species suggest there may be increased relative abundance around the vent region, but the data are not clear. We suspect that even closed nets might sometimes be contaminated as they pass through dense layers of *A. digitale* in the near-surface waters. Depth distributions of another common trachymedusa, *Halicreas minimum* (Fig. 5b), clearly show higher percent abundance in both shallow and deep-water samples over vent fields than at off-axis sites. Other Trachymedusae of the family Rhopalonematidae (including *Pantachogon* sp., *Crossota rufobrunnea*, and unidentified specimens) were collectively higher in relative abundance over the vents between 1200 and 1800 m depth than off-vent in the same depth range (Fig. 5c).

Although few in number, the large size of the giant red scyphomedusa *Stygiomedusa gigantea* (about 30 cm diameter) meant that each animal contributed considerable biomass to a given sample (Fig. 6). Because these medusae lack tentacles, it is not clear how or what they eat (cf. Harbison et al., 1973; Larson, 1986). One or more of these 30 cm diameter jellyfish were caught either partially or intact in many deep nets (400 m or deeper) at the Endeavour Ridge vent field between 1991 and 1994.

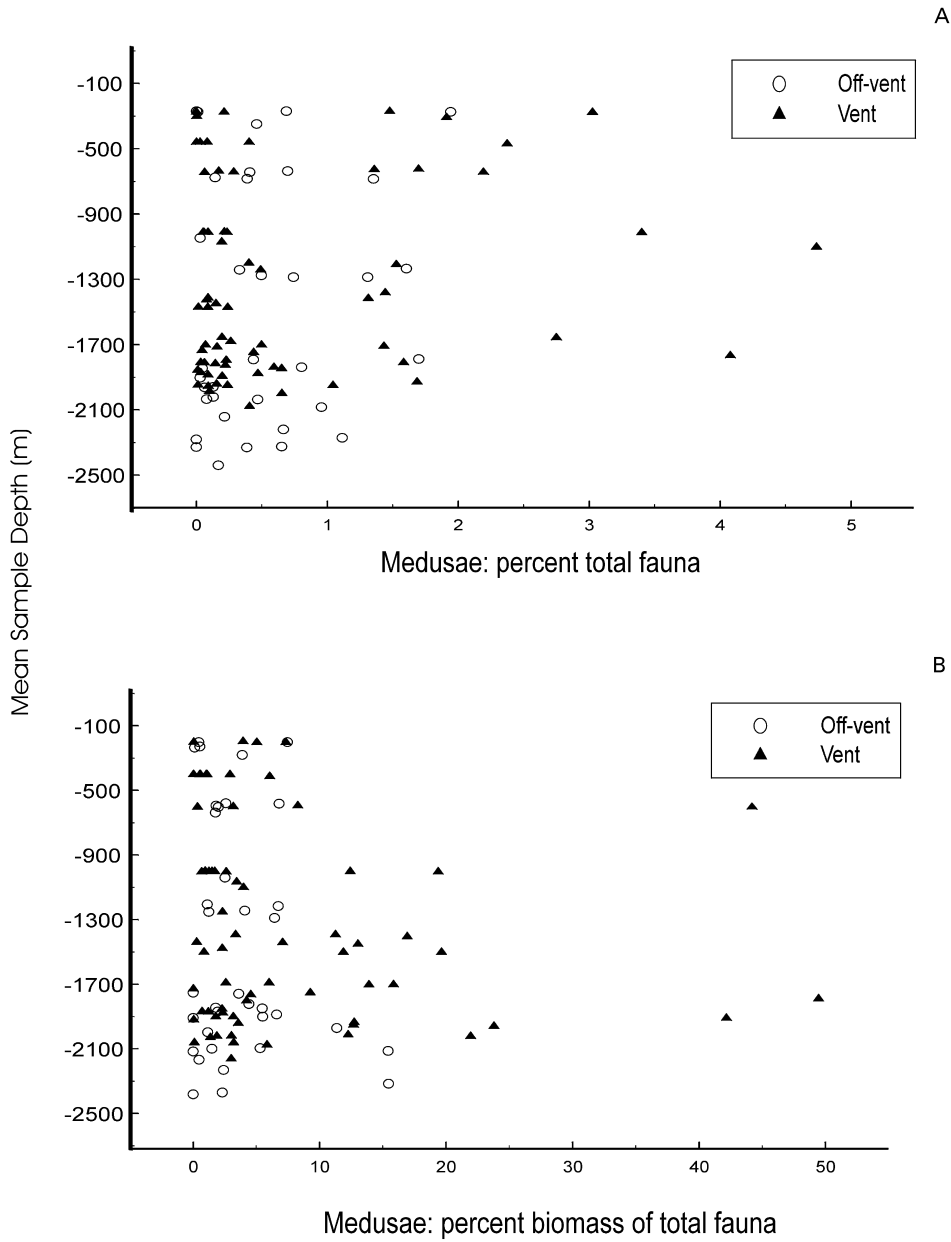


Fig. 4. (a) Relative abundance (percent of total fauna) versus depth contributed by medusae for off-vent and vent samples, and (b) Relative biomass (percent total fauna) versus depth contributed by medusae for off-vent and vent samples.

Table 3

Anova results for comparison of vent and off-vent biological factors

Dependent variable	TSS	RSS	S.E.	F	p (F)
Medusae biomass	7657.0	9347.0	8.6	4.2	0.04
Medusae abundance	80.6	79.6	0.9	1.3	0.26
Medusae abundance – <i>A. digitale</i>	10.4	10.2	0.3	2.0	0.16
Siphonophore biomass	289.5	289.0	1.7	0.2	0.68
Fish biomass	3957.2	3943.5	6.7	0.3	0.58
Chaetognath biomass	8175.9	8175.3	9.6	0.01	0.94

In addition, when recovered the towed equipment package was often covered in pieces of *S. gigantea* for tows in which they were found in nets. Only one off-axis net had a specimen; this sample was located about 10 km south of the main vent field and was the “off-vent” tow closest to the vent field (tow 914). Acoustic profiles at this location showed a substantial deep scattering layer even at this distance from the main vent field (see Burd and Thomson, 1994).

A single specimen of *Periphyllopsis galatheae* (Kramp, 1959) was recovered intact below 1000 m at the Endeavour Ridge vent field. The specimen was 30 cm diameter, deep red, and reasonably rigid. It is rare, and single specimens are known to have been collected twice originally off Mombassa, East Africa and again off Hawaii in May 1993 (C. Mills, Friday Harbor Marine Laboratory, pers. comm.).

Siphonophore relative biomass values (Fig. 7) were not significantly different on and off-axis (Table 3). However, the distribution suggests that relative biomass was higher in some deep samples near vents, with the exception of one very deep off-axis sample, which had one (1) nectophore each of *Praya* sp. and *Muggieae* sp. and very few other specimens in the net. This resulted in a high relative siphonophore biomass for that one sample. Relative biomass of fish and chaetognaths were also not significantly different with depth on and off-axis (Table 3).

5. Discussion

Despite problems with underestimation of gelatinous animals using towed nets, it is evident that these animals are important throughout the water column, particularly in higher latitudes (Angel and Baker, 1982). In the present study, medusae composed up to 24% of the total faunal biomass on a dry weight basis near the Endeavour Ridge vent fields. Based on wet weight, this percentage would be much higher. For example, Angel and Baker (1982) estimated that the contribution to live biomass of micronekton (based on displacement volume) from medusae in the northeast Atlantic was as high as 70%.

Assuming that the sampling bias of our net system was consistent from year to year, we conclude that medusae percent biomass and abundance were greater in the region

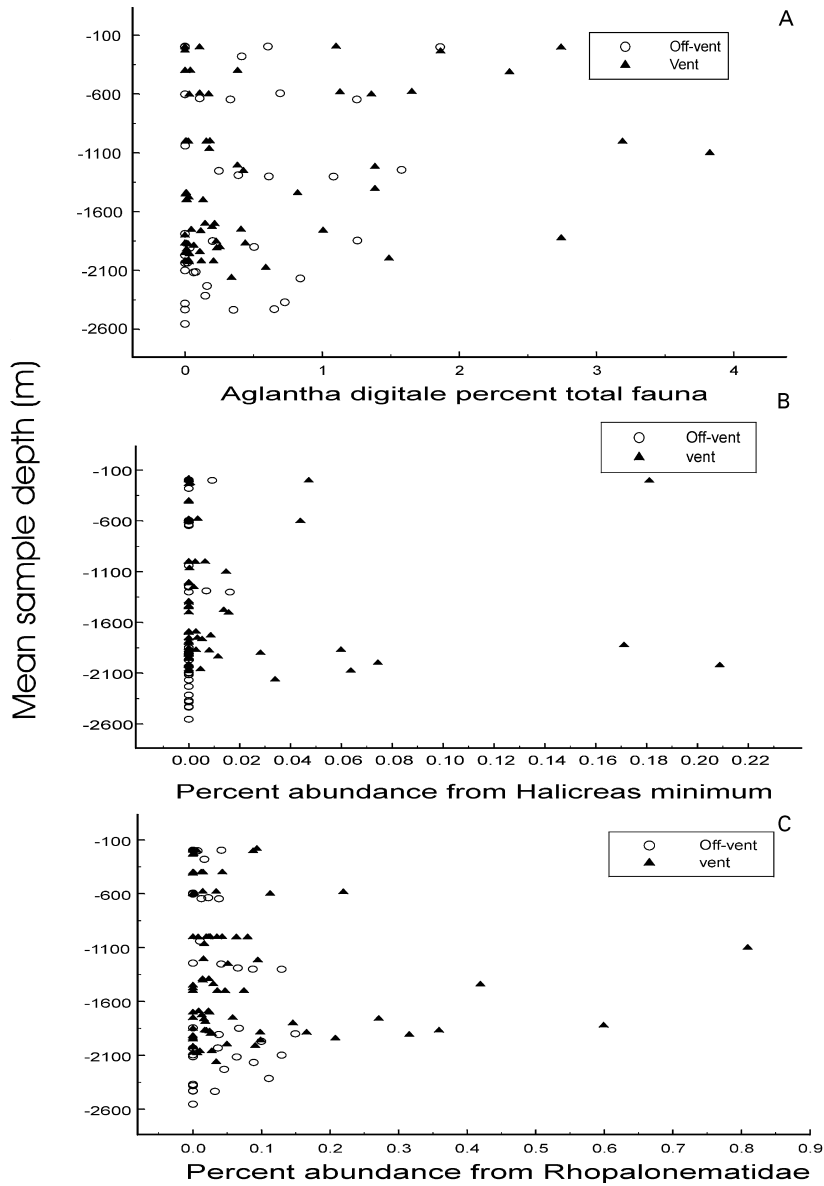


Fig. 5. (a) Relative abundance of *Aglantha digitale* (family Rhopalonematidae — percent of total fauna) related to depth for off-vent and vent samples, (b) Relative abundance versus depth contributed by the medusa *Halicreas minimum* (family Rhopalonematidae — percent of total fauna) for off-vent and vent samples, and (c) Relative abundance (percent of total fauna) versus depth contributed by the the remaining Rhopalonematidae for off-vent and vent samples.

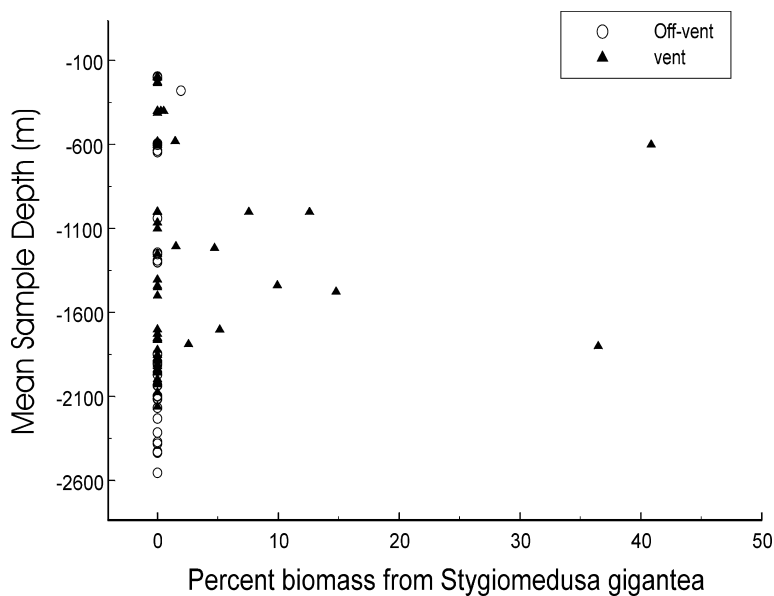


Fig. 6. Relative biomass (percent of total fauna) versus depth contributed by the medusa *Stygiomedusa gigantea* (family Semaestomae) for off-vent and vent samples. Note that the only specimen found in off-vent samples was in tow 914, about 10 km south of the main vent field.

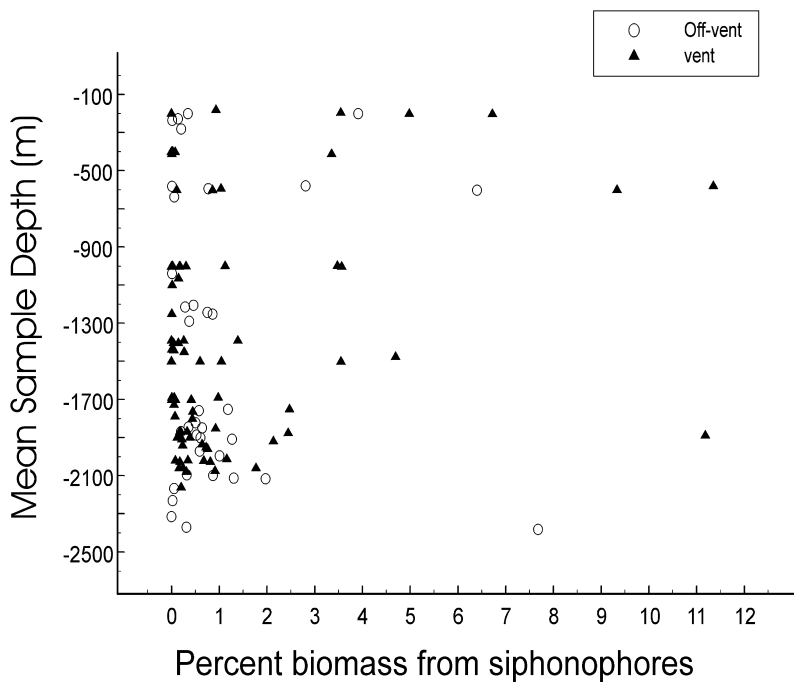


Fig. 7. Relative biomass contributed by siphonophores for off-vent and vent samples.

of deep-water (> 1000 m depth) scattering layers at the Endeavour vent field than in the surrounding northeast Pacific, where deep zooplankton scattering layers were not present and total standing stock was lower.

The enhanced relative importance of medusae observed below 1000 m depth in close proximity to the Endeavour Ridge vents suggests that predaceous medusae are associated with the deep zooplankton aggregations unique to the venting region (Burd and Thomson, 1994; Burd et al., 1992; Thomson et al., 1992a). The deep zooplankton scattering layers are composed mainly of copepods, chaetognaths, small shrimp and fish, which are typically the diet of carnivorous jellyfish (Arai, 1988; Arai et al., 1993) and are presumably the only concentrated source of food available to carnivores in these depth ranges.

Biomass enhancement of medusae was more evident than abundance enhancement, suggesting that the medusae at the vent region were generally larger taxa than those captured off-vent. In particular, the presence of two very large species (*Stygiomedusa*, *Periphylliopsis*) in the venting region (but not at the off-axis sites) is indicative of an increase in relative jelly biomass and size compared with the surrounding area. The common occurrence of *Stygiomedusae gigantea* in deep nets around the venting region, and the presence of gelatinous debris on the instrument package suggests that swarms of these medusae may be present. Schyphomedusae swarms have been noted off the west coast of North America and other locations (for review see Arai, 1988). Large *Stygiomedusa gigantea* also have been identified at 1200 m depth in the San Clemente basin off California (March, 1995; C. Mills, pers. comm.; Thuesen and Childress, 1994). These jellyfish are undoubtedly present elsewhere in the northeast Pacific, but in seemingly lower numbers, such that our off-vent net samples did not encounter them.

Siphonophores, which are generally considered to be more limited to the epi- and meso-pelagic water column in the open ocean (Angel and Baker, 1982) and can make up some proportion of deep micronekton, were found to be important in the upper ocean throughout the current study area. There was an observable increase in relative biomass of siphonophores in some deep vent samples compared with off-axis samples. However, the difference was not significant in the ANOVA analysis. Therefore, it is not entirely clear whether siphonophores were enhanced in relative proportion at vent areas.

Salps and ctenophores were rare in net samples, partly because of the fragility of these organisms (cf. Laval et al., 1989) and also because of the relatively short time periods they tend to be abundant. Net surveys taken earlier in the year (in June) in 1995 (Burd and Thomson, unpub. data) suggest that salps were much more abundant than in the July samples described in this paper.

The lack of a concurrent increase in relative importance of non-gelatinous predaceous taxa (fish and chaetognaths) in the deep, enhanced biomass region around the vent field suggests that other predators do not respond as opportunistically to the local, seasonal enrichment at Endeavour Ridge as medusae do. This supports the contention by Mills (1995) and Parsons (1979) that predaceous medusae are poised to take advantage of ecological opportunities which other taxa cannot.

Acknowledgements

We thank the crew of the CFAV *Endeavour*, personnel at the Institute of Ocean Sciences, Sidney, BC, for technical assistance, and Val MacDonald of Victoria, BC, for taxonomic expertise. We also thank Claudia Mills, Friday Harbour Marine Laboratory, for her taxonomic expertise and invaluable ecological knowledge about jellyfish.

References

- Angel, M.V., Baker, A. de C., 1982. Vertical distribution of the standing crop of plankton and micronekton at three stations in the northeast Atlantic. *Biological Oceanography* 2, 1–30.
- Arai, M.N., Brinkmann-Voss, A., 1980. Hydromedusae of British Columbia and Puget Sound. *Canadian Bulletin Fisheries and Aquatic Science* 204, 192.
- Arai, M.N., Fulton, J., 1973. Diel migration and breeding cycle of *Aglantha digitale* from two locations in the northeastern Pacific. *Journal of the Fisheries Research Board Canada* 30, 551–553.
- Arai, M.N., 1988. Interactions of fish and pelagic coelenterates. *Canadian Journal of Zoology* 66, 1913–1927.
- Arai, M.N., McFarlane, G.A., Saunders, M.W., Mapston, G.M., 1993. Spring abundance of medusae, ctenophores and siphonophores off southwest Vancouver Island: possible competition or predation on saffish larvae. *Canadian Technical Report on Fisheries and Aquatic Sciences* 1939, 37.
- Baker, E.T., Massoth, G.J., Feely, R.A., 1987. Cataclysmic hydrothermal venting on the Juan de Fuca Ridge. *Nature* 329, 149–151.
- Burd, B.J., Thomson, R.E., 1993. Flow volume calculations based on three-dimensional current and net orientation data. *Deep-Sea Research (I)* 40, 1141–1153.
- Burd, B.J., Thomson, R.E., 1994. Hydrothermal venting at Endeavour Ridge, effect on zooplankton biomass throughout the water column. *Deep-Sea Research* 41, 1407–1423.
- Burd, B.J., Thomson, R.E., 1995. Distribution of zooplankton associated with the Endeavour Ridge hydrothermal plume. *Journal of Plankton Research* 17, 965–997.
- Burd, B.J., Thomson, R.E., Jamieson, G.S., 1992. Composition of a deep scattering layer overlying a mid-ocean ridge hydrothermal plume. *Marine Biology* 113, 517–526.
- Cann, J., Strens, R., 1987. Venting events in hot water. *Nature* 329, 104.
- Cowen, J.P., Massoth, G.J., Baker, E.T., 1986. Bacterial scavenging of Mn and Fe in a mid- to far-field hydrothermal particle plume. *Nature* 322, 169–171.
- Cowen, J.P., Massoth, G.J., Feely, R.A., 1990. Scavenging rates of dissolved manganese in a hydrothermal vent plume. *Deep-Sea Research* 17, 1619–1637.
- Cowen, J.P., Bertram, M.A., Wakeham, S., Thomson, R.E., Lavelle, J.W., Baker, E.T., Feely, R.A., Burd, B.J., 2000. Ascending and descending particle flux from hydrothermal plumes at Endeavour segment, Juan de Fuca ridge. *Deep-Sea Research*, submitted for publication.
- Dymond, J.S., Roth, S., 1988. Plume dispersed hydrothermal particles: a time-series record of settling flux from the Endeavour Ridge using moored sensors. *Geochimica et Cosmochimica Acta* 52, 2525–2536.
- Feely, R.A., Geiselman, T.L., Baker, E.T., Massoth, G.J., 1990. Distribution and composition of hydrothermal plume particles from the ASHES vent field at Axial volcano, Juan de Fuca Ridge. *Journal of Geophysical Research* 95, 12855–12873.
- Feely, R.A., Massoth, G.J., Baker, E.T., Geiselman, T.L., 1992. Tracking the dispersal of hydrothermal plumes over the Juan de Fuca ridge using suspended matter compositions. *Journal of Geophysical Research* 97, 3457–3468.
- Greve, W., Parsons, T.R., 1977. Photosynthesis and fish production: hypothetical effects of climatic change and pollution. *Helgolander Wissenschaftliche Meeresuntersuchungen* 30, 666–672.
- Hamner, W.M., Madin, L.P., Alldredge, A.L., Gilmer, R.W., Hamner, P.P., 1975. Underwater observations of gelatinous zooplankton: sampling problems, feeding biology and behaviour. *Limnology and Oceanography* 20, 907–917.

- Harbison, G.R., Smith Jr., K.L., Backus, R.H., 1973. Stygiomedusa fabulosa from the north Atlantic: its taxonomy, with a note on its natural history. *Journal of Marine Biology Association* 53, 615–617.
- Karl, D.M., Knauer, G.A., 1984. Vertical distribution, transport, and exchange of carbon in the north-east Pacific Ocean: evidence for multiple zones of biological activity. *Deep-Sea Research* 31, 221–243.
- Larson, R.J., 1986. Pelagic scyphomedusae (Scyphozoa: coronatae and Semaestomeae) of the southern ocean. In: Kornicker, L.S. (Ed.), *Biology of the Antarctic Seas XVI Antarctic Research Series*, Vol. 41. American Geophysical Union, Washington, DC, pp. 59–166.
- Laval, J., Braconnot, C., Carre, C., Goy, J., Morand, P., Mills, C.E., 1989. Small-scale distribution of macroplankton and micronekton in the Ligurian Sea (Mediterranean Sea) as observed from the manned submersible *Cyana*. *Journal of Plankton Research* 11, 665–685.
- Longhurst, A.R., 1985. The structure and evolution of plankton communities. *Progress in Oceanography* 15, 1–35.
- Lupton, J.E., Delaney, J.R., Johnson, H.P., Tivey, M.K., 1985. Entrainment and vertical transport of deep-ocean water by buoyant hydrothermal plumes. *Nature* 316, 621–623.
- Mackie, G.O., 1985. Midwater macroplankton of British Columbia studies by submersible PISCES IV. *Journal of Plankton Research* 7, 753–777.
- Mackie, G.O., Mills, C.E., 1983. Use of the Pisces IV submersible for zooplankton studies in coastal waters of British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 40, 763–776.
- Miller, C.B., Frost, B.W., Batchelder, H.P., Clemons, M.J., Conway, R.E., 1984. Life histories of large, grazing copepods in the subarctic ocean gyre: *Neocalanus plumchrus*, *Neocalanus cristatus*, and *Eucalanus bungii* in the northeast Pacific. *Progress in Oceanography* 13, 201–243.
- Mills, C.E., 1995. Medusae, siphonophores and ctenophores as planktivorous predators in changing global ecosystems. *ICES Journal of Marine Science* 52, 575–581.
- Moeller, H., 1979. Jellyfish are also strongly fishing. *Fischcherblatt* 27 (9), 249–253.
- Moeller, H., 1980. Scyphomedusae as predators and food competitors of larval fish. *Meerestechnik Report on Marine Research* 28, 90–100.
- Moeller, H. 1984. Data on the biology of jellyfish and youngfish in Kiel Bight. Kiel FRG – Verlag, London, 182pp.
- Parsons, T.R., 1979. Some ecological, experimental and evolutionary aspects of the upwelling ecosystem. *South African Journal of Science* 75, 536–540.
- Roth, S.E., Dymond, J., 1989. Transport and settling of organic material in a deep-sea hydrothermal plume: evidence from particle flux measurements. *Deep-Sea Research* 36, 1237–1254.
- Shushkina, E.A., Musayeva, E.I., 1983. The role of jellyfish in the energy system of Black Sea plankton communities. *Oceanology Academy of Science USSR* 23, 92–96.
- Theusen, E.V., Childress, J.J., 1994. Oxygen consumption rates and metabolic enzyme activities of oceanic California medusae in relation to body size and habitat depth. *Biological Bulletin* 187, 84–98.
- Thomson, R.E., Burd, B.J., Dolling, A.G., Gordon, R.L., Jamieson, G.S., 1992a. The deep scattering layer associated with the Endeavour Ridge hydrothermal plume. *Deep-Sea Research* 39, 55–73.
- Thomson, R.E., Delaney, J.R., McDuff, R.E., Janechy, D.R., McClain, J.S., 1992b. Physical characteristics of the Endeavour Ridge hydrothermal plume during July 1988. *Earth and Planetary Science Letters* 111, 141–154.
- Thomson, R.E., Gordon, R.L., Dymond, J., 1989. Acoustic Doppler Current Profiler observations of a mid-ocean ridge hydrothermal plume. *Journal of Geophysical Research* 94, 4709–4720.
- Thomson, R.E., Gordon, R.L., Gast, J.A., 1990. Reply to comment on “Acoustic Doppler Current Profiler observations of a mid-ocean ridge plume” by D.R. Palmer P.A. Rona. *Journal of Geophysical Research* 95, 5413–5415.
- Thomson, R.E., Gordon, R.L., Dolling, A.G., 1991. An intense acoustic back-scattering layer at the top of a mid-ocean ridge hydrothermal plume. *Journal of Geophysical Research* 96, 4839–4844.
- Vereshchaka, A.L., Vinogradov, G.M., 1999. Visual observations of the vertical distribution of plankton throughout the water column above the Broken Spur vent field Mid-Atlantic Ridge. *Deep-Sea Research* I 46, 1615–1632.

- Vinogradov, M.Ye., Shushkina, E.A., 1982. Estimate of the concentration of Black Sea jellyfish, ctenophores and Calanus, based on observations from the Argus submersible. *Oceanology Academy of Science USSR* 22, 351–355.
- Vinogradov, M.Ye., Shushkina, E.A., Lebedeva, L.P., Gagarin, V.I., 1994. Mesoplankton in the eastern Kara Sea and in estuaries of the Ob and Yenisey Rivers. *Oceanology (English Translation)* 34, 716–723.
- Zelickman, E.A., 1972. Distribution and ecology of the pelagic hydromedusae, siphonophores and ctenophores of the Barents Sea based on perennial plankton collections. *Marine Biology* 17, 256–264.