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PART I

Observations on depth distribution, diversity and abundance of pelagic nemerteans from the Pacific Ocean off California and Hawaii

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Abstract

Meso- and bathypelagic nemerteans were collected during five cruises west of Pt. Conception, California, and one west of Oahu, Hawaii, from depths of 0–3800 m, using a 10 m^2 Tucker Trawl modified with a thermally protected closing cod end, as well as MOCNESS-10 and MOCNESS-1D trawls. In this study, about 53 putative species were collected off California and about 23 off Hawaii, with little taxonomic overlap between the two groups, as compared to 16 and 0 species previously known from these regions. Numbers of nemertean individuals and species were greatest between 625 and 1750 m off California, and 1300–2500 m off Hawaii. Abundance of nemerteans off California was about 10 times that off Hawaii. The Shannon–Wiener diversity index (H') was higher for Hawaii than for California due to numerical dominance by two species, *Phallonemertes* cf *murrayi* and *Nectonemertes* cf *mirabilis*, off California and a more even species distribution off Hawaii. Neither of the two dominant California species showed evidence of nocturnal vertical migration to shallow water. This is the first report of a *Phallonemertes* species from the Pacific and the first report of pelagic nemerteans from waters off Hawaii. © 1999 Elsevier Science Ltd. All rights reserved.

Keywords: Nemerteans; Pelagic; Abundances; Depth distribution; Diversity

1. Introduction

Pelagic nemerteans are commonly sampled permanent residents of the meso- and bathypelagic fauna, but their biology and systematics are poorly understood.

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Although deep-sea biologists have recognized that pelagic nemerteans can attain great abundance (e.g. J. Childress, University of California, Santa Barbara, California, personal communication), these potentially significant predators usually have been ignored because their taxonomy is so difficult.

To date, about 98 species of polystiliferous pelagic nemerteans, most from deep-sea areas, have been described. Coe (1946, 1954a, b) suggested that pelagic nemerteans are transported long distances by deep currents and that species should therefore have wide distributions. However, few pelagic nemertean species are known to have wide distributions; only 23 species have been recorded as occurring in more than one oceanic region, and 14 are recorded as occurring in more than one ocean (calculated from Gibson, 1982, 1995). Fifty-four species are known from the entire Pacific Ocean, 48 from the Atlantic Ocean, and 11 from the Indian Ocean. Of the 54 Pacific species, 39 are known from the North Pacific, 15 from the tropical Pacific and 10 from the far South Pacific (primarily the Antarctic Pacific) (calculated from Gibson, 1982, 1995). Sixteen species are known from California waters (Coe, 1954a) and none from Hawaii. Ten of the California species described by Coe (1954a) have not been recorded from elsewhere. The Western North Pacific (especially the Bering Sea, Sea of Okhotsk and near Japan), with 22 species, and the Eastern North Pacific (Gulf of Alaska to the equator), with 27 species, share only five species (calculated from Coe, 1954a and Gibson, 1982). Of the North Pacific species, nine are known from the tropical Pacific, two from the South Pacific and seven from the Atlantic (calculated from Gibson, 1982, 1995). However, many of the known species are based on single specimens or single collection lots. Two monostiliferan pelagic species have been described (Crandall and Gibson, 1998) and a third was encountered in this study (Norenburg and Roe, 1998), but here we address only polystiliferan pelagic nemerteans.

In this study, living specimens in unusually good condition were obtained by means of a Tucker Trawl modified with a 30 l thermally insulated closing cod end (Childress et al., 1978) usually towed at less than 1.5 knots. We are using these collections to re-examine morphology, taxonomy and systematics in this group, which previously was known only through poorly preserved specimens. Specifically, for the California collection we analyzed depth distribution of individuals and of species, temperature and salinity parameters at collecting depths of nemertean presence, effects of collecting with three net types, vertical migration, and relative nemertean size with increasing depth. For the collection off Hawaii we analyzed depth distribution of individuals and of species, and temperature parameters at collecting depths. Diversity and abundances of pelagic nemerteans from off California and Hawaii were compared.

2. Materials, methods and data

2.1. Specimen collection

Collections were made during five oceanographic cruises west of California in September 1992 and 1993, March 1993, February and June 1994 and one cruise west of Hawaii in April–May 1993. Collections off California were taken along a transect covering an area approximately 81 km north–south by 53 km east-west, north of Point Conception, parallel to the coastline and about 160 km off shore between latitudes 34°32.6′N and 35°16.4′N and longitudes 122°34.4′W and 123°08.85′W. Because of rough seas, tows during the last four days of the September 1992 cruise were taken closer to shore, extending the usual eastern limits to 121°45.81′W. Rough seas in June 1994 made sampling from the transect area possible for only three tows. Collections off Hawaii were taken along a transect about 16 km north–south between latitudes 21°14.66′N and 21°63.0′N by about 84 km east–west between longitudes 158°10.48′W and 158°58.73′W, approximately 13 km west of Waianae, Oahu. On all cruises, depths sampled ranged from 0 m (surface) to approximately 3800 m; tows were made for various lengths of time and during day and night periods. Individual tows extended through various depth ranges and covered only a small distance within the transect areas. Table 1 provides specific reference data for each cruise.

Three types of nets were used for mid-water trawls. On all cruises but one (September 1993), a modified Tucker Trawl, the Mother Tucker Trawl (MTT) was used, with 10 m^2 opening, 6 mm mesh, and 30 l thermally insulated closing cod end (Childress et al., 1978). A time-depth recorder used with many of these tows provided measurements of depth fished. For tows where measured quantitative data were not available, volume of water filtered was estimated from amount of time the net was open at depth, speed of towing and size of the net mouth. Speed of towing was the least accurate variable in this estimate, since differences between towing speed recorded on shipboard and actual net speed at depth can occur because of local currents and other water conditions. The MTT was towed mostly at speeds of 1–1.5 kt (average speed, California = 1.26 kt, Hawaii = 1.38 kt), and usually it was pulled horizontally when open, so that it fished at a single depth. However, in February 1994, oblique tows from deeper to shallower depths were made in order to fish depth intervals of 500, 250 and 125 m. For the September 1993 cruise, two types of MOCNESS (Multiple Opening/Closing Net and Environmental Sensing System, see Wiebe et al., 1985) were used (Table 1). The MOCNESS is equipped with electronic instrumentation for recording temperature, salinity, depth fished and volume of water filtered through the net. We used a MOCNESS-10 (10 m^2 opening, with six individual nets, each 3 mm mesh) and a MOCNESS-1D (1 m^2 opening, with ten pairs of nets, each 0.505 mm mesh). Each MOCNESS net or pair of nets was spaced to fish a given, different depth interval, from deeper to shallower, and each opened and closed independently of the other nets, resulting in six (MOCNESS-10) or ten pairs (MOCNESS-1D) of independent samples per MOCNESS tow. Thus, there were 66 individual (MOCNESS-10) or 100 pairs (MOCNESS-1D) of potentially available depth-interval samples for September 1993, of which 43 and 61, respectively, were used for quantitative data (Table 1). Only one of each pair of MOCNESS-1D samples was sorted quantitatively. Readily observed nemerteans were removed from the other sample, referred to hereafter as the qualitatively sorted sample, and the remainder of that sample was preserved in bulk for use by other researchers. To prevent the nets from becoming tangled, the MOCNESS usually was towed faster than the MTT (J. Childress, University of California, Santa Barbara, California, personal communication); average towing speed during September 1993

Table 1
Reference data for University-National Oceanographic Laboratory System Cruises included in this study. "Tows" = number tows/number quantitative tows (for MOCNESS = number of depth intervals sampled quantitatively – see methods text)

Date	Ship name	Cruise	Site	Latitude extremes	Longitude extremes	Trawl type	Tows
Sept 9–19, 1992[a]	*R.V. Point Sur*	92–29	CA	35°04.14′N 34°32.58′N	123°08.85′W 122°43.23′W	MTT	35/25
March 8–17, 1993	*R.V. New Horizon*	Calm Seas	CA	35°10.17′N 34°40.39′N	123°07.56′W 122°37.77′W	MTT	47/46
Sept 10–19, 1993	*R.V. New Horizon*	93–15	CA	35°16.4′N 34°38.1′N	123°08.0′W 122°43.1′W	MOCNESS-10 MOCNESS-1D	11/43 10/61
Feb 13–24, 1994	*R.V. New Horizon*	94–02	CA	35°13.62′N 34°38.25′N	123°06.24′W 122°39.32′W	MTT	24/12
June 11–22, 1994	*R.V. Point Sur*	94–19	CA	34°39.46′N 34°38.13′N	122°41.25′W 122°34.40′W	MTT	3/3
Apr 2–May 14, 1993	*R.V. New Horizon*	Calm Seas II	HI	21°63.0′N 21°14.66′N	158°58.73′W 158°10.48′W	MTT	94/87

[a] During the last four days of September 1992 cruise, towing extended east of usual limits, to 121°45.81′W.

was 2.2 kt (MOCNESS-10) and 1.94 kt (MOCNESS-1D). The depth intervals fished by the individual MOCNESS nets were similar to the oblique tows of the MTT in February 1994. Tows were considered to be non-quantitative, with either the MTT or MOCNESS, if time for fishing depth was not recorded, the net did not open, or the net or cod end did not close. Nemerteans collected in non-quantitative tows were included in analyses for which specific depth of collection or volume of water filtered during the tow were unimportant.

2.2. Data analysis

Specimen length and width, wet-weight (for specimens collected September, 1993 and February 1994) and sex were recorded, and specimens were preserved. Some specimens were photographed or videotaped prior to preservation. Taxonomic identification of pelagic nemerteans requires microscopic analysis of serial sections. In the present study, prior to histological examination, features visible in intact specimens were used to assign them to putative species (here specified by numerals). Characteristics used to differentiate species included: color of body, brain and proboscis; opacity/transparency; relative rhynchocoel length; number and branching pattern of intestinal diverticula; testis arrangement; presence/absence of caudal fin and its appearance; general body shape; large size differences between sexually mature individuals of otherwise similar appearance; presence of epidermal glandular patches and any unique features. In addition, all preserved specimens were compared to each other, to descriptions in the literature, and to specimens previously deposited at the

Smithsonian Institution. This process led us at first to combine several morphotypes as putative species, but subsequent preliminary histological study supported our original hypotheses of distinct species. The actual number of species is unlikely to differ from our estimate by more than a few species in either direction. Representatives of all putative species recognized in this study, at the conclusion of relevant taxonomic studies, will be deposited in the Smithsonian Institution's National Museum of Natural History, Washington, DC.

Because different numbers of tows, for different durations, were made at each depth with each type of net (MTT, MOCNESS-10 and MOCNESS-1D), tows were grouped by depth or depth interval by cruise; the volume of water filtered and number of worms from grouped samples were summed to get totals. To make samples reasonably comparable, the total number of worms per depth interval was divided by the total estimated volume of water filtered at those depths. These normalized quantities were used to compare nemertean abundance and species distribution by depth, net type, and region, and to test the hypothesis of vertical migration. For analysis of abundance of individuals per depth interval, all individuals collected from quantitative tows in September 1992 and 1993, April–May 1993 and February 1994 were included. Day–night depth distribution for each of the two most abundant species was evaluated by comparison of mean depths based on an analysis of variance of specimen density at each depth (SAS Institute Inc., Ver 6.12 for Windows). For number of species collected per depth interval, all individuals from quantitative tows from September 1992 and 1993, April–May 1993 and February 1994 studies were used, except a few unidentifiable specimens and specimens collected from the qualitative samples of the MOCNESS-1D. Collections from March 1993 were not included because tow data for each individual collected were not recorded. Sizes of *N.* cf *mirabilis* specimens collected by MOCNESS-10 and -1D were compared using the Mann–Whitney rank test (Minitab Inc., State Coll. Pennsylvania).

The Shannon–Wiener diversity index (H') (Rolan, 1973) was calculated and used as a measure of nemertean diversity. Calculations of diversity in California were based on all identifiable specimens collected from the California transect during all five California cruises, regardless of type of net used, depth, or other collection variable; likewise, all identifiable specimens from Hawaii were used. Since equal numbers of samples are required to compare H' of two areas (Cox, 1980), the September 1992 California cruise was chosen as most comparable to the single Hawaii cruise in trawl type, towing method and data recording (California: 131 identifiable specimens in 18 of 29 tows that could have contained nemerteans, i.e., the net opened; Hawaii: 43 identifiable specimens in 26 of 88 tows that could have contained nemerteans, i.e., 87 quantitative tows plus one non-quantitative tow in which two nemerteans were retrieved). Tows with worms were listed (1–18 or 1–26) in order of occurrence for each cruise. The two cruises were compared by using five ad hoc methods to equalize samples, as follows: (A) the 18 California tows with worms were matched with 18 Hawaii tows with worms that were selected by eliminating eight tows whose ordinal numbers first appeared in a random numbers list; (B) the 18 California tows with worms were matched with 18 randomly chosen tows from the 26 Hawaii tows with worms; (C) all 29 potential worm-containing California tows were matched with 29 randomly chosen tows from Hawaii's 88 potential worm-containing tows; (D) 10 tows with worms were chosen randomly for each site; and (E) all 43 specimens from Hawaii were matched with the first 43 specimens collected from California in September 1992.

Only MTT data were used to compare overall abundance of pelagic nemerteans between California and Hawaii. Three methods were used: (A) the average number of specimens/tow, i.e., dividing the respective total number of specimens by the total number of quantitative tows for Hawaii and the four MTT California cruises (Table 1); (B) the average number of specimens/tow in quantitative and non-quantitative tows (excluding those in which the net did not open and the March 1993 California cruise, which lacked data for number of worms/tow); (C) the average number of worms/10^5 m^3 water, for all depth intervals sampled (below 400 m for Hawaii or 350 m for California, with September 1992 and February 1994 combined).

3. Results

Based on comparative morphological observations, we were able to discern 53 putative species from California waters and 23 from Hawaii among the specimens deemed identifiable (425 of 463 collected off California and 43 of 44 collected off Hawaii). In waters off California, members of two species, *Phallonemertes* cf *murrayi* Brinkmann, 1912, and *Nectonemertes* cf *mirabilis* Verrill, 1892, made up 36.7 and 28.2% of all identifiable nemerteans, respectively. Two other species, with 24 specimens each, *Cuneonemertes elongata*, Coe 1954, and *Proarmaueria pellucida*, Coe 1926, together made up about 11% of California specimens. These four species constituted 76% of all pelagic nemerteans collected off California. Species 9 (Family Protopelagonemertidae) included 10 specimens; all other species from California were collected in single digit numbers, with 38 species represented by only one or two specimens each. In waters off Hawaii, species 51 and species 52 made up 23.5 and 14% of the total collected. Both of these species appear to be undescribed. Species 15A included three specimens, and the remaining 20 species from Hawaii were represented by only one or two specimens. Almost no species overlap was found between California and Hawaii; one specimen of *Phallonemertes* cf *murrayi* was collected from Hawaii, and three other putative species (awaiting further study) may include specimens from both Hawaii and California. Thus, at best, four of 73 species may occur in both regions.

Abundance of individuals per depth is detailed for each net type used off California (Figs. 1–4). Collections from all three net types reflect several similar trends: (1) pelagic nemerteans off California were never retrieved from depths shallower than 350 m and rarely from depths shallower than 500 m; (2) the depth range for the most abundant species, *Phallonemertes* cf *murrayi*, overlapped that of the second most abundant species, *Nectonemertes* cf *mirabilis*; however (3) *P.* cf *murrayi* was most abundant between 625 and 875 m (Figs. 1–3) or at least above 1000 m (Fig. 4); (4) *N.* cf *mirabilis* was most abundant between 1000 and 1250 m (Figs. 2 and 3) or 1000 and 1750 m (Figs. 1 and 4); (5) the highest abundance of individuals for all species, including or

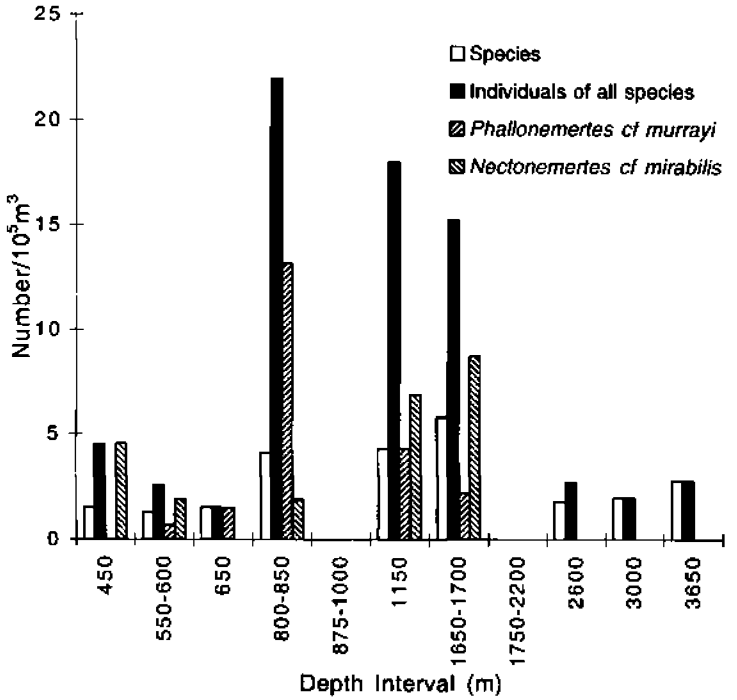

Fig. 1. Number of pelagic nemertean species (open bars) and density of individuals (filled and partly filled bars) per estimated volume of water using Mother Tucker Trawl, at different depths 160 km west of Point Conception, California, September 1992. Total number of individuals = 131, total number of tows = 25, total number of species = 27. No tows were made at depths from 875–1000 or 1700–2200 m; these depths are included for ease of between-figure comparisons.

excluding *P.* cf *murrayi* and *N.* cf *mirabilis*, occurred between 625 and 1250 m (extrapolated from Figs. 1–4); (6) abundance of pelagic nemerteans was reduced in deeper waters.

Depths of greatest number of species per volume of water filtered generally parallel depths of greatest abundance of individuals, for each cruise and net type off California (Figs. 1–4). Fig. 1 shows the number of species in deeper waters (2600–3650 m) to be high when compared to September 1993 (Figs. 2 and 3) and February 1994. Collections from February 1994 (Fig. 4) show a higher number of species in shallower waters (350–750 m) than seen in the other samples from California.

Temperature and salinity recordings over all depths from which nemerteans were collected ranged from 1.59 to 5.56°C and 35.45 to 34.37‰, at 3250 and 500 m, respectively. Temperature and salinity in September 1993, at depths of maximum abundance of all species except *Nectonemertes* cf *mirabilis* averaged 4.86–4.1°C and 34.48–34.65‰, whereas they averaged 3.78–2.35°C and 34.73–35.03‰ at depths of maximum abundance of *N.* cf *mirabilis* (1000–1750 m).

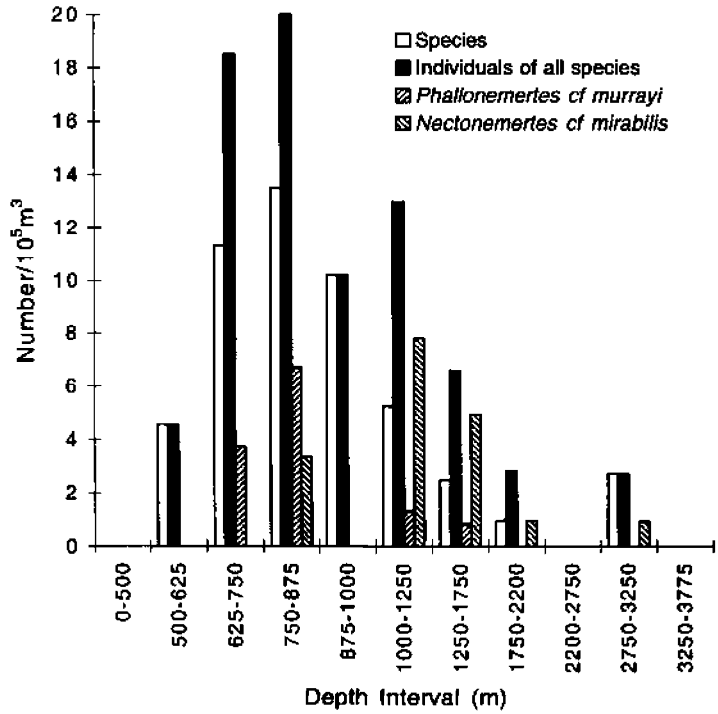

Fig. 2. Number of pelagic nemertean species (open bars) and density of individuals (filled and partly filled bars) per volume of water using MOCNESS-10, at different depth intervals, 160 km west of Point Conception, California, September 1993. Total number individuals = 39, total number of tows = 43, total number of species = 14. Number of individuals used in species calculations is only 34; 5 unidentifiable specimens are not included. No specimens were collected from 0–500 m in 11 tows through 112, 452 m^3 of water, or from 2200–2750 m in 3 tows through 89610 m^3 of water. No tows were made at 3250–3775 m.

Collections resulting from the three net types used on California cruises (Table 1) were different in number of specimens, size of specimens, and species captured (using February 1994 cruise data for the MTT since the MTT was towed similarly to the MOCNESS then). The number of specimens/10^5 m^3 water, averaged over all depth intervals between 350 and 3250 m (Figs. 2–4), was 32.9 for the MOCNESS-1D, 8.7 for the MOCNESS-10 and 12.8 for the MTT. The actual number of specimens retrieved from the MOCNESS-1D was comparatively low. In 7.8 h collecting with the MOCNESS-1D, 15 specimens were collected in 11 of 61 quantitative depth-interval tows from five general tows (Table 1), compared to 33 specimens over 12.8 h in 35 quantitative depth-interval tows from eight MOCNESS-10 general tows (Table 1) and 39 specimens over 12.2 h in 12 quantitative tows at comparable depths with the MTT. For all general tows that captured worms, including non-quantitative tows, results were: MOCNESS-1D, five tows, 31.9 h, 16 specimens; MOCNESS-10, eight tows, 39.5 h, 43 specimens; MTT, 17 tows, 30.6 h, 89 specimens. Maximum number of nemerteans/general tow was: MOCNESS-1D, 7; MOCNESS-10, 9; and MTT, 12. The

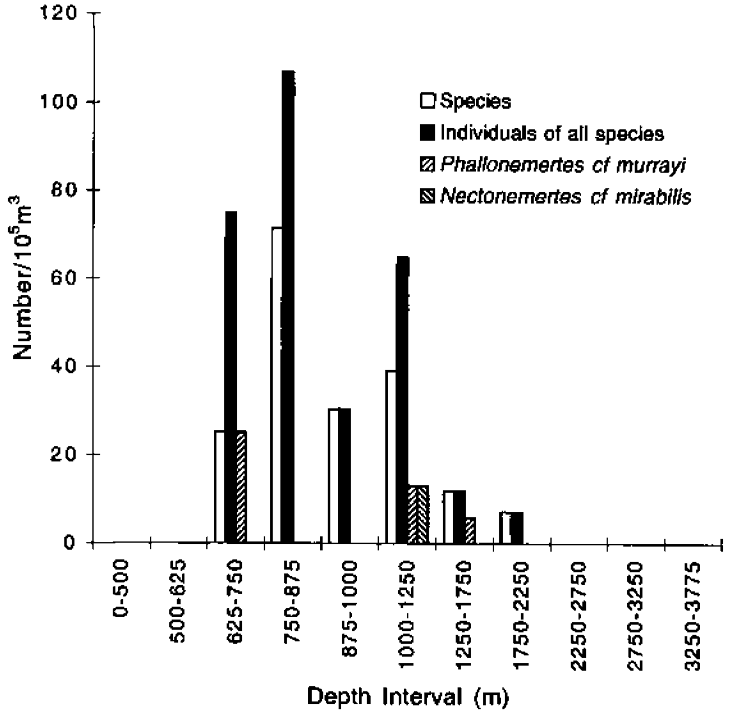

Fig. 3. Number of pelagic nemertean species (open bars) and density of individuals (filled and partly filled bars) per volume of water using MOCNESS-1D, at different depth intervals, 160 km west of Point Conception, California, September 1993. Total number of individuals = 15, total number of tows = 61, total number of species = 7. Only individuals from the quantitative half of each tow pair are included. An additional 9 individuals in 3 species were captured from 7 of the qualitative halves of sample pairs. No specimens were collected from depths shallower than 625 m in 26 tows through 25, 254 m^3 of water, from depths between 2250 and 2750 m in 4 tows through 9,614 m^3 of water, or from depths between 2750 and 3250 m in 4 tows through 5,731 m^3 water. No tows were made below 3250 m.

average size of all individuals collected, as measured by length or by wet weight, was significantly less (Mann Whitney U, length, $P = 0.0001$; wet wt, $P = 0.0000$) for specimens collected by the MOCNESS-1D than for specimens collected by the MOCNESS-10 (Table 2). In September 1993 the MOCNESS-10 captured 18 individuals of *Nectonemertes* cf *mirabilis*, half showing sexual development and all greater than 4 cm length; the MOCNESS-1D captured only five individuals of *N.* cf *mirabilis*, all immature and none more than 4.2 cm long (Table 2). Samples from the MOCNESS-1D had less species overlap with samples from other cruises or net types than samples from the MOCNESS-10 or the MTT (Table 3). Three of the four most abundant species, *Phallonemertes* cf *murrayi* (sp 1), *Nectonemertes* cf *mirabilis* (sp 2) and *Cuneonemertes elongata* (sp 14), were found in samples from all three net types. Besides these three, only two other species (34c and 35) were caught in both the MOCNESS-1D and either of the larger nets (Table 3).

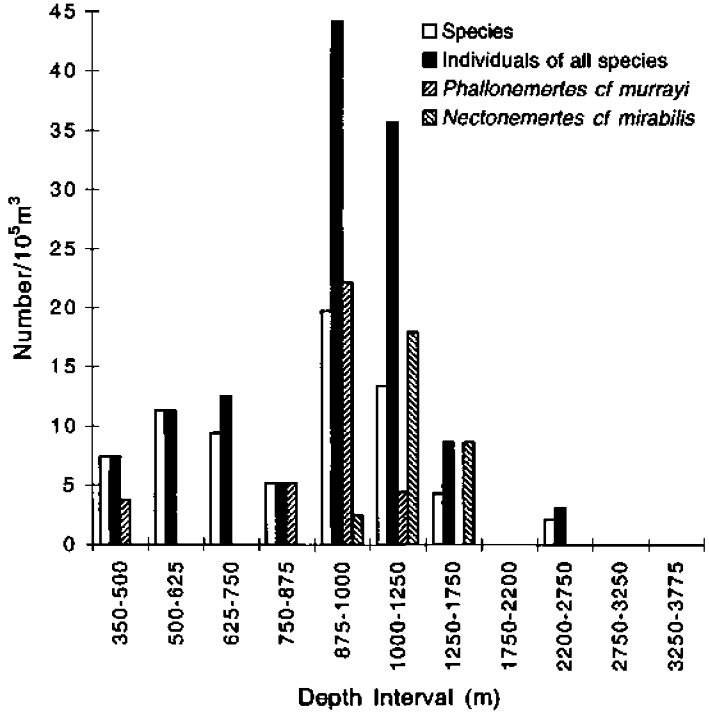

Fig. 4. Number of pelagic nemertean species (open bars) and density of individuals (filled and partly filled bars) per estimated volume of water using Mother Tucker Trawl, at different depth intervals, 160 km west of Point Conception, California, February 1994. Total number of individuals = 39, total number of tows = 12, total number of species = 13. Five additional species were collected from non-quantitative tows. No tows were made between 1750 and 2200 m or below 2750 m.

Mean depths were not significantly different between day and night samples (Table 4) of *Nectonemertes* cf *mirabilis* and *Phallonemertes* cf *murrayi*, based on an analysis of variance of density at each depth ($P = 0.617$ and 0.453, respectively). Among the specimens of *N.* cf *mirabilis* retrieved at night, three were from 450–250 m, whereas the most shallow specimens retrieved during the day were from 500–625 m; the density of specimens was similar for both depth intervals (Table 4). The depths of maximum numbers for *N.* cf *mirabilis* remained at 1000–1750 m during both day and night, although more specimens occurred shallower than 1000 m in the day while more occurred deeper than 1750 m at night. Maximum abundance of *P.* cf *murrayi* was slightly deeper at night (875–1000 m) than during the day (750–1000 m).

The average size of individual nemerteans appeared to be larger below 1250 m than it was for specimens from shallower depths (Table 5). However, this trend is strongly influenced by the fact that all of the exceptionally large specimens (wet weight greater than 2 g or area larger than 600 mm^2) collected throughout the five California cruises came from depths deeper than 1250 m, including: two individuals from 1250–1750 m,

Table 2
Lengths and wet weights of individuals for all species, and for adults and immatures of *Nectonemertes* cf *mirabilis* collected with MOCNESS-10 and MOCNESS-1D (n = number of worms, $\bar{x}$ = mean, r = range)

	All species		*Nectonemertes* cf *mirabilis*			
			Adults		Immatures	
Net type	Length (cm)	Wet weight (g)	Length (cm)	Wet weight (g)	Length (cm)	Wet weight (g)
MOCNESS-10	$n = 39$ $\bar{x} = 3.43$ $r = 0.9–5.9$	$n = 42$ $x = 0.374$ $r = 0.03–2.12$	$n = 9$ $\bar{x} = 4.96$ $r = 4.0–5.7$	$n = 8$ $\bar{x} = 0.473$ $r = 0.31–0.66$	$n = 9$ $\bar{x} = 3.19$ $r = 1.7–4.3$	$n = 9$ $\bar{x} = 0.168$ $r = 0.04–0.25$
MOCNESS-1D	$n = 27$ $\bar{x} = 1.87$ $r = 0.2–4.4$	$n = 28$ $\bar{x} = 0.08$ $r = 0.003–0.52$	$n = 0$	$n = 0$	$n = 5$ $\bar{x} = 3.58$ $r = 2.7–4.2$	$n = 5$ $\bar{x} = 0.136$ $r = 0.06–0.21$

Table 3
California morpho-species (designated by numerical identifier) occurring in more than one cruise or trawl type (MTT, MOCNESS-10 and MOCNESS-1D), in descending order of overlap. Names of species collected on four or more cruises: 1 = *Phallonemertes* cf *murrayi*, 2 = *Nectonemertes* cf. *mirabilis*, 14 = *Cuneonemertes elongata*, 69 = *Nectonemertes* cf *primitiva*

Species	September 92 MTT	March 93 MTT	February 94 MTT	September 93 MOCNESS-10	September 93 MOCNESS-1D
1	+	+	+	+	+
2	+	+	+	+	+
14	+	+	+	+	+
69	+	+	+	+	
8	+		+	+	
9	+	+	+		
10	+		+	+	
6a	+	+			
12	+	+			
15	+	+			
16	+		+		
18	+			+	
19a		+		+	
22	+	+			
34a		+	+		
34c				+	+
35		+			+
35b		+	+		
72		+		+	
Total species/ cruise	27	27	18	14	10

Table 4
Depth distributions of *Nectonemertes* cf *mirabilis* and *Phallonemertes* cf *murrayi* in daylight (Day) and dark (Night) quantitative trawls. Data combined from September 1992, September 1993, February 1994 and June 1994; Depth = depth intervals (finite depths for September 1992 assigned to appropriate intervals); Tows = number of tows made; n = total number of worms; D = worms per 10^5 m^3 water filtered (measured MOCNESS and estimated Mother Tucker Trawl volumes). Mean depth distributions between day and night captures are not significantly different (Analysis of variance, $P = 0.617$ for *N*. cf *mirabilis*; $P = 0.453$ for *P*. cf *murrayi*)

		Day				Night				
		N. cf *mirabilis*		*P*. cf *murrayi*			*N*. cf *mirabilis*		*P*. cf *murrayi*	
Depth (m)	Tows	*n*	*D*	*n*	*D*	Tows	*n*	*D*	*n*	*D*
0–500	24	0	0	0	0	16	3	3.13	1	1.05
500–625	8	3	2.91	1	0.97	5	0	0	0	0
625–750	8	0	0	3	2.78	4	0	0	0	0
750–875	10	7	2.25	43	13.83	6	0	0	2	1.68
875–1000	5	1	2.22	6	13.33	5	0	0	3	10.71
1000–1250	8	17	8.37	8	3.94	4	2	10.00	1	5.00
1250–1750	4	4	3.60	1	0.90	7	16	8.47	4	2.12
1750–2250	1	0	0	0	0	6	1	1.30	0	0
2250–2750	1	0	0	0	0	9	5	1.06	4	0.85
2750–3250						8	1	0.313	0	0
3650						1	0	0	0	0
Totals		30		64			23		12	

Table 5
Average wet weight of individual nemerteans from quantitative tows off California, September 1993 and February 1994 combined

Depth interval (m)	Number of worms weighed	Average wet weight (g)
500–625	2	0.186
625–750	9	0.100
750–875	7	0.236
875–1000	21	0.152
1000–1250	18	0.296
1250–1750	9	0.597
1750–2250[a]	3	0.189
1750–2250[b]	12	0.809
2250–2750	3	0.591
2750–3250	3	0.681

[a] Using only data from quantitative tows September 1993. There were no quantitative tows at these depths in February 1994.
[b] Using data from a non-quantitative tow in February 1994 in which cod end did not close, so sample was from 2250 m to surface. One worm in this tow weighed 5.992 g; without this specimen, combined September and February average is 0.338 g.

with wet weights of 2.27 and 2.12 g; the largest individual collected (*Dinonemertes* cf *investigatoris*), from 1700 m, over 18 cm in length and wet weight of 92.12 g; one specimen from 1750–2200 m with wet weight 5.99 g; and two specimens from 2500–0 m with wet weights 3.00 and 2.00 g. Weights were not taken in September 1992, but all specimens, from that cruise, with surface area greater than 600 mm^2 also were from deep water, including: two specimens from 1700 m, at 1092 mm^2 and 675 mm^2; two specimens from 3000 m at 744 mm^2 (*Pelagonemertes rollestoni*) and 1050 mm^2; and one specimen from 3650 m at 724.5 mm^2. Except for *P. rollestoni*, these all appear to belong to families Dinonemertidae, Protopelagonemertidae or Planktonemertidae.

Pelagic nemerteans were not collected from depths shallower than 500 m off Hawaii. The two most common species, although not separated in Fig. 5, had overlapping depth distributions between 1000 and 1300 m: species 51 occurred at depths of 1000 m ($n = 1$), 1300–1400 m ($n = 5$), 1700 m ($n = 1$) and 2500 m ($n = 1$); and species 52 occurred at depths of 750 m ($n = 1$), 1200 m ($n = 2$), and 1300 m ($n = 3$). Maximum abundance of individuals of all species occurred between 1300 and 2500 m,

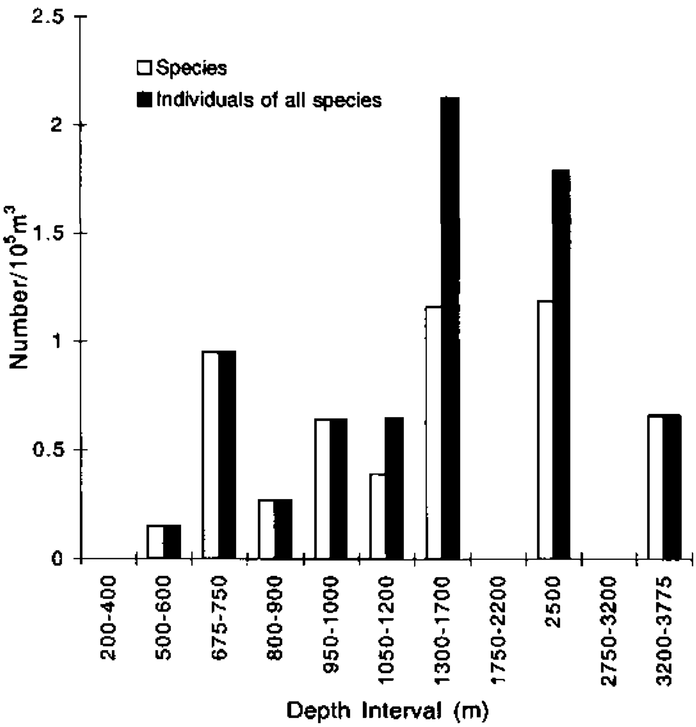

Fig. 5. Number of pelagic nemertean species (open bars) and density of individuals (filled bars) per estimated volume of water using Mother Tucker Trawl, at different depths 13 km west of Waianae, Hawaii, April–May 1993. Total number of individuals = 41, total number of tows = 87, total number species = 22. One additional species was collected from non-quantitative tows. No specimens were collected above 500 m in 15 tows through an estimated 444,350 m^3 of water. No tows were taken between 1750 and 2200 m or between 2750 and 3250 m.

although there was a minor peak at 675–750 m (Fig. 5). The highest number of species per volume of water filtered off Hawaii occurred at 1300–2500 m (Fig. 5). The number of species per depth was moderately high at most depths deeper than about 675 m, including the deepest depths (3200–3775 m). Depths of maximum abundance (Fig. 5) were deeper than for California samples (Figs. 1–4). The few temperature recordings from Hawaii for depths at which nemerteans were found were 3.9°C at about 850 m, 6.6°C at about 600 m, and 5° and 6.05° for 1100 m of wire out (actual depth unavailable).

California, with 53 putative species of pelagic nemerteans, has higher species rich ness than Hawaii, with 23 species, based on this study's collections. The Shannon–Wiener diversity index (H') for the 43 identifiable specimens from Hawaii is 4.1, whereas it is 3.25 for the 425 identifiable California specimens. Five comparisons of either equal numbers of tows or specimens, made between California (September 1992) and Hawaii, gave similar results (Table 6). In all cases (Table 6, A–D) except equal number of specimens (Table 6, E), California had higher species richness but lower diversity (H') than Hawaii. When comparing equal numbers of specimens (Table 6, E), both species richness and H' were lower for California.

California is an area of high abundance of pelagic nemerteans, with 463 individuals collected from 130 tows during five cruises. In contrast, 44 specimens were caught off Hawaii in 94 tows during one cruise. Various comparisons of the two sites, using California results from MTT tows only, show: (A) 86 quantitative tows off California (September 1992, March 1993, February 1994 and June 1994) yielded 339 worms, an average of 3.94/tow; whereas 87 quantitative tows off Hawaii yielded only 41 specimens, an average of 0.47/tow; (B) for all tows in which nemerteans could have been collected, California yielded 235 specimens in 54 tows (excluding March 1993, which lacked individual tow data), an average of 4.35 worms/tow (range 0–21; September 1992, 4.6/tow; February 1994, 4.1/tow; June 1994, 4.0/tow), whereas Hawaii yielded 43 specimens in 91 tows, 0.47 worm/tow (range 0-5); (C) specimens/10^5 m^3 water filtered was 9.1 worms for California and 0.7 for Hawaii, averaged over all depth intervals below 350 m for California (Figs. 1 and 4) or 400 m for Hawaii (Fig. 5). All

Table 6
Number of species, number of individuals, and diversity (H') comparisons of pelagic nemerteans from transects 160 km west of Point Conception, California, September 1992 and 13 km west of Waianae, Hawaii, April–May 1993. A–E = ad hoc methods of "equalizing" samples, as described in methods section

	California			Hawaii		
Comparison	Species	Individuals	H'	Species	Individuals	H'
A	24	131	2.83	19	29	4.05
B	24	131	2.83	15	26	3.76
C	24	131	2.83	8	10	2.92
D	15	84	2.54	9	12	3.02
E	14	43	2.84	23	43	4.1

comparisons show pelagic nemerteans to be 8 to 13 times more abundant off California than off Hawaii.

4. Discussion and conclusions

Although most of the morpho-species recognized in this study are not and, as yet, cannot be explicitly named, a range of important inferences can be drawn from the surprising diversity encountered. This study also underscores the dismal state of knowledge about pelagic nemerteans and the powerful effect of having specialists assessing diversity of groups within their expertise. The latter issue and the related lack of person-hours to name all the species in difficult groups are frequently cited as major deficits in more general, regional evaluations of biodiversity (e.g., Lawton et al., 1998).

This is the first explicit record of pelagic nemerteans off Hawaii and the first study of them off California since 1954 (Coe, 1954a). The number of ostensible species of pelagic nemerteans found in this study far exceeds that previously recorded for deep waters off California (53 here versus 16 for Coe, 1954a), whereas no species were previously recorded off Hawaii (23 here). The two groups combined exceed the recorded total of 54 species known for the entire Pacific Ocean (calculated from Gibson, 1982, 1995). One obvious reason for this is the shipboard presence of experienced observers familiar with the range of subtle morphological variation characterizing accepted nemertean species groups. The ability to recognize morphological differences is and was enhanced by having the advantage of living specimens collected in uniquely excellent condition. Repeated sampling along the same transect in California at different seasons and over different years also has been an important factor in retrieving so many species; species that had not been encountered previously were obtained on every trip. This contrasts with the one-time visits of many expeditions, including this one off Hawaii.

Identification of the pelagic nemerteans in this study is greatly hampered by a broad lack of comparative material and by the mutilated condition of much of the type and voucher material that is available in museum collections. This contrasts markedly with the overall high-quality capture condition of specimens in this study, which, combined with onboard annotation and individual preservation, made it relatively easy to sort specimens into putative species on the basis of a standard suite of taxonomic characters observable on intact pelagic nemerteans. Subsequent histological study of several groupings of assumed conspecific opaque worms uncovered anatomical differences standardly used to discriminate species of pelagic nemerteans. Hence, we are confident that the number of morpho-species in this study is likely to be slightly underestimated.

The lack of species overlap between California and Hawaii in our samples supports the hypothesis of relatively high endemism in the pelagic fauna of the North Pacific (Brodsky, 1967, cited in Dunbar, 1979) and it may challenge Coe's hypothesis (1946, 1954a, b) that pelagic nemerteans generally have very wide geographic distributions. The two dominant species off California, identified here as *Phallonemertes* cf *murrayi* and *Nectonemertes* cf *mirabilis* do appear to have wide distributions, as both were originally described from the Atlantic. However, it is not possible to state confidently that they are indeed those species; they may represent currently synonymized or undescribed species. Our findings, although from narrowly focused geographic locales, agree with studies that support relatively high endemism for the eastern Pacific off California for both epi- and mesopelagic organisms (e.g., Van der Spoel, 1983). Brodsky (1967, cited in Dunbar, 1979) showed that about 50% of the bathypelagic fauna of the North Pacific is comprised of endemic species. Hawaii and California are in different distributional zones for virtually all species reviewed by Van der Spoel and Heyman (1983). Van der Spoel's (1983) assertion that "cosmopolitan species (of plankton) are far from common" is supported by the fact that most species of pelagic nemerteans are described from single or closely connected regions (as calculated from Gibson, 1982, 1995). Indeed, our taxonomic study to date suggests that several, and probably many, of the putative species in this study are new to science rather than being range extensions from the Atlantic, Indian or western Pacific. These inferences are bolstered significantly by the recent molecular lineage study (mitochondrial DNA sequence) of *Cyclothone alba*, one of the most abundant and, presumably, well-known deep-sea fish, recorded as occurring circumglobally along tropical and subtropical latitudes (Miya and Nishida, 1997). The study showed that fish assigned to this species, which we can expect to be much more motile than pelagic nemerteans, segregated into five anciently separated monophyletic lineages showing high regional endemism.

Pelagic nemertean diversity in waters off central California is dominated by *Phallonemertes* cf *murrayi* and *Nectonemertes* cf *mirabilis*. In this study, *P.* cf *murrayi* is the most abundant pelagic nemertean off central California, at sites 16–80 km offshore over Monterey Canyon (Roe, unpublished observation) and 160 km offshore throughout an 81 km stretch from Pt. Conception north. It is an enigma that it was not recognized or observed by Coe (1954a) in a study that covered essentially the same area over Monterey Canyon. Although our 1992 and 1993 sampling was within the time frame of an El Niño, it seems likely that higher sea surface temperatures, increased fresh water runoff and other effects from El Niño should be damped out at depths of 500 m or more. Preserved specimens of *P. murrayi* can be mistaken for *N. mirabilis*, especially if retrieved in poor condition or poorly prepared, as appears to be the case with most museum specimens that we have seen. In addition, only four specimens of *P.* cf *murrayi* were collected with the MOCNESS-1D. If the small net used in Coe's (1954a, b) study were towed more rapidly than our speed of 2 kt, more water would have flowed around the net mouth, further reducing the chance of catching relatively large and relatively good swimmers such as *P.* cf *murrayi* (Roe, personal observation). *Nectonemertes mirabilis* is described as a cosmopolitan species (in part, a consequence of synonymies), with a range of 100° of latitude (34°S to 64°N), nearly 6°C of temperature (3.5–9°C), a depth range of 200–4000 m, and records from throughout the Atlantic and Pacific Oceans (Coe, 1954a; O'Sullivan, 1983; Van der Spoel, 1985). We suspect that many records of this species actually pertain to other species of *Nectonemertes* or even other genera. Our findings suggest that it is very likely that specimens collected off California and attributed to *N. mirabilis* by Thuesen and Childress (1993) are likely to have been a mix of *N.* cf *mirabilis* and *P.* cf *murrayi* (E. Thuesen, The Evergreen State College, Olympia, Washington, personal communication).

In our studies off California, net size (as well as other parameters of collection methods) showed differences in the numbers of specimens collected, the size of individuals collected, and even which species were collected. Both greater numbers of individuals and larger numbers of species were collected using nets with a large mouth opening and towing for long time periods. The amount of water filtered/time by the MOCNESS-1D was an order of magnitude less than that of the larger nets, resulting in apparent increased rate of capture but decrease in actual numbers captured. In addition, it appears probable that even relatively feeble swimmers can escape the small mouth (1 m^2) of the MOCNESS-1D. Shipboard observations and video film show that some of these nemerteans are capable of energetic swimming behavior for bursts of at least tens of seconds (unpublished observations). Specimens collected by the MOCNESS-1D were significantly smaller than those collected from large nets. Of the *Nectonemertes* cf *mirabilis* specimens collected by the MOCNESS-1D, all were less than 4.2 cm length and all were immature. In contrast, during the same cruise, the MOCNESS-10 captured 18 individuals, all over 4 cm length, with nine showing sexual development. Average lengths of mature males and females of *N.* cf *mirabilis* were 4.8 and 4.7 cm, respectively, and individuals usually do not commence sexual development until they reach approximately 4 cm (P. Roe, personal observation). Of 29 specimens collected by the MOCNESS-1D, only four were of *Phallonemertes* cf *murrayi* and five were of *N.* cf *mirabilis*, well below the 65% combined representation of these species across all California samples. Had only the MOCNESS-1D been used, the reproductive patterns (Norenburg and Roe, 1998) and dominance patterns of the most abundant species would have been missed. However, several of the species (Table 3) caught by the MOCNESS-1D mature at very small sizes. These species were underrepresented in the larger nets, presumably because they escaped through the coarser mesh or escaped notice in samples dominated by many more, and larger specimens.

Vertical migration, defined as daily migration by organisms into deeper waters during daylight and into surface waters at night, occurs in several groups of deep-sea midwater animals and is best developed in areas of high surface productivity (summarized in Nybakken, 1993). The only evidence known to the authors for vertical migration of pelagic nemerteans is an apparent seasonal migration by *Nectonemertes mirabilis* in the North Atlantic, which, north of 41°N, moves into shallow water (300 m) in winter/spring and deeper than 500 m in summer/fall, with the upper limit following the 9° isotherm (Van der Spoel, 1985). In the same study, Van der Spoel (1985) reported one shallow night sample from 45°N with only a few specimens, which he said might indicate vertical migration. In our samples, specimens of *N.* cf *mirabilis* and *Phallonemertes* cf *murrayi* were collected in large enough numbers off California that vertical migration could have been detected if it had occurred in these species. Our data show no significant evidence of nocturnal vertical migration into shallow water by either species. In fact, visual inspection of the data (Table 4) could lead one to conclude the opposite for *N.* cf *mirabilis*. Few specimens of either species were found above 500 m and almost none above 350 m, and both species were actually more abundant in deeper water during night tows. We concluded that these two dominant species off California do not migrate vertically in the widely understood sense. Although we included them in our statistical analysis, we consider it probable that all four specimens retrieved from very shallow night tows had been left in the trawl from the preceding tows, all of which were from deeper water.

General biomass decreases exponentially with depth, especially below 1000 m (Vinogradov, 1970; Childress, 1996). This decrease also is apparent in abundance data of nemerteans below about 1750 m in our samples from California (Figs. 1–4), although nemerteans were collected in even the deepest tows from waters off both Hawaii and California. It also appears, from limited data, that deeper-water (>2000 m) nemerteans are often large, muscular and robust. When present, they can make up a large portion of the biomass of an entire sample, due to the low numbers of other taxa also living at these depths. However, obtaining suitable quantitative data at such depths to test this hypothesis is prohibitively difficult.

Among the several definitions for the term diversity, two of the most general are: (1) the number of species in an area, i.e., species richness, and (2) a measure of the number of species and their relative abundance, with low diversity resulting from either few species or unequal abundances (Lincoln et al., 1983). Abundance is an important component of the Shannon Wiener diversity index, H' (Cox, 1980). In the present study, waters off California appear to have higher species richness (53 species) than those off Hawaii (23 species). California waters were sampled on five cruises (130 tows) compared to only one cruise (94 tows) off Hawaii; so, the two areas were sampled differently. Additional species were recognized on each California cruise as well as from other sites off California not reported here (Roe, personal observation). Probably, additional sampling off Hawaii would yield additional species as well. However, H' consistently is higher for nemerteans from Hawaii, even though California shows higher species richness in most comparisons (Table 6). The lower H' values reflect the impact on diversity by dominance of *Phallonemertes* cf *murrayi* and *Nectonemertes* cf *mirabilis*, which together make up 65% of all identifiable nemerteans collected off California, whereas there appears to be no such dominant species off Hawaii.

Pelagic nemerteans were about 10 times more abundant off California than off Hawaii. Even though California waters were sampled five times in different seasons, compared to only one sampling period off Hawaii, the various abundance comparisons indicate that the much higher abundance of pelagic nemerteans off California is not an artifact of unequal sampling. The overall average number of nemerteans/tow, average number/tow for each cruise, and average number/volume water filtered over all depth intervals sampled, were consistently 8–13 times greater off California than off Hawaii. Waters off California are generally characterized as having higher primary productivity and greater macrozooplankton biomass than waters in the Central Pacific, including those off Hawaii (Childress et al., 1990). This higher productivity might account, at least in part, for the greater abundance of pelagic nemerteans off California.

The high abundance of pelagic nemerteans off California was a surprise, because this is not evident in the few relevant published reports. Part of the reason so many specimens were collected was the large size of net used and long towing times, especially with the MTT. In Coe's (1954a, b) studies of nemerteans from Monterey Canyon, a 1 m^2 net made 141, 1 h tows between depths of 650 and 1160 m over the course of 2 yr. One or two nemerteans were retrieved from each of only 29 of those tows (Coe, 1954b), comparable to the numbers we obtained with the MOCNESS-1D. Our data show this net to be particularly poor at sampling specimens larger than about 4 cm length. A rough estimate of average length of all specimens measured (Norenburg and Roe, 1998) of *Phallonemertes* cf *murrayi* (36.7 mm) and *Nectonemertes* cf *mirabilis* (40.2 mm), suggests that small nets may provide a biased sample of the pelagic nemertean community. In addition to the two studies cited above, the most extensive previous quantitative study of pelagic nemerteans was off Bermuda (Coe, 1945, 1946). In that study, several nets 1 m^2 in diameter were towed simultaneously, for 4 h, at 200 m intervals between 1000 and 2000 m. Tows were made in the course of three summers, 1929–31, in an area 8 miles in diameter, for a total of 1042 tows, and yielded 105 nemertean specimens (Coe, 1945, 1946). Coe (1954b) considered his studies off Bermuda and California to be highly productive; yet, they provided far fewer specimens or species than did the present study off California when large nets were used. The use of small nets in earlier studies may account for the long-held belief that pelagic nemerteans are uncommon. The fact that so few specimens were retrieved off Hawaii with the same large net (MTT) as used off California supports the conclusion that pelagic nemerteans are much less abundant in Hawaii than in waters off California. The overriding conclusion of this study must be that abundance and diversity of pelagic nemerteans has been widely misjudged and, consequently, ignored.

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