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Cephalopod paralarvae assemblages in Hawaiian Islands waters

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ABSTRACT: The distribution and abundance of cephalopod paralarvae near the Hawaiian Islands are described. Paralarvae were collected during 5 plankton surveys in 1991 to 1993. The 404 tows at 59 stations collected 10375 paralarvae from 21 families and 57 species. The most numerous families were the Ommastrephidae (23% of total catch), Pyroteuthididae (17%), Enoploteuthididae (16%), Onychoteuthididae (14%), and Chtenopterygidae (8%). The most numerous species were *Ommastrephes bartramii* (18%), *Pterygioteuthis microlampas* (15%), *Chtenopteryx sicula* (8%), and *Onychoteuthis compacta* (6%). Analysis of paralarval distribution patterns identified 2 paralarval assemblages: 'island associated' and 'oceanic' The 15 'island-associated' species showed increased paralarval abundance near the islands, suggesting preferential spawning in this area. Epipelagic nearshore spawners included *Onychoteuthis* sp. C, *Sthenoteuthis oualaniensis*, and *Nototodarus hawaiiensis*. Mesopelagic nearshore spawners included 3 reported members of the Hawaiian Mesopelagic Boundary Community (*Abralia trigonura*, *Liocranchia reinhardti*, and *Chiroteuthis picteti*) and 3 probable new members (*Liocranchia valdiviae*, *Histioteuthis hoylei* and *Enoploteuthis jonesi*).

KEY WORDS: Paralarvae · Cephalopod · Hawaiian Islands · Distribution · Assemblage

INTRODUCTION

Cephalopod paralarvae are more numerous and more easily sampled than adults. Knowledge of paralarval distribution and abundance patterns is useful for determining when and where adults spawn, particularly for species whose adults are difficult to catch. Knowledge of the early life stages can also help in understanding cephalopod population dynamics and in developing stock-recruitment models for commercially important species (Vecchione 1987). Yet, despite their importance, the early life stages of most species are seldom studied and poorly understood (Boyle 1990).

A diverse community of cephalopods occurs near the Hawaiian Islands (Berry 1914, Young 1978). It includes inhabitants of the mesopelagic-boundary region (Reid et al. 1991, Young 1995), one of the most poorly investigated habitats in the ocean. Benthic adults are particularly difficult to sample because the steep and jagged seafloor near the islands restricts benthic trawling. As a result, the species composition and distribution of cephalopods around the islands remain uncertain.

To date, the paralarval distribution patterns of only 1 cephalopod species (*Ommastrephes bartramii*) near the Hawaiian Islands have been described (Young & Hirota 1990, Bower 1994, 1996). In this paper, we present the paralarval distribution patterns of 58 cephalopod species collected near the islands during 5 surveys in 1991 to 1993. We then identify species-assemblage groups based on capture distance from the islands and compare onshore-offshore abundance patterns to infer which species may spawn preferentially near the islands.

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MATERIALS AND METHODS

Sampling. Five plankton surveys were conducted near the Hawaiian Islands to collect cephalopod paralarvae. Stations were located 9 to 1169 km windward (northeast) and 11 to 256 km leeward (southwest) of the islands. Samples were collected aboard the Hokkaido University ship 'Hokusei Maru' (HM) during 6 to 15 February 1991 (HM-91 survey; 7 stations, 3 to 5 tows station^{-1}), 5 to 26 February 1992 (HM-92 survey; 16 stations, 7 to 10 tows station^{-1}), and 4 to 19 February 1993 (HM-93 survey; 12 stations, 7 to 10 tows station^{-1}), and aboard the NOAA ship 'Townsend Cromwell' (TC) during 5 to 20 February 1991 (TC-91 survey; 10 stations, 1 to 7 tows station^{-1}) and 22 March to 7 April 1992 (TC-92 survey; 14 stations, 4 to 8 tows station^{-1}). The standard sampling procedure in all surveys was to conduct 30 min open oblique tows from 100 m depth to the surface during the day. This depth range was chosen to sample through the depths known for paralarval *Ommastrephes bartramii*. Species with paralarval distributions deeper than this depth range will thus be underrepresented. In total, 404 tows were conducted at 59 stations. All HM surveys used a 4 m^2 ring net equipped with 0.505 mm mesh, a General Oceanics flowmeter, and a Benthos time-depth recorder (TDR). The TC-91 survey also used a 4 m^2 ring net. The TC-92 survey used a 2 m^2 ring net for 94 tows and a 4 m^2 ring net for 4 tows. TC nets carried a Wildlife Computers TDR. Bower (1996) described the sampling procedure in detail.

Net collections were fixed at sea in 4 to 6% buffered formalin for 3 to 6 h, then preserved in 50% isopropyl alcohol. During the HM-91 survey, paralarvae were sorted from the plankton at sea with dissecting microscopes. Samples from subsequent TC and HM surveys were sorted on shore. Paralarvae were identified to genus and species level with the aid of published figures and descriptions (Harman & Young 1985, Young & Harman 1985, 1987, 1989, Young et al. 1985, Young & Hirota 1990, Young 1991). In some genera, more than 1 species was present, but identification was not possible either because a growth series connecting paralarvae to known adults was not available or the adults were known but undescribed. In such cases, species were given letter designations. Abundances of each species were standardized (individuals per 50 m^2 of sea surface sampled) for each tow (Smith & Richardson 1977). Station abundances were calculated as the average of all station tows.

Assemblage groups. Assemblage groups were determined with the 2-way indicator species analysis program TWINSPAN (Hill 1979, Gauch & Whittaker 1981) using PC-ORD software (McCune & Mefford 1997). Analyses are based on abundance data from all surveys for species with total catches greater than 15. Abundances at each station were used for comparisons of onshore-offshore distribution to determine which species preferentially spawn near the islands (Spearman rank test, $p < 0.05$).

RESULTS

Family and species composition

The 404 tows at 59 stations collected 10375 paralarvae from 21 families and 58 species (Table 1). The most numerous families were the Ommastrephidae (23% of total catch), Pyroteuthididae (17%), Enoploteuthididae (16%), Onychoteuthididae (14%), and Chtenopterygidae (8%). The most numerous species were *Ommastrephes bartramii* (18%), *Pterygioteuthis microlampas* (15%), *Chtenopteryx sicula* (8%), and *Onychoteuthis compacta* (6%). Interannual catch rates for most species varied widely. Catches of the most abundant species showed a general decline over the 3 survey years. Results for the more frequently taken taxa are presented below.

Species distribution: squids

A total of 8848 squids from 16 families and 44 species were collected.

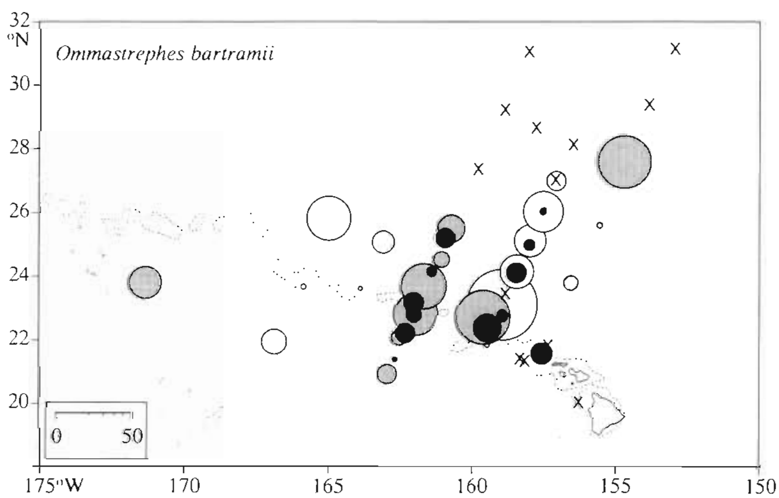

Fig. 1. Distribution and abundance of *Ommastrephes bartramii* paralarvae collected near the Hawaiian Islands during 5 cruises in 1991 to 1993. Circles represent mean station abundance (ind./50 m^2). White circles: 1991 catches; gray circles: 1992 catches; black circles: 1993 catches. Circle area represents catch abundance. X: no catch

Family Ommastrephidae. *Ommastrephes bartramii* was the most numerous cephalopod species collected, composing 18% of the cephalopod catch and 80% of the ommastrephid catch; catches occurred at 41 stations (Fig. 1), and 40% were collected more than 200 km offshore. *Hyaloteuthis pelagica* was also widely distributed, occurring at 37 stations; 35% were collected more than 200 km offshore. Catches of the other 2 ommastrephids represented in the collections occurred farther inshore. *Sthenoteuthis oualaniensis* was collected at 26 stations (Fig. 2); 40% occurred less than 25 km offshore. *Nototodarus hawaiiensis* was collected at 15 stations; 54% occurred less than 25 km offshore.

Family Pyroteuthididae. All 3 pyroteuthid species were widely distributed. *Pterygioteuthis microlampas* composed 89% of the pyroteuthid catch and was the most commonly collected cephalopod species, occurring in 68% of the tows and at 56 stations (Fig. 3); 41% occurred more than 200 km offshore. *Pterygioteuthis giardi* was collected at 26 stations; 54% occurred more than 200 km offshore. *Pyroteuthis addolux* was collected at 17 stations; 81% occurred more than 200 km offshore.

Family Enoploteuthididae. *Abraliopsis* sp. A (Young & Harman 1985) was collected at 46 stations (Fig. 4) and composed 30% of the enoploteuthid catch; 66% occurred more than 200 km offshore. *Enoploteuthis*

Table 1. Cephalopod paralarvae collected near the Hawaiian Islands during 5 surveys in 1991 to 1993. Numbers for higher taxa include specimens that could not be further identified. HM: 'Hokusei Maru'; TC: 'Townsend Cromwell'. 91: 1991; 92: 1992; 93: 1993. Mean abundance: ind./50 m^2 NE: distance (km) from archipelago to northeasternmost point of capture; SW: distance (km) from archipelago to southwesternmost point of capture. This point will lie windward (northeast) of the archipelago if no captures were made south of the archipelago. W: windward of the archipelago; L: leeward of the archipelago. na: not applicable

	HM-91	TC-91	HM-92	TC-92	HM-93	Total	Positive tows (%)	Positive-tow mean abundance (SD)	Offshore range NE	Offshore range SW	% collected <50 km offshore
Order Octopoda	29	333	82	17	128	589					
Family Argonautidae	2	3	3	2	4	14					
Argonauta argo	2	3	3	2	4	14	3	0.8 (0.4)	486-W	14-W	21
Family Bolitaenidae	1	1	6	0	9	17					
Eledonella pygmaea	1	1	6	0	9	17	3	0.9 (0.3)	736-W	204-W	0
Family Octopodidae	26	325	70	12	111	544					
Octopus cyanea	14	250	38	3	83	388	18	4.3 (7.9)	264-W	256-L	82
Octopus ornatus	0	2	3	0	0	5	1	1.0 (0.3)	26-W	9-W	100
Octopus Type A[a]	1	3	0	0	2	6	1	1.0 (0.6)	26-W	113-L	83
Octopus Type B[a]	0	13	2	4	7	26	3	2.0 (1.1)	143-W	113-L	73
Octopus Type C[a]	1	11	1	1	5	19	4	1.0 (0.5)	264-W	34-L	84
Octopus Type D[a]	1	1	1	1	0	4	1	1.2 (0.4)	59-W	126-L	50
Octopus Type E[a]	4	18	1	2	0	25	3	2.2 (2.4)	59-W	11-L	92
Octopus Type H[a]	2	14	8	1	13	38	7	1.0 (0.6)	351-W	113-L	66
Octopus Type I[a]	3	13	9	0	1	26	5	1.1 (0.6)	238-W	34-L	73
Family Tremoctopodidae	0	4	3	3	4	14					
Tremoctopus violaceus	0	4	3	3	4	14	3	1.1 (0.5)	762-W	215-L	14
Order Sepioidea	1	1	0	0	0	2					
Family Sepiolidae	1	1	0	0	0	2					
Euprymna scolopes	1	1	0	0	0	2	1	1.0 (0.1)	26-W	34-L	100
Order Teuthida	1790	1874	2263	1293	1628	8848					
Family Ancistrocheiridae	3	9	4	7	2	25					
Ancistrocheirus lesueurii	3	9	4	7	2	25	5	1.1 (0.8)	721-W	212-L	36
Family Brachioteuthididae	101	73	117	45	56	392					
Brachioteuthis sp.	101	73	117	45	56	392	42	2.1 (2.2)	1169-W	256-L	43
Family Chiroteuthididae	31	20	48	18	12	129					
Chiroteuthis picteti	3	10	5	0	3	21	4	1.3 (0.6)	183-W	113-L	57
Chiroteuthis sp. nov.[b]	27	7	43	16	8	101	17	1.2 (0.9)	762-W	126-L	28
Grimalditeuthis bonplandi	0	3	0	2	1	6	1	1.4 (0.6)	1169-W	113-L	50
Planctoteuthis danae	1	0	0	0	0	1	0.2	1.6 (na)	106-W	106-W	0
Family Chtenopterygidae	192	103	272	65	141	773					
Chtenopteryx sicula	192	103	272	65	141	773	59	2.7 (2.9)	1169-W	256-L	26

(Table continued overleaf)

Table 1 (continued)

	HM-91	TC-91	HC-92	TC-92	HM-93	Total	Positive tows (%)	Positive-tow mean abundance (SD)	Offshore range NE	Offshore range SW	% collected <50 km offshore
Family Cranchiidae	96	214	209	32	188	739					
Cranchia scabra	29	28	95	7	69	228	34	1.2 (0.8)	736-W	256-L	29
Galiteuthis pacifica	1	0	5	1	5	12	3	0.7 (0.3)	1169-W	9-W	25
Helicocranchia sp. B[c]	40	59	15	4	52	170	14	3.0 (4.9)	979-W	207-L	43
Leachia pacifica	16	25	25	12	16	94	18	1.1 (0.7)	721-W	256-L	49
Liocranchia reinhardti	6	67	50	4	25	152	22	1.3 (1.3)	471-W	256-L	70
Liocranchia valdiviae	4	33	18	4	19	78	14	1.2 (1.0)	721-W	207-L	62
Megalocranchia fisheri	0	2	1	0	2	5	1	0.8 (0.2)	230-W	30-L	60
Family Cycloteuthididae	0	1	0	0	0	1					
Cycloteuthis sirventi	0	1	0	0	0	1	0.2	0.8 (na)	14-W	14-W	100
Family Enoploteuthididae	357	351	416	121	270	1515					
Abralia astrosticta	0	6	0	0	1	7	1	1.7 (1.1)	71-W	14-W	86
Abralia trigonura	108	185	34	17	27	371	20	4.4 (5.1)	264-W	113-L	88
Abraliopsis pacificus	39	39	82	39	80	279	38	1.5 (1.2)	1169-W	256-L	50
Abraliopsis sp. A[d]	101	38	180	48	86	453	45	2.2 (2.3)	1169-W	256-L	24
Enoploteuthis higginsi	78	67	78	13	52	288	37	1.7 (1.6)	721-W	256-L	39
Enoploteuthis jonesi	1	6	8	0	6	21	4	1.0 (0.6)	264-W	207-L	81
Enoploteuthis reticulata	30	10	34	4	15	93	16	1.3 (1.4)	736-W	256-L	27
Family Histioteuthididae	8	26	7	5	8	54					
Histioteuthis hoylei	0	14	6	0	4	24	3	1.6 (1.2)	143-W	207-L	79
Histioteuthis sp. B[c]	0	3	0	0	1	4	1	1.8 (1.6)	230-W	204-W	0
Histioteuthis sp. C[c]	7	9	1	1	3	21	4	1.2 (1.0)	581-W	113-L	33
Histioteuthis sp. D[c]	1	0	0	4	0	5	1	1.3 (0.3)	979-W	351-W	0
Family Lepidoteuthididae	2	0	0	1	0	3					
Lepidoteuthis grimaldii	2	0	0	1	0	3	1	1.2 (0.3)	955-W	16-W	33
Family Mastigoteuthididae	0	5	1	0	0	6					
Mastigoteuthis famelica	0	5	1	0	0	6	1	0.9 (0.2)	183-W	14-W	83
Family Octopoteuthididae	10	9	10	9	12	50					
Octopoteuthis nielseni	10	9	10	9	8	46	9	1.2 (0.7)	1169-W	207-L	30
Taningia danae	0	0	0	0	4	4	1	1.0 (0.2)	30-L	207-L	50
Family Ommastrephidae	403	210	378	634	519	2144					
Hyaloteuthis pelagica	22	65	90	34	40	251	27	2.1 (4.0)	736-W	256-L	49
Nototodarus hawaiiensis	6	11	11	1	6	35	6	1.0 (0.4)	264-W	113-L	80
Ommastrephes bartramii	368	100	242	556	453	1719	47	8.1 (11.9)	721-W	256-L	34
Sthenoteuthis oualaniensis	7	34	35	43	20	139	19	1.9 (2.2)	581-W	256-L	63
Family Onychoteuthididae	156	444	343	103	251	1297					
Onychoteuthis compacta	79	226	114	26	93	538	46	2.4 (3.3)	1169-W	256-L	33
Onychoteuthis sp. B[e]	0	3	4	0	7	14	3	0.8 (0.3)	264-W	256-L	64
Onychoteuthis sp. C[e]	34	166	117	13	87	417	36	2.3 (2.3)	721-W	256-L	73
Onykia sp. A[c] (*O. carriboea?*)	38	47	103	61	58	307	43	1.5 (1.1)	721-W	256-L	36
Onykia sp. B[c] (*O. rancureli?*)	5	1	5	3	0	14	3	1.5 (0.7)	979-W	16-W	29
Family Pholidoteuthididae	10	11	0	1	2	24					
Pholidoteuthis sp.	10	11	0	1	2	24	3	1.7 (1.0)	721-W	22-W	8
Family Pyroteuthididae	411	377	419	234	147	1588					
Pterygioteuthis giardi	16	40	35	1	15	107	13	1.8 (1.2)	955-W	215-L	45
Pterygioteuthis microlampas	373	331	360	227	125	1416	68	5.0 (6.2)	955-W	256-L	40
Pyroteuthis addolux	22	6	21	6	7	62	8	2.2 (3.0)	979-W	215-L	8
Family Thysanoteuthididae	10	21	39	18	20	108					
Thysanoteuthis rhombus	10	21	39	18	20	108	18	1.2 (0.7)	721-W	256-L	42
Unidentified	185	180	371	133	67	936					
Total cepalopods	2005	2388	2716	1443	1823	10375					
Total species	45	52	46	41	47	57					

[a]Young & Harman (1989); [b]Young (1991); [c]identified from growth series; [d]Young & Harman (1985); [e]Young & Harman (1987)

higginsi, *Abraliopsis pacificus* and *E. reticulata* also had wide latitudinal distributions. *Abralia trigonura* (Fig. 5) and *E. jonesi* were collected much closer to shore; 40% and 67% of their respective catches occurred less than 25 km offshore.

Family Onychoteuthididae. *Onychoteuthis compacta* was collected at 50 stations (Fig. 6) and composed 43% of the onychoteuthid catch; 59% occurred more than 200 km offshore. *Onykia* sp. A was also widely distributed at 50 stations, but less abundant than *O. compacta*; 40% occurred more than 200 km offshore. *Onychoteuthis* sp. C (Young & Harman 1987) was widely distributed at 41 stations (Fig. 7), yet 53% occurred less than 25 km offshore. *Onychoteuthis* sp. B (Young & Harman 1987) was collected at 9 stations; 50% occurred less than 25 km offshore.

Family Chtenopterygidae. *Chtenopteryx sicula* was the most widely distributed cephalopod collected, occurring at 97% of the stations (Fig. 8); 57% were collected more than 200 km offshore.

Family Cranchiidae. *Cranchia scabra* was collected at 42 stations (Fig. 9) and composed 31% of the cranchiid catch; 58% occurred more than 200 km offshore. *Helicocranchia* sp. B was collected at 22 stations and composed 23% of the cranchiid catch; 50% occurred more than 200 km offshore. *Leachia pacifica* was also widely distributed; catches occurred at 38 stations, and 37% were collected more than 200 km offshore. *Liocranchia reinhardti* and *Liocranchia valdiviae* occurred closer to shore; 46 and 41% of their respective catches occurred less than 25 km offshore.

Species distribution: octopods

A total of 589 octopods from 4 families and 12 species were collected. The 9 octopodid species composed 92% of the octopod numeric catch. All octopodids were collected less than 352 km from the islands; 59% occurred less than 25 km offshore. *Octopus cyanea* was collected at 23 stations (Fig. 10) and composed 72% of the octopodid numeric catch. *Octopus* Type H (Young & Harman 1989) had the furthest offshore distribution of the octopodids; 29% were collected more than 200 km off-

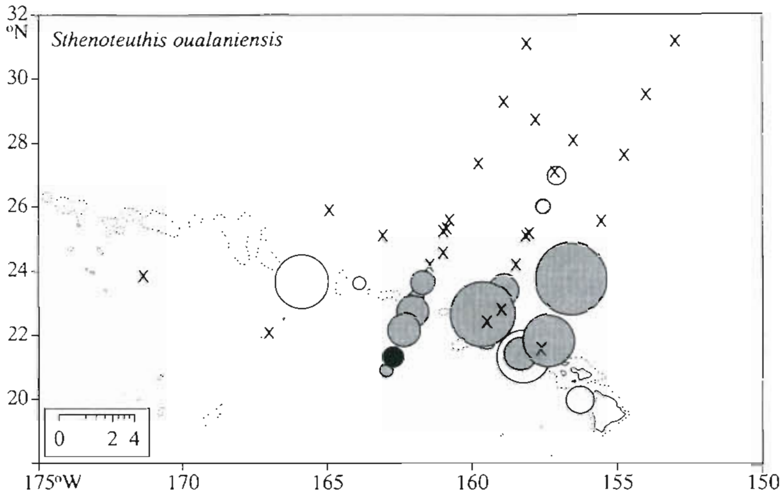

Fig. 2. Distribution and abundance of *Sthenoteuthis oualaniensis*. Symbols described in Fig. 1

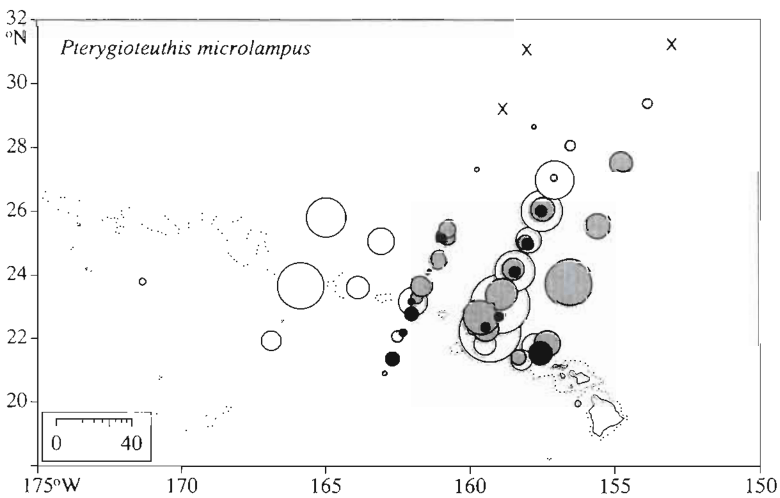

Fig. 3. Distribution and abundance of *Pterygioteuthis microlampus*. Symbols described in Fig. 1

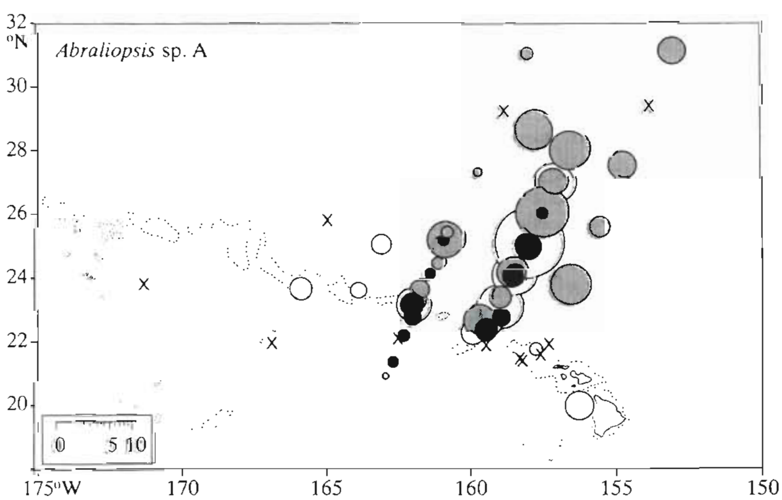

Fig. 4. Distribution and abundance of *Abraliopsis* sp. A. Symbols described in Fig. 1

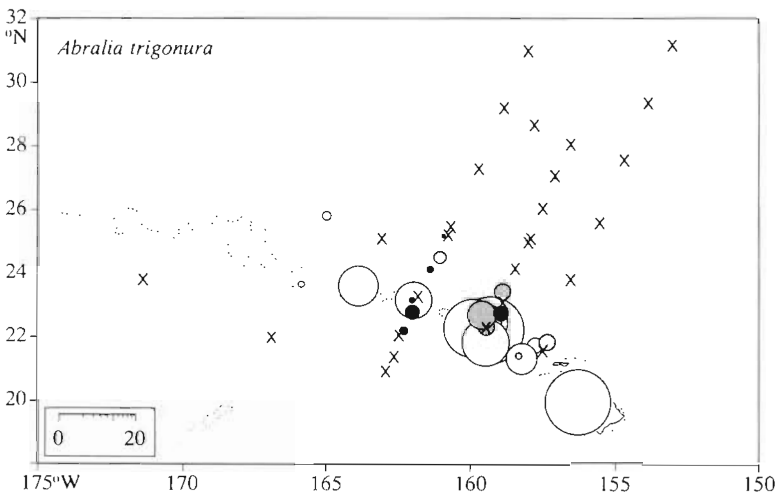

Fig. 5. Distribution and abundance of *Abralia trigonura*. Symbols described in Fig. 1

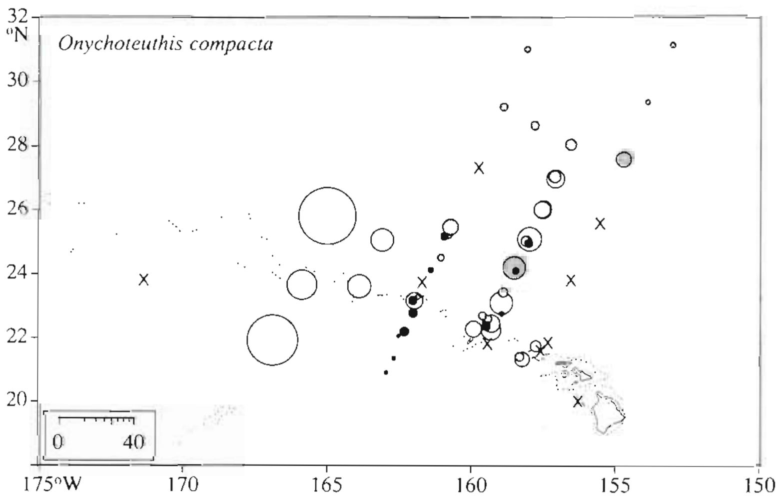

Fig. 6. Distribution and abundance of *Onychoteuthis compacta*. Symbols described in Fig. 1

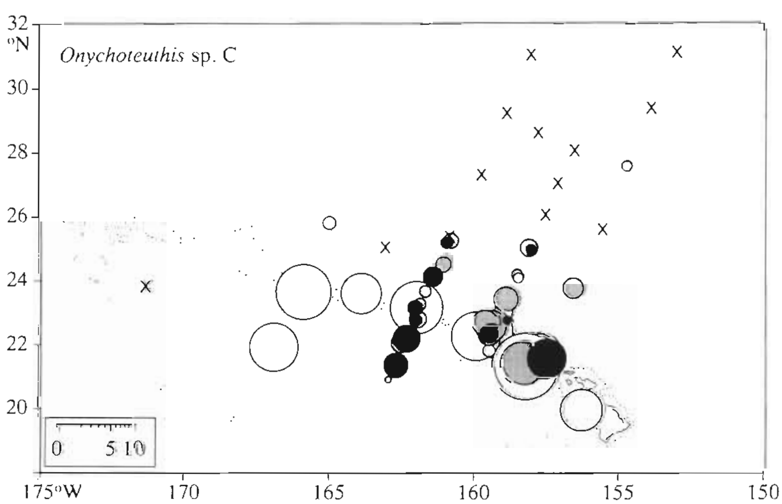

Fig. 7. Distribution and abundance of *Onychoteuthis* sp. C. Symbols described in Fig. 1

shore. *Eledonella pygmaea* was the only cephalopod collected exclusively offshore; catches occurred at 8 windward stations north of 25° 02' N greater than 200 km offshore. *Tremoctopus violaceus* was collected at 11 stations and had the widest latitudinal range of all octopods (21° 20' to 29° 14' N); 79% occurred more than 200 km offshore.

Assemblages

Assemblage analysis using the 2-way indicator species analysis program defined 2 distributional assemblages: 'island associated' and 'oceanic' (Table 2). The 15 'island-associated' species include 6 species with benthic adults (*Octopus* spp.), 6 species with mesopelagic adults (*Abralia trigonura*, *Liocranchia reinhardti*, *L. valdiviae*, *Histioteuthis hoylei*, *Chiroteuthis picteti*, and *Enoploteuthis jonesi*) and 3 species with epipelagic adults (*Onychoteuthis* sp. C, *Sthenoteuthis oualaniensis* and *Nototodarus hawaiiensis*). Analysis of onshore-offshore abundance patterns showed that all 'island-associated' species decreased significantly in abundance with increasing distance offshore and had more than 50% of their paralarvae collected within 50 km of shore.

DISCUSSION

Paralarval distribution patterns provide further evidence that *Abralia trigonura*, *Liocranchia reinhardti* and *Chiroteuthis picteti* are members of the Hawaiian Mesopelagic Boundary Community (MBC). However, the present data lend no support to Young's (1995) suggestion that *Pterygioteuthis giardi* is a probable facultative boundary species.

Paralarval catch data indicate that *Liocranchia valdiviae*, *Histioteuthis hoylei*, and *Enoploteuthis jonesi* are also probable MBC members. *L. valdiviae* adults were rarely caught near the Hawaiian Islands during MBC studies; however, the subadults of this deep-living species, unlike those of their congener, do not vertically migrate (Young 1978) and were thus mostly out of the sampling range of those studies. *H. hoylei* is widely distributed in the Pacific (Voss et al. 1998), but appears to spawn preferentially near land masses. Mature *H. hoylei* females collected off Japan occur in aggregations near an isolated oceanic rise, suggesting this species might spawn near the seafloor, as reported for *H. miranda* and *H. celetaria pacifica* (Nesis 1993a). *H. reversa* paralarvae also commonly occur near land masses (Clarke 1966). *E. jonesi* occurs in Hawaiian and equatorial waters (Burgess 1982) and has not been considered a member of the Hawaiian MBC (Young 1995); however, the present study indicates that this species is a nearshore spawner. Some other *Enoploteuthis* species have been reported to spawn only over the slopes or in nearshore oceanic regions (Nesis 1993a, 1996).

The paralarvae of *Sthenoteuthis oualaniensis*, an abundant member of the oceanic nekton throughout the tropical and subtropical Indo-Pacific region (Roper et al. 1984, Young & Hirota 1998), were also 'island associated'. Increased catches of *S. oualaniensis* paralarvae in nearshore waters also have been reported from the Saya de Malha Bank, Seychelles, and its slopes (Nesis 1993b) and the Arabian Sea (Piatkowski et al. 1993). Most mature *S. oualaniensis* females collected in the present study area occur along the windward slope of the islands (Suzuki et al. 1986, Young & Hirota 1998), further suggesting that nearshore waters are favorable for spawning.

Some epipelagic squids near the Hawaiian Islands, including *Sthenoteuthis oualaniensis* and possibly *Onychoteuthis* sp. C, may migrate inshore before spawning. Nesis (1993a) has suggested that other oceanic squids (*Todarodes sagittatus*, *Ornithoteuthis* spp. and *Pholidoteuthis* spp.) similarly migrate to seamounts to spawn (Nesis 1993a). Inshore-offshore spawning migrations are common in the Loliginidae (Mangold 1987); these squid must find a solid substrate where they can attach their egg capsules.

Possibly good feeding conditions near the Hawaiian Islands could explain why some oceanic cephalopods appear to spawn preferentially nearshore. Young pelagic squids can consume 80 to 100% of their body weight per day (LaRoe 1971, Hurley 1976). Meeting such a high food requirement may be difficult, particularly in oligotrophic

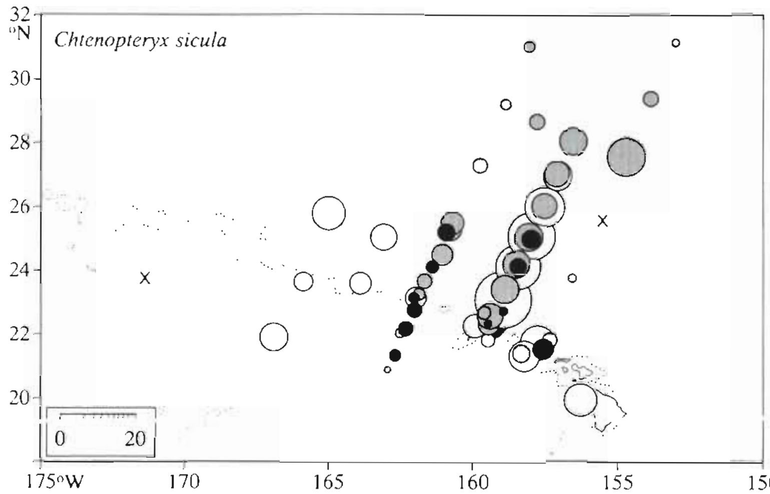

Fig. 8. Distribution and abundance of *Chtenopteryx sicula*. Symbols described in Fig. 1

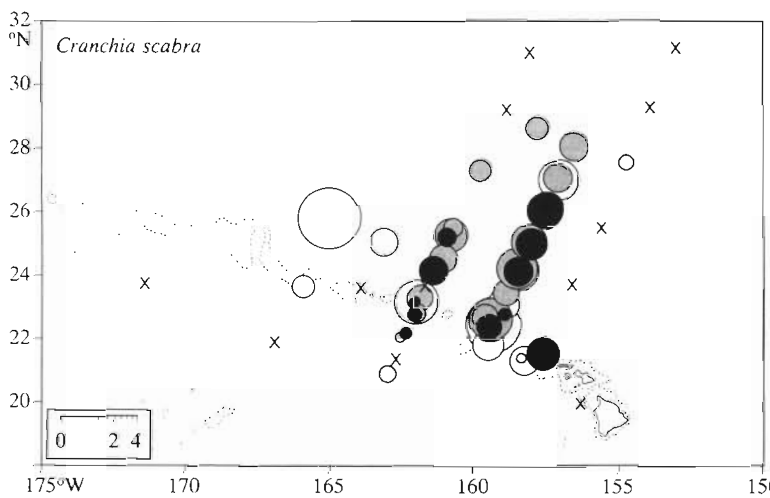

Fig. 9. Distribution and abundance of *Cranchia scabra*. Symbols described in Fig. 1

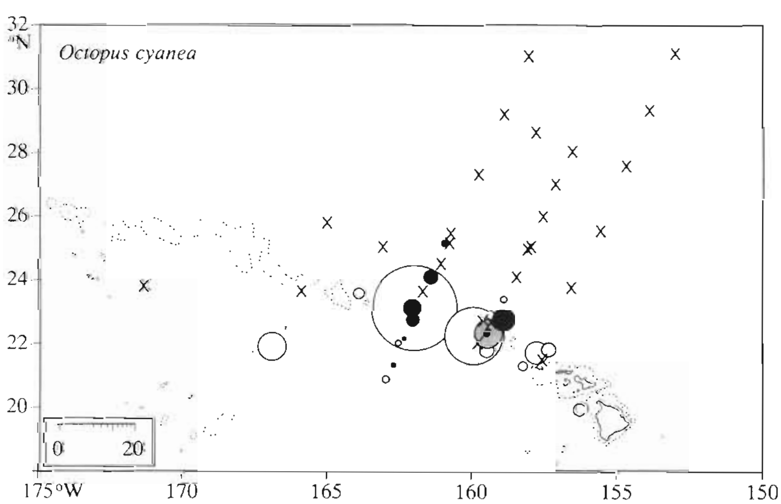

Fig. 10. Distribution and abundance of *Octopus cyanea*. Symbols described in Fig. 1

Table 2. Paralarval assemblages identified from 5 plankton surveys near the Hawaiian Islands. Species groups within assemblages were determined with a 2-way synthesis table technique (TWINSPAN). Only species with ≥15 paralarvae collected were considered in the analyses. Literature references for species with letter designations are listed in Table 1

Island-associated assemblage	Oceanic assemblage
Abralia trigonura	*Abraliopsis pacificus*
Chiroteuthis picteti	*Abraliopsis* sp. A
Enoploteuthis jonesi	*Ancistrocheirus lesueurii*
Histioteuthis hoylei	*Brachioteuthis* sp.
Liocranchia reinhardti	*Chiroteuthis* sp. nov.
Liocranchia valdiviae	*Cranchia scabra*
Nototodarus hawaiiensis	*Chtenopteryx sicula*
Octopus cyanea	*Eledonella pygmaea*
Octopus Type B	*Enoploteuthis higginsi*
Octopus Type C	*Enoploteuthis reticulata*
Octopus Type E	*Helicocranchia* sp. B
Octopus Type H	*Histioteuthis* sp. C
Octopus Type I	*Hyaloteuthis pelagica*
Onychoteuthis sp. C	*Leachia pacifica*
Sthenoteuthis oualaniensis	*Octopoteuthis nielseni*
	Ommastrephes bartramii
	Onychoteuthis compacta
	Onykia sp. A
	Pholidoteuthis sp.
	Pterygioteuthis giardi
	Pterygioteuthis microlampas
	Pyroteuthis addolux
	Thysanoteuthis rhombus

oceanic environments. The islands and seamounts that form the crest of the Hawaiian Ridge result in a number of mesoscale features, including seamount-induced biological and nutrient concentration disturbances (Boehlert & Genin 1987), which could result in advantageous feeding conditions near the islands. Higher productivity and plankton biomass levels very near the Hawaiian Islands (Gilmartin & Revelante 1974) may enhance paralarval survival for some species (see Dandonneau & Charpy 1985). Unfortunately specific conditions that would provide a superior paralarval nursery ground are not known for these waters.

Waters near the Hawaiian Islands also may serve as favorable feeding grounds for spawning adults. Boehlert & Mundy (1994) have suggested that this may be the case for spawning tuna. Pelagic species such as tuna and squid typically aggregate in waters near islands and banks (Uda & Ishino 1958) and above seamounts (Inoue 1983, Yasui 1986) to feed. Increasing evidence indicates that some cephalopods, including *Sthenoteuthis oualaniensis* (Harman et al. 1989, Nigmatullin & Laptikhovsky 1994), are multiple (i.e. iteroparous *sensu lato*) rather than single/terminal (i.e. semelparous *sensu lato*) spawners. Mature females spawning multiple batches of eggs on spawning grounds presumably must feed to survive and reproduce again.

In conclusion, the paralarval fauna near the Hawaiian Islands is the most diverse yet reported (Table 3). Species that showed evidence of increased spawning near the islands include not only those with bottom or nearshore spawning, such as *Abralia trigonura*, *Nototodarus hawaiiensis*, and *Octopus* spp., but also oceanic species not connected with the bottom of nearshore areas, such as *Sthenoteuthis oualaniensis*. Improved feeding conditions in waters near the archipelago might be one reason for the apparent increase in nearshore spawning by some oceanic species.

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Table 3. Numbers of families and species of cephalopod paralarvae collected from different regions. •Octopods not reported

	Hawaiian Islands[a]	Pacific coast of Japan[b,c,d,e,f]	Gulf Stream east of 60° W[g]	Gulf of Guinea[h]	Northwest Pacific[i,j,k,l,m]	Arabian Sea[n,o,p]	California Current[q]
Order Octopoda							
Alloposidae	0		1	0	0	0	
Argonautidae	1		1	1	0	0	
Bolitaenidae	1		0	0	1	1	
Octopodidae	9		2	3	1	1	
Ocythoidae	0		0	1	0	0	
Tremoctopodidae	1		0	0	0	0	
Order Sepioidea							
Idiosepiidae	0	1	0	0	0	0	0
Sepiolidae	1	3	0	0	0	0	0
Order Teuthida							
Ancistrocheiridae	1	1	0	1	0	0	0
Bathyteuthididae	0	0	0	0	0	1	0
Brachioteuthididae	1	1	1	1	1	0	0
Chiroteuthididae	4	1	1	0	0	1	1
Chtenopterygidae	1	1	1	1	0	1	1
Cranchiidae	7	7	3	3	1	2	4
Cycloteuthididae	1	0	0	1	0	0	0
Enoploteuthididae	7	4	3	2	2	3	1
Gonatidae	0	2	2	0	9	0	1
Histioteuthididae	4	0	1	1	1	0	1
Joubiniteuthididae	0	0	1	0	0	1	0
Lepidoteuthididae	1	0	0	0	0	0	0
Loliginidae	0	2	0	0	0	0	1
Lycoteuthididae	0	0	1	0	0	0	0
Mastigoteuthididae	1	0	1	1	0	0	0
Neoteuthididae	0	0	0	0	0	0	0
Octopoteuthididae	2	1	1	0	1	1	1
Ommastrephidae	4	6	1	2	1	2	1
Onychoteuthididae	5	3	2	3	1	1	1
Pholidoteuthididae	1	0	0	0	0	0	0
Psychroteuthididae	0	0	0	0	0	0	0
Pyroteuthididae	3	1	4	2	0	0	1
Thysanoteuthididae	1	1	0	1	1	0	0
No. of families	21	15•	17	15	11	11	11•
No. of species	57	35•	27	24	20	15	14•

References: [a]Present study; [b]Okutani (1968); [c]Okutani (1969); [d]Sato & Sawada (1974); [e]Yamamoto & Okutani (1975); [f]Saito & Kubodera (1993); [g]Dawe & Stephen (1988); [h]Arkhipkin et al. (1988); [i]Okutani (1966); [j]Kubodera & Okutani (1981); [k]Kubodera & Jefferts (1984a); [l]Kubodera & Jefferts (1984b); [m]Kubodera (1991); [n]Nesis (1974); [o]Piatkowski & Welsch (1991); [p]Piatkowski et al. (1993); [q]Okutani & McGowan (1969)

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