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Cephalopods eaten by pelagic fishes in the tropical East Pacific, with special reference to the feeding habitat of pelegic fish

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Abstract: Cephalopods removed from stomachs of pelagic fish in tropical East Pacific were examined. From 131 stomachs of 14 pelagic fish species, more than 40 cephalopod species of 20 families were identified. 30% of prey cephalopods were occupied by the onychoteuthids consisting by at least 3 species followed by the Ommastrephidae (14%), and the Bolitaenidae (7.0%). Predominant prey species for *Xiphias gladius* was epipelagic octopus, *Tremoctopus violaceus*, which shared 17% in number. There were some differences between prey species composition between two species of tunas, *Thunnus obesus* and *T. albacares*. *T. obesus* fed on more deeply distributed, mesopelagic species than *T. albacares*. A coincidence in time and depth was detected between predatory fish and prey cephalopods. Small onychoteuthid species, *Onykia rancureli* was most abundant in number among prey cephalopods (21%). It shared 29% of prey cephalopods for *Thunnus obesus*. From frequency of occurrences in fish stomach contents, *O. rancureli* seems to live in epipelagic or upper mesopelagic waters, abundant around the bottom of mixing layer, and thus plays an important role among food of *T. obesus* and *T. albacares*. From the species composition of eaten cephalopods, the major large pelagic fish discrete feeding depth with minor overlaps, such as, surface layer for bill- and swordfish, around bottom of mixing layer for tunas, and midwater for midwater scombrids. Only *Alepisaurus ferox* seems to be a vertical wonderer.

1. Introduction

The tuna and billfish are well known as the major predators of cephalopods (e.g., DRAGOVICH, 1970; MATTHEWS *et al.*, 1977; PINKAS, 1971; TOLL and HESS,1981). Also, many species of pelagic fish, such as *Alepisaurus ferox*, consume pelagic cephalopod stock (e.g., MOTEKI *et al.*, 1993). However, the detailed taxonomic analyses of prey cephalopods have been rather scarce(RANCUREL, 1970; OKUTANI and TSUKADA, 1988; TOLL and HESS, 1981). The information from the pelagic fish stomach contents is very useful, especially in the toropical waters, of which pelagic cephalopod fauna has seldom been studied (DUNNING *et al.*, 1993; SMALE, 1996).

National Research Institute fo Far Seas Fisheries has promoted the survey on the pelagic fish resources in the tropical East Pacific. During the survey, they investigated the stomach contents of pelagic fish caught by longline. The present study aims to discuss the feeding habitat of pelagic fish based on exact identification of cephalopods in fish stomach contents, and to clarify niches of prey cephalopods in oceanic food web.

2. Materials and Methods

Materials examined in the present study were collected during the fisheries surveys on the potential resources of tuna and billfish undertaken by the National Research Institute of Far Seas Fisheries (NRIFSF). The surveys were carried out in the tropical East Pacific in June and July 1994, and June and July 1995 on board the fishing boat FR/V *Kaihatsu-Maru*, chartered by Japan Marine Resource Research Center (JAMARC), and R/V *Shoyo-Maru*, Fisheries Agency of Japan, respectively. The fish were all collected with the longline from 56 stations (Fig. 1).

The total nomber of fish examined were 131 of 14 species of 8 families (Table 1). More than

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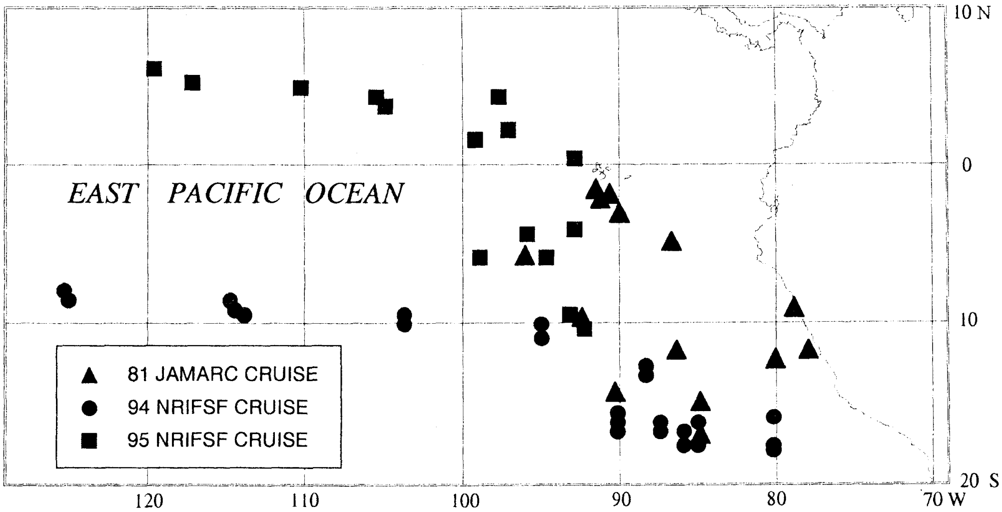

Figure 1. Sampling stations.

Table 1. Number of stomachs by fish species examined in the present study

Survey month	81 Dec.-Apr.	94 Jun.-Jul.	95 Jun.-Jul.	Total	SL (cm)
Family Alopiidae					
Alopias pelagicus			2	2	
Family Carcharhinidae					
Prionace glauca			6	6	
Carcharinus falciformis			1	1	
Family Odontaspididae					
Pseudocarcharias kamoharai		1		1	
Family Alepisauridae					
Alepisaurus ferox			2	2	
Family Lampridae					
Lamprius regius		1		1	
Family Istiophoridae					
Tetrapturus audax		1	7	8	
T. angustirostris		1		1	
Istiphorus platypterus				1	
Family Xiphiidae	1				
Xiphias gladius		18	5	23	63–166
Family Scombridae					
Thunnus albacares	3	21	3	27	94–157
T. obesus	13	39	4	56	70–161
T. alalunga		1		1	
Acanthocybium solandri		1		1	
Total (8 fam. 14 spp.)	17	84	30	131	

60% in total number was occupied by two species of tunas. The majority of tunas and shordfish were almost similar in body size.

The stomachs were removed and frozen, or fixed by 50% formalin-sea water solution on board. The frozen samples were thawed in the university laboratory, and fixed in 10% formalin.

Table 2. Cephalopods identified from the fish stomach contents

Family Heteroteuthidae	*Eucleoteuthis luminosa*
Heteroteuthis sp.	*Hyaloteuthis pelagicus* *
Family Ctenopterygiidae	?*Dosidicus gigas* *
Ctenopteryx sicula *	Family Pholidoteuthidae
Family Histioteuthidae	*Pholidoteuthis boschmai* *
Histioteuthis spp.	Family Lepidoteuthidae
Family Lycoteuthidae	*Lepidoteuthis grimaldi*
Lampadioteuthis megalea	Family Architeuthidae
Family Enoploteuthidae	*Architeuthis* sp.
Enoploteuthis ?leptura	Family Thysanoteuthidae
Enoploteuthis reticulate	*Thysanoteuthis rhombus* *
Enoploteuthis (s.s.) sp.	Family Chiroteuthidae
ENOPLOTEUTHIDAE sp.	*Chiroteuthis* spp.* (part)
Family Pyroteuthidae	*Grimalditeuthis bonplandii* *
Pyroteuthis sp.	CHIROTEUTHIDAE sp. indet
PYROTEUTHIDAE sp.	Family Cranchiidae
Family Ancistrocheiridae	*Cranchia scabra* *
Ancistrocheirus lesueuri *	*Liocranchia reinhardti* *
Family Onychoteuthidae	*Leachia* sp.*
Onychoteuthis sp.*	*Helicocranchia* sp.*
Onykia rancureli	?*Taonius* sp.
Moroteuthis robsoni *	Family Argonautidae
Moroteuthis sp.	*Argonauta? argo*
Family Octopoteuthidae	*Argonauta hians* *
Octopoteuthis sp.*	Family Tremoctopodidae
Taningia danae	*Tremoctopus violaceus* *
Family Ommastrephidae	Family Bolitaenidae
Sthenoteuthis oualaniensis *	*Japetella diaphana* *
Sthenoteuthis sp.	Family Allopodidae
Ornithoteuthis volatilis	*Haliphron atlanticus*

*Asterisk suggests the common species with NESIS (1973) and ALEXEYEV (1994).

3. Results

Cephalopods from fish stomachs were identified more than 40 species of 20 families (Table 2).

Predator which used most divergent prey species was *T. obesus* feeding on more than 35 species of cephalopods. This number of prey species occupies about 90% in number of total prey cephalopods. In contrast to this, *T. albacares* fed on 16 cephalopod species which attains 40% in prey cephalopods. *Xiphias gladius* fed only on 10 cephalopod species (25%) (Table 3).

Most abundant family of prey cephalopods was the Onychoteuthidae which occupies 30% consisting at least of 3 species, followed by the Ommastrephidae (14%, six species), the Bolitaenidae (7%, a single species, *Japatella diaphana*), the Argonautidae and the Cranchiidae (5% each).

Cephalopod species that were not common for two tuna species were 25, such as *Onykia* spp. (10%) which was peculiar to *T. obesus*. In contrast, three pelagic octopods, *Argonauta hians*, *Tremoctopus violaceus* and *Japatella diaphana* were not found from stomachs of *T. obesus*. Among bill- and swordfish species, there was no specific prey species unlike in case of two tuna species.

Among the species occurred, *Onykia rancureli* was dominant one occupying 21% in number of all.

From stomachs of *T. albacares* and *T. obesus*, *O. rancureli* was most frequent (12% and 29%, respectively) (Table 4). Among bill- and swordfishes, mainly *Xiphias gladius*, *O. rancureli* was

Table 3. Number and occupancy of prey species in stomachs of main predator fishes

	T. albacares		*T. obesus*		*X. gladius*		Others		Total	
	no.	%	no.	%	no.	%	no.	%	no.	%
Heteroteuthis sp.	0	0.0	1	0.4	0	0.0	0	0.0	1	0.2
Chtenopteryx sicula	1	1.0	1	0.4	0	0.0	0	0.0	2	0.4
Lampadioteuthis megaleia	1	1.0	0	0.0	0	0.0	0	0.0	1	0.2
Enoploteuthis ? leptura	0	0.0	4	1.5	0	0.0	0	0.0	4	0.9
Enoploteuthis reticulata	3	3.0	2	0.7	0	0.0	1	1.7	6	1.3
Enoploteuthis (s.s.) sp.	0	0.0	2	0.7	0	0.0	0	0.0	2	0.4
ENOPLOTEUTHIDAE sp.	2	2.0	3	1.1	0	0.0	0	0.0	5	1.1
Pyroteuthis sp.	1	1.0	6	2.2	0	0.0	0	0.0	7	1.5
PYROTEUTHIDAE sp.	0	0.0	1	0.4	0	0.0	0	0.0	1	0.2
Onychoteuthis sp.	0	0.0	12	4.4	0	0.0	2	3.4	14	3.1
Ancistrocheirus lesueuri	0	0.0	1	0.4	0	0.0	1	1.7	2	0.4
Moroteuthis robsoni	0	0.0	2	0.7	0	0.0	0	0.0	2	0.4
Moroteuthis sp.	0	0.0	24	8.9	0	0.0	0	0.0	24	5.2
Onykia rancureli	12	12.0	79	29.3	2	6.7	2	3.4	95	20.7
ONYCHOTEUTHIDAE sp.	0	0.0	3	1.1	1	3.3	0	0.0	4	0.9
Octopoteuthis sp.	0	0.0	1	0.4	0	0.0	0	0.0	1	0.2
Taningia danae	1	1.0	0	0.0	0	0.0	0	0.0	1	0.2
Histioteuthis spp.	0	0.0	3	1.1	0	0.0	0	0.0	3	0.7
Chiroteuthis sp.	0	0.0	2	0.7	0	0.0	2	3.4	4	0.9
Grimalditeuthis bonplandi	0	0.0	2	0.7	0	0.0	0	0.0	2	0.4
Lepidoteuthis grimaldi	0	0.0	0	0.0	0	0.0	1	1.7	1	0.2
CHIROTEUTHIDAE sp.	0	0.0	1	0.4	0	0.0	4	6.8	5	1.1
Architeuthis sp.	0	0,0	1	0.4	0	0.0	0	0.0	1	0.2
Pholidoteuthis boschmai	4	4.0	7	2.6	1	3.3	0	0.0	12	2.6
Eucleoteuthis luminosa	0	0.0	0	0.0	1	3.3	0	0.0	1	0.2
?Dosidicus gigas	1	1.0	9	3.3	0	0.0	0	0.0	10	2.2
Sthenoteuthis oualaniensis	10	10.0	28	10.4	1	3.3	1	1.7	40	8.7
Sthenoteuthis sp.	0	0.0	1	0.4	0	0.0	0	0.0	1	0.2
Ornithoteuths volatilis	0	0.0	1	0.4	0	0.0	0	0.0	1	0.2
Hyaloteuthis pelagicus	3	3.0	0	0.0	2	6.7	8	13.6	13	2.8
OMMASTREPHIDAE spp.	16	16.0	5	1.9	3	10.0	1	1.7	25	5.4
Thysanoteuthis rhombus	3	3.0	7	2.6	3	10.0	1	1.7	14	3.1
Cranchia scabra	0	0.0	4	1.5	1	3.3	1	1.7	6	1.3
Liocranchia reinhardti	0	0.0	1	0.4	0	0.0	0	0.0	1	0.2
Leachia sp.	2	2.0	3	1.1	0	0.0	1	1.7	6	1.3
Helicocranchia sp.	0	0.0	1	0.4	0	0.0	0	0.0	1	0.2
Taonius sp.	0	0.0	1	0.4	0	0.0	0	0.0	1	0.2
CRANCHIIDAE spp.	2	2.0	3	1.1	0	0.0	1	1.7	6	1.3
Argonauta hians	6	6.0	2	0.7	0	0.0	0	0.0	8	1.7
Argonauta sp.	2	2.0	3	1.1	2	6.7	6	10.2	13	2.8
Tremoctopus violaceus	7	7.0	3	1.1	8	26.7	3	5.1	21	4.6
Japetella sp.	9	9.0	19	7.0	2	6.7	2	3.4	32	7.0
Haliphron atlanticus	0	0.0	1	0.4	0	0.0	0	0.0	1	0.2
Pelagic octopus	0	0.0	0	0.0	0	0.0	10	16.9	10	2.2
Unidentified oegopsids	0	0.0	1	0.4	0	0.0	0	0.0	1	0.2
Unidentified squids	12	12.0	12	4.4	3	10.0	6	10.2	33	7.2
Unidentified	2	2.0	7	2.6	0	0.0	5	8.5	14	3.1
Total	100	100	270	100	30	100.0	59	100.0	459	100.0

Table 4. Ranking of occupancy in total cephalopod population in major fish stomachs

Species	*T. obesus* (56)	*T. albacares* (27)	Bill-& Swordfish (33)	*A. ferox** (45)
1	*O. rancureli* (29.3%)	*O. rancureli* (12.0%)	*T. violaceus* (16.7%)	*J. diaphana* (23.8%)
2	*S. oualaniensis* (10.6%)	*S. oualaniensis* (9.3%)	*H. pelagicus* (11.7%)	*O. rancureli* (19.0%)
3	*Moroteuthis* sp. (9.1%)	*J. diaphana* (8.4%)		*A. boettgeri* (16.7%)

*Collected from north off Hawaiian Islands, Dec. 25, 1979 (TSUCHIYA, pers. obs.).

scarce (5% in total bill-and swordfish).

Most abundant cephalopod eaten by bill- and swordfish is *Tremoctopus violaceus* (16.7%), followed by *Hyaloteuthis pelagicus* (11.7%), but there was no pronouncedly dominant species among prey cephalopods. Such a high utilization by bill- and swordfish of *H. pelagicus* (11.7% versus 3% in *T. albacares*) and *T. violaceus* (16.7% versus 7% in *T. albacares*) was quite characteristic in contrast to tunas that seldom fed on these cephalopods. The occurrence of large-sized *Thysanoteuthis rhombus* from the billfish stomach was also characteristic, though not so frequent.

4. Discussion

The pelagic fish are considered to be good samplers for pelagic cephalopods (CLARKE, 1996; VOSS, 1973; DUNNING *et al.*, 1993). Adult tunas are generally considered to be opportunitic feeders with low prey selectivity (SMALE, 1996). *X. gladius* predation also suggests that it exhibits opportunistic nature (SCOTT and TIBBO, 1968; TOLL and HESS, 1981). The result of the present study suggests that the stomach contents of pelagic fish are reflected directly to the pelagic cephalopod fauna of the tropical East Pacific.

Almost of all species occurred in the pelagic fish diet are epipelagic and upper mesopelagic species, and none of lower mesopelagic species, such as cycloteuthids or *Mastigoteuthis* species (ROPER and YOUNG, 1975) were eaten.

From the tropical East Pacific, 42 species of cephalopods have been reported by NESIS (1973) and ALEXEYEV (1994). 19 species in the listed species in the present study are common to those in NESIS (1973) and ALEXEYEV (1994). They are all epipelagic or upper mesopelagic species (ROPER and YOUNG, 1975). The major families of prey cephalopod are consisted of strong swimming squids (e.g., Onychoteuthidae, Ommastrephidae). This fact suggests that the swimming speeds of predators exceed that of prey, and a low possibility of negative food selection occurs by avoidance of prey. Sporadically occurred species are considered to live in mesopelagic life in adult stage (e.g., *Taningia danae*, *Lepidoteuthis grimaldii*). But, those found in the present material are all in early juvenile stages which inhabit epipelagic zone(ROPER and YOUNG, 1975; LU and CLARKE, 1975; ROPER and VECCHIONE, 1993). The possibly abundant species in the survey area, viz. *Abraliopsis* spp., never occurred in the present stomachs.

The main fishing depth of *T. obesus* is 100–250m which coincides with the depth of thermocline or just below it (SUDA *et al.*, 1969; HANAMOTO, 1975, 1987). While, HANAMOTO (1987) and BOGGS (1992) estimated that *T. obesus* inhabits the depth of 200–400m, the lower boundary of which almost agrees with 10℃-isotherm. Tracking study suggests that *T. albacares* spends most of the time in the layer shallower than the habitat of *T. obesus*, at about 30–80 m on the bottom of the mixing layer (HOLLAND *et al.*, 1990). Tunas are foraging and feeding both in day and night, but seemingly mainly in daytime (SHAFER *et al.*, 1963; KUME and MORITA, 1966). *X. gladius* is fished at 50–60 m deep during night (GUERRA *et al.*, 1993). Tracking study elucidated that *X. gladius* spends almost all the time at the layer shallower than 50m, which agrees with 20–25 ℃-isotherm during night, while descends to 600 m during daytime (CAREY and ROBINSON, 1981; CAREY, 1990). The main fishing depth seems to be almost coincident with foraging and feeding depths of these fish. Thus, the vertical distributions of pelagic fish well indicate those of prey cephalopod species.

Among pelagic fish under the study, there are some differences in stomach contents composition. Pelagic octopod species of which *Tremoctopus violaceus* is most abundant, are confined to bill-and swordfish. This octopod is a cosmopolitan in the tropical to warm temperate waters of the world (THOMAS, 1977). On diel vertical migration, *T. violaceus* is probably limited to upper 100 m and does not descend below thermocline (THOMAS, 1977). BEARSLEY (1978) has indicated that *X. gladius* migrates towards the surface at night to feed and returns to deeper waters in daytime. The fact of occurrence of *T. violaceus* in.stomach of *X. gladius* supports his view.

In the stomach of *X. gladius* in the Florida Straits, *Illex* species were predominant, and the majority of prey cephalopods were shared by five ommastrephid species (TOLL and HESS, 1981). GUERRA *et al.* (1993) also reported the dominant occupancy of ommastrephids in the diet of *X. gladius* in the Northeast Atlantic. In the present material, ommastrephids are not so much abundant nor predominant. Predominant occurrence of ommastrephids seems to relate the massive schooling behavior of squids. Occurrences of *Thysanoteuthis rhombus* and *Argonauta species* are also characteristic to *X. gladius* diet (TOLL and HESS, 1981).

All epipelagic or near-surface cephalopods mostly inhabit in the water shallower than 100m at night (ROPER and YOUNG, 1975 ; NESIS, 1977; LU and ROPER, 1979). *T. rhombus* shared 7.0% of prey cephalopods for *X. gladius,* while only 2.6% for tunas. *T. rhombus* stays at upper mixing layer during daytime, while shifts to surface water during night (ROPER and YOUNG, 1975; NESIS, 1977, 1992). This vertical migration causes the possible availability to feeding depth of both bill- and swordfish. Occurrence of *T. violaceus* was not recognized by TOLL and HESS (1981), and no *T. rhombus* was reported by GUERRA *et al.* (1993).

Between two species of tunas, *T. obesus* exhibits higher diversity of prey. Characteristic prey items of *T. obesus* are mainly lower epipelagic or upper mesopelagic species, such as *Ancistrocheirus lesueuri, Chiroteuthis* spp. and *Grimalditeuthis bonplandi* (ROPER and YOUNG, 1975; NESIS, 1977; LU and ROPER, 1979). Juvenile *G. bonplandi* is distributed in 200–900m deep without distinct vertical migration (LU and CLARKE, 1975). In contrast to this, the prey items of *T. albacares* do not include such deep dwelling species. This difference well agrees with the difference of foraging and feeding depth between two species of tunas as mentioned above, suggesting that *T. obesus* has broader feeding depth than *T. albacares.*

The species most frequently occurred was *Onykia rancureli* which shared 20.7% in all cephalopods. *O. rancureli* is a small-sized species. The male reaches in spent stage at about 15 cm, and the maximum female is 13 cm in dorsal mantle length (TSUCHIYA, pers. obs.). This species is widely distributed in the warm waters of the Indo-Pacific. Distribution pattern almost agrees with the isotherm of 25℃ surface temperature in winter (TSUCHIYA and OKUTANI, MS).

Although such an abundant and frequent occurrence of *O. rancureli* from fish stomach, the vertical distribution of this species has never been studied. This species is very scarce in tow net samples, and almost all of the materials hitherto known (RANCUREL, 1970; OKUTANI, 1981; OKUTANI and TSUKADA, 1988) were collected from stomachs of lancetfish or tunas. Table 5 shows the frequency of *O. rancureli*-fed fish versus total fish, and occupancy of *O. rancureli* versus the total prey cephalopod in number. In the present study, about a half of *T. obesus* fed on *O. rancureli.* In OKUTANI and TSUKADA (1988), the frequency of this squid in tuna stomach from the study area exceeds 70% (Table 6). For the occupancy of prey cephalopods, *T. obesus* also shows the high value. In the material treated by OKUTANI and TSUKADA, *O. rancurele* occupied 40% of prey cephalopods. dominant occurrence (26%) of *O. rancureli* from 18 stomachs of tuna was also observed in sample of the 1981 cruise.

The frequency and occupancy of *O. rancureli* in *T. albacares* stomachs were not so high. In RANCUREL'S (1976) material, *O. rancureli* occupied only 5% of the total prey cephalopod from

Table 5. Frequency in number of stomachs and occupancy of *Onykia rancureli* to the total prey cephalopods

	Frequency *1		Occupancy *2	
Tunas	39.3%	[33/84]	24.3%	[92/379]
T. albacares	22.2%	[6/27]	12.0%	[12/100]
T. obesus	46.4%	[26/56]	29.3%	[79/270]
Bill-& Swordfish	9.1%	[3/33]	5.0%	[3/60]
T. audax	12.5%	[1/8]	6.7%	[1/27]
X. gladius	8.7%	[2/23]	3.7%	[2/30]

*1 Numerals in brackets mean no. of *O. rancureli*-eating fish/total no of fish.
*2 Numerals in brackets mean no. of *O. rancureli* eaten by fish/total no. of eaten squids.

Table 6. Frequency in number of stomachs and occupancy of *Onykia rancureli* to total prey cephalopods

	Frequency *1		Occupancy *2	
Tunas *3	72.2%	[13/18]	40.0%	[38/95]
T. albacares *4	19.3%	[40/207]	4.6%	[54/1158]
G. melampus *5	0%	[0/16]	0%	[0/62]
A. ferox *6	24.4%	[11/45]	19%	[16/84]
A. ferox *7	24.0%	[37/154]	13.8%	[46/33]

*1 Numerals in brackets mean no. of *O. rancureli*-eating fish/total no. of fish.
*2 Numerals brackets mean no. of *O. rancureli* eaten by fish/total no. of eaten squids.
*3 East Pacific, Oct. 8–Mar. 7, 1980 (OKUTANI and TSUKADA, 1988).
*4 SW off New Guinea (RANCUREL, 1976).
*5 Collected from 20°–40° S, 80°–120° W (TSUCHIYA and SAWADAISHI, 1997).
*6 Collected from N off Hawaiian Islands, Dec. 25, 1979 (TSUCHIYA, pers. obs.).
*7 Tropical Indo-West Pacific and Central Pacific (OKUTANI and TSUKADA, 1988).

207 stomach samples of *T. albacares* in the Southwest Pacific. This value is similar to the results of the present study.

MOTEKI *et al.* (1993) studied the stomach contents of *Alepisaurus ferox* in the Hawaiian waters and central equatorial Pacific. In 42 stomachs, the most abundant species was *Japetella diaphana* (31% in frequency), but *O. rancureli* occupied only 7.14% among 22 cephalopod taxa. *J. diaphana* was also dominant (36%) in the sample from Southwest Pacific, while *O. rancureli* was only 1% (MOTEKI *et al.*, 1993). RANCUREL (1970) also reported 4% of occurrence of *O. rancureli* (as *Onychia* sp.) in the stomach of *A. ferox* in the equatorial Pacific. *Gasterochisma melampus* is also a large predator distributed in the study area. TSUCHIYA and SAWADAISHI (1997) examined 15 stomachs of *Gasterochisma melampus* from the Southeast Pacific, but no occurrence of *O. rancureli* was recognized. These low values seem to suggest the main feeding depth of these pelagic fish is separated from the habitat dapth of *O. rancureli.*

The vertical distributions of predator fishes are shown in Table 7 on the basis of fishing data. These pelagic fish feed on different prey species according to their swimming depth at feeding time. KORNILOVA (1980) also concluded that sympatric two species of tunas, *T. albacares* and *T. obesus* overlap in prey items, the considerable differences of feeding depth are recognized between them. From the results of RANCUREL (1970) and MOTEKI *et al.* (1993), the lancetfish feeds the cephalopods over wide bathymetirical range, and seems to be a vertical wanderer. In the epipelagic water of the tropical East Pacific, *Tremoctopus violaceus*, *Thysanoteuthis rhombus* and small ommastrephids are key prey cephalopods for large

Table 7. Vertical distributions of predator fish with the characteristic prey cephalopods

Predator fish	Main fishing depth	Depth(m)	Characteristic prey cephalopods	*O. rancureli*
Bill-& Swordfish	shallower	(50–150)	*T. violaceus, H. pelagicus*	+
T. ablacares	↓	(50–180)	*S. oualaniensis*	++
T. obesus	↓	(100–230)	*S. oualaniensis*	+++
A. ferox	↓	(100–300)	*J. diaphana*	++
G. melampus *	deeper	(150–300)	*G. bonplandi, E. luminosa*	−

*From 25°–40° S(TSUCHIYA and SAWADAISHI, 1997).

predator (e.g., *X. gladius*). Food of *T. albacares* shows the dominant occurrence of ommastrephids, and also loliginids, especially in coastal and shelf waters (DRAGOVICH, 1970; SMALE, 1986). Epipelagic scombrid fish *Allotunus fallai* in Southeast Pacific also takes ommastrephids as a dominant food (YATSU, 1995). In the upper mesopelagic water, *O. rancureli* is one of key species as the prey for pelagic fishes. In the mesopelagic water, the gelatinous cephalopods such as *Japetella diaphana, Grimalditeuthis bonplandi* and *Chiroteuthis* species, are the important food items for large predator fishes. These mesopelagic cephalopods are usually not so abundant in tow-net samples (e.g., YOUNG, 1972; OKUTAI, 1974).

From the view point of cephalopod ecology, the large pelagic fish that feed in nighttime, possibly discrete the feeding layer into three, namely, near surface water, bottom of mixed layer and mesopelagic water. The prey species also discrete their habitat into the above-mentioned vertical strata. The fish that take abundant epipelagic species, could feed on any prey species regardless their swimming ability. Their diet includes both muscular storong swimmers (e.g., ommastrephids) and drifter (e.g., argonautids). In contrast to them, the midwater fish that take mainly gelatinous cephalopods (e.g., chiroteuthids, cranchiids) and weak muscular midwater species (e.g., brachioteuthids) having no relation to natural abundance (CLARKE *et al*., 1979). *O. rancureli* is muscular, nonbuoyant species. Its short and globose mantle, broad and round fins adapt to directional control rather than high speed swimming (CLARKE, 1988). As the boundary of vertical distribution of two tuna species almost coincides with bottom of mixed layer (KORNILOVA, 1980; HOLLAND *et al*., 1990), *O. rancureli* that is eaten commonly and dominantly by these two tuna species, is proved to inhabit that depth with large biomass. The bottom of mixed layer is a boundary of vertical distribution and diel vertical migration of ichthyopankton. High abundance of ichthyoplankton is shown in both upper and lower peripheries of this layer at night (LOEB, 1986). This layer seems to be an important foraging area for two species of tunas.

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