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FEEDING ECOLOGY OF MARINE CORMORANTS IN SOUTHWESTERN NORTH AMERICA

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ABSTRACT.—The diets of Pelagic, Brandt's and Double-crested cormorants (*Phalacrocorax pelagicus, P. penicillatus* and *P. auritus*) were compared. Data were based on 1,695 pellets and 71 chick regurgitations analyzed by us and information on 34 stomach samples published in the literature. A total of 19 sites between Kodiak, Alaska and central Mexico is represented. The three cormorants often fed in the same areas at the same time using the same technique. They exploited different microhabitats as defined by prey behavior; the prey species overlapped substantially between Brandt's and Pelagic cormorants, but those of the Double-crested Cormorant were quite different. Double-crested Cormorants fed on schooling fish usually occurring well above flat bottoms; Pelagic Cormorants fed on solitary prey on or concealed in rocky substrates; and Brandt's Cormorants fed on prey on or just above the bottom in rocky areas and in areas of flat sand or mud. The latter species fed over flat bottoms more in the northern part of their range than in the southern part where they fed almost exclusively in or near rocky habitat. Double-crested and Pelagic cormorants showed no geographic shift in their feeding habits.

The feeding ecology of marine birds has been defined in five major ways: the distance offshore at which a species feeds (inshore, offshore or pelagic; Wynne-Edwards 1935), the depth to which it dives (bottom, mid-water or surface; Balz and Morejohn 1977), the prey species consumed (Ainley and Sanger 1979), prey size (Ashmole 1968), and the methods of food capture (Ashmole 1971). Except for diving depth, little has been said about differences in feeding habitat. This contrasts markedly with land birds, whose use of microhabitats for feeding is a well-known phenomenon. In the present article we attempt to define much more narrowly the feeding habitats of three sympatric, closely related seabird species: the Pelagic, Brandt's and Double-crested cormorants (*Phalacrocorax pelagicus, P. penicillatus* and *P. auritus*). Heretofore, all have been regarded as feeding similarly, by diving beneath the surface, from the bottom to mid-depths, in inshore waters. So similar has their feeding ecology appeared that Cody (1973) was led to postulate that, in areas of sympatry, breeding seasons have become staggered as a means to distribute demand on available food resources.

We obtained information on prey from the analysis of fish otoliths and invertebrate hard parts in pellets. Pellets, which cormorants apparently produce almost daily, have received very little attention from seabird researchers, yet they prove invaluable in a study such as ours. In cormorants, these pellets are equivalent to stomach samples in terms of what they indicate about diet (Jordán 1959, Schlatter and Moreno 1976; Ainley, unpubl. data). Birds do not have to be collected for their stomachs nor harassed in order that they regurgitate their stomach contents; thus, large samples and time series of samples can be gathered. The attainment of adequate samples to allow valid comparisons between species has posed problems in studies of marine birds (Balz and Morejohn 1977).

Jordán (1959) gave a detailed description of cormorant pellets and the mechanism and frequency of their production. Why cormorants produce pellets is not known, but the fact that pellets often contain many nematodes indicates that they may aid in parasite control (Jordán 1959; Ainley, unpubl. data). They are produced only by adult and subadult cormorants; younger birds begin producing them at about the time they are able to fly. In forming the pellet, the stomach contents are enveloped in mucus secreted by the stomach wall. Upon drying, the pellet becomes very hard. A cormorant regurgitates one pellet during the night, usually just before dawn, when it departs for daily feeding. Regurgitation before daylight not only allows maximum time for the previous day's meal to be digested, but also allows deposition without the notice of gulls. Gulls fight one another for pellets, an activity that disrupts the cormorant colony. (This consumption of cormorant pellets may explain the remains of deepwater prey in gull pellets and stomachs [e.g., Martini 1966]—an enigma since gulls do not dive for food.)

METHODS

Pellets were collected just after the breeding season from the vicinity of nest sites at 11 localities between central California and central Mexico (see below). Although cormorants produce pellets throughout the year, it is easiest to find them among closely-spaced nests where gulls do not scavenge. Additional information from stomach samples and chick regurgitations collected by ourselves and other persons at other sites was used for comparison. Since cormorants feed young by regurgitation, stomach samples, chick regurgitations and pellets are equivalent (Jordán 1959). We compared data on cormorant diets from 19 localities from Alaska to Mexico.

Fish were identified by otoliths (sagittae), cephalopods by beaks, and other invertebrates by various hard parts. The number of otoliths of each fish species was divided by two in order to estimate the number of individuals eaten. In the case of cephalopods, we took the number present to be the greater number of upper or lower beaks.

Fish size can be related to otolith size, but in practice this has been done for only a few commercially important species, and we found few of these in our samples. The prey discussed in this paper, including both fish and invertebrates, ranged in lengths from 5 to 15 cm. Such a size range rules out, in most cases, the possibility that significant numbers of the prey we ascribed to cormorants could actually have been eaten by the cormorants' prey, an important consideration in a study such as ours (Owre 1967).

Feeding habitats of cormorants were ascertained by comparing the behavior and habitat preferences of the prey they consumed. This information was gleaned from the literature, tabulated, and then given to ichthyologists for confirmation. This list is available upon request from the senior author. Key references used in habitat identification were Hobson (1965), Fitch (1967), Fitch and Lavenberg (1968, 1971, 1973), Frey (1971), Miller and Lea (1972), Hart (1973), and Ebeling and Bray (1976).

The following is a summary of samples at each site (PC = Pelagic Cormorant, BC = Brandt's Cormorant, DCC = Double-crested Cormorant): Kodiak Is., Alaska 1977—9 PC stomachs (Sanger, unpubl. data); Mandarte Is., British Columbia 1969–71—unknown numbers of PC and DCC chick regurgitations (Robertson 1974); Vancouver Is. (1969–70—13 BC stomachs (Robertson, unpubl. data); Yaquina Head, Oregon 1969–70—29 BC chick regurgitations (Scott 1973); South Farallon Is., California 1973–77—199 PC pellets, 31 BC regurgitations and 283 BC pellets, as well as 175 DCC pellets; Monterey Bay, California 1974—6 BC stomachs (Balz and Morejohn 1977); Santa Rosa Is., California 1977—50 BC pellets; Santa Cruz Is., California 1976–77—175 BC pellets; San Miguel Is., California 1976–78—39 DCC chick regurgitations; San Nicolas Is., California 1976–77—135 BC pellets; Anacapa Is., California 1977—1 DCC chick regurgitation; San Clemente Is., California 1976–75 BC pellets; Is. Coronados, Baja California 1969—15 BC stomachs (Hubbs et al. 1970); I. San Martín, Baja California 1975—35 DCC pellets; Bahia de los Angeles, Gulf of California 1975–77—191 BC and 106 DCC pellets; I. San Esteban, Gulf of California 1974—14 BC pellets; I. Sal Si Puedes, Gulf of California 1974—29 BC pellets; Bahia de Kino, Sonora 1973–75—208 DCC pellets; and Bahia de Pabellon, Sinaloa 1975—20 DCC pellets.

TABLE 1. Prey species of cormorants that contribute at least 1% and 10% of the diet, sorted by habitat and behavior characteristics. Percentages of prey that fit into various categories are shown.

	Diet contribution					
	Pelagic		Brandt's		Double-crested	
Prey characteristics	1% (9)[a]	10% (5)	1% (50)	10% (17)	1% (41)	10% (15)
Behavior						
Schooling	22	40	60	53	66	67
Non-schooling	78	60	40	47	34	33
Substrate						
Rocky	78	80	36	40	24	20
Flat	22	20	38	33	63	67
Rocky/flat			18	20	7	
Mid-water			8	7	6	13
Depth						
Surface–mid-depth	11		14	12	22	33
Mid-depth–bottom	11	20	47	47	39	27
Bottom	22		27	29	39	40
Bottom–cryptic	56	80	12	12		

[a] Number of prey species.

RESULTS

Pelagic Cormorants range from the Bering Sea to southern California, but few occur south of central California (Palmer 1962). The three sample sites compared span the species' range (Appendix 1). The only prey common to all sites were large decapod "shrimp." Beyond that there was little similarity in major species consumed, except at the two northern sites where these cormorants ate many sandlance (*Ammodytes*). Only at Mandarte Island were pholids important prey, and Pelagic Cormorants at the Farallones ate mostly sculpins (cottids) and rockfish (*Sebastes*). In all places, most prey were non-schooling inhabitants of rocky reefs. Many were species that remain in close contact with, and even conceal themselves in, the rock and kelp substrate (Tables 1 and 2). This diet indicates that the name "Pelagic" Cormorant is inappropriate, because these substrates occur in inshore neritic areas.

Diets of Brandt's Cormorant were represented for 12 sites, including four sampled by other researchers. All but the Vancouver Island and Monterey Bay samples were gathered during the spring and summer. This species was thus studied throughout

TABLE 2. Percentage of prey in cormorant diets by geographic location and substrate preference.

	Substrate preferences of prey[a]											
	Pelagic				Brandt's				Double-crested			
Locality	R	F	R/F	N	R	F	R/F	N	R	F	R/F	N
Kodiak Island	54	45										
Mandarte Island	65	35							49	49		2
Vancouver Island					76	24						
Yaquina Head					55	17		24				
Farallon Islands	99	1	1	1	72	23	3	2	3	78	4	14
Monterey Bay					32	36	4	28				
Santa Rosa Island					92	7	1					
Santa Cruz Island					86	8	4	2				
San Miguel Island									54	1	22	23
San Nicolas Island					78	5	14	3				
San Clemente Island					89	3	4	4				
Coronados Islands					22	42	33	3				
San Martín Island									2	79	4	15
Bahia de los Angeles					47	22	28	1	6	85	6	3
San Esteban Island					30	5	65					
Sal Si Puedes Island					51	26	23					
Kino Bay									1	77	8	12
Pabellon										97	3	

[a] Symbols denoting habitat of prey: R = rocky reef; F = flat sand or mud; R/F = flat area near rocks; N = no substrate designated because fish dwell from mid-depths to the surface.

its entire range, the major part of which extends from the Gulf of California north through Oregon (Palmer 1962). Small isolated populations occur from there northward as far as southeastern Alaska (Sowls et al. 1978). Several prey species or species groups were common to diets at many Pacific Coast sites and other groups were common to Gulf of California sites. Especially prevalent as food among Pacific populations were *Engraulis, Oxyjulis, Chromis,* and *Sebastes*; several other fishes were found in diets at several sites but were much less important (Appendix 2). In the Gulf of California, *Apogon, Abudefduf, Chromis,* pomadasyids and serranids were among the important prey common to diets at several sites. Predominant prey of the Brandt's Cormorant apparently shifted from *Sebastes* and *Engraulis* in the north to *Chromis* in the south. The high proportion of squid in the diet at Monterey Bay was exceptional and was probably related to the important squid spawning ground there (Reckseik and Frey 1978).

Included in Brandt's Cormorant diets were equal proportions of schooling and non-schooling prey. Though the majority of prey species occurred on or just above the bottom over both rocky and flat substrates, appreciable numbers occurred from mid-depths to the surface and others hid in the substrate (Table 1). From north to south, prey that associated with purely rocky substrate decreased in prevalence and were replaced by those that associated with sandy or muddy substrate beneath rocky overhangs. Prey species that occurred higher in the water column, and were unassociated with a substrate, also decreased (Table 2).

Diets of Double-crested Cormorants were sampled at seven sites spanning the southern two-thirds of the species' range, which extends from the Alaska Peninsula to central Mexico (Palmer 1962). Atherinids, *Porichthys*, embiotocids, engraulids and sciaenids were common in diets along the Pacific Coast and in the Gulf of California. Pomadasyids, especially *Orthopristis*, were important only in the Gulf (Appendix 3). Diet preferences defined Double-crested Cormorant feeding as being rather narrow since these birds ate mostly schooling prey that occurred from the surface to near, but not on, bottoms having no relief (Table 1). This pattern was common to the species throughout that part of its sampled range (Table 2).

We found no clear differences in the diversity of prey eaten by the three cormorants. Diversity indices based on numbers of each prey species eaten (the Shannon-Weaver index H; see Tramer 1969) ranged from 0.894 to 1.527 in Pelagic Cormorants (Appendix 1; $\bar{x} = 1.167$, $s = 0.325$, $n = 3$ sites), from 0.381 to 2.284 in Brandt's Cormorants (Appendix 2; $\bar{x} = 1.337$, $s = 0.615$, $n = 12$), and from 0.861 to 2.530 in Double-crested Cormorants (Appendix 3; $\bar{x} = 1.697$, $s = 0.519$, $n = 7$). In the latter two species, where an appreciable series of sample sites was available, highest prey diversities occurred in the Gulf of California. This may reflect greater diversity in the fish fauna in subtropical waters.

We also compared the degree of diet overlap among cormorants in certain regions. The proportions of prey items in the diet of cormorants from several adjacent sites were averaged and these average proportions were used to calculate Morisita's Index (Horn 1966; a value of 0 represents no overlap, while a 1 represents complete overlap). In the region from British Columbia to the Farallon Islands, the index of overlap between Pelagic (two sites sampled) and Brandt's cormorants (two sites) was 0.492, between Pelagic and Double-crested cormorants (two sites) was 0.204, and between Double-crested and Brandt's cormorants was 0.138. The index of dietary overlap between the latter two species from sites in the central Gulf of California (not including Pabellon) was 0.140. There was thus relatively high overlap in the prey eaten by Brandt's and Pelagic cormorants, much less in those eaten by Pelagic and Double-crested cormorants, and virtually none in those eaten by Brandt's and Double-crested cormorants. For Brandt's and Double-crested cormorants, greatest separation in diet occurred in the central part of their common range. Exceptional was the situation in the Channel Islands: the overlap index there between Brandt's and Double-crested cormorants was 0.757, caused by an unusually high proportion of rockfish eaten by Double-crested Cormorants at San Miguel Island. Calculations of the index without inclusion of *Sebastes* resulted in the more typical figure of 0.105. Actually, several species of *Sebastes* were represented in each of the birds' diets and thus there could have been less overlap than it at first appeared. In our samples, it was difficult to identify the small otoliths of this group to species.

DISCUSSION

Pelagic Cormorants fed on solitary prey that hid in rocky reef substrates, Double-crested Cormorants fed on aggregating prey that occurred above the substrate (usually flat if the prey orient to it at all), and Brandt's Cormorants showed a range of preferences that overlapped those of the others. In part of their respective ranges, Brandt's and Pelagic cormorants were especially similar, but more than the others, Brandt's Cormorants ate prey that occurred on or near to bottoms having no relief or having rock nearby. The behavior of organisms thus affected their suitability as prey and because of its behavior, a potential prey species was or was not suitable for a particular cormorant species. This suggests why diets differ among cormorants, or other seabirds, feeding in the same region at the same time and using the same feeding technique. It further indicates that in future research on seabird trophic relations the ocean should be perceived as a habitat more complex than having just the two dimensions of depth and distance from land. Indeed, at least for cormorants, the ocean is comprised of microhabitats, like a terrestrial ecosystem.

Of the three species, Double-crested Cormorants showed the greatest constancy in prey type throughout their range. Their diet preferences showed almost no overlap with the other two species. Pelagic Cormorants also appeared to be rather specialized in the type of prey they ate. Brandt's Cormorants were more variable in their diet, though in a regular manner. Their choice of prey overlapped extensively with that of the Pelagic Cormorant in the area of sympatry, but other information suggests that the two were probably catching the same prey in different habitats: the Pelagic Cormorant in rocky substrate and Brandt's Cormorant just above that substrate. In the area of sympatry, Brandt's Cormorants also fed heavily near substrates having no relief. Farther south, however, where Pelagic Cormorants did not occur, Brandt's Cormorants fed almost exclusively in rocky habitats or near rocks on flat bottoms. Could the Pelagic Cormorant have competitively excluded Brandt's Cormorants from feeding in rocky habitat? The question is a difficult one and requires additional information, for instance, on the geographic changes in the availability of suitable prey in various habitats.

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APPENDIX 1. Percent composition of the diet of Pelagic Cormorants at three localities (see Methods).

Prey	Kodiak I.	Mandarte I.	Farallon I.
AMMODYTIDAE			
Ammodytes hexapterus	26.7	31.1	
BATRACHOIDIDAE			
Porichthys notatus			<0.1
BOTHIDAE			
Citharichthys sordidus			0.1
BROTULIDAE			
Brosmophycis marginata			0.1
CARANGIDAE			
Trachurus symmetricus			<0.1
COTTIDAE			
Artedius sp.			<0.1
Hemilepidotus sp.			0.2
Leptocottus armatus		2.9	<0.1
Unidentified cottids			35.5[a]
CYNOGLOSSIDAE			
Symphurus atricauda			<0.1
GADIDAE	6.7		
GOBIESOCIDAE			
Gobiesox maeandricus		2.9	<0.1
GOBIIDAE			
Coryphopterus nicholsii			0.6
Lepidogobius lepidus			<0.1
MYCTOPHIDAE			
Tarletonbaenia crenularis			<0.1
OPHIDIIDAE			
Chilara taylori			0.2
PHOLIDAE			
Apodichthys flavidus		4.9	
Pholis laeta		34.9	
PLEURONECTIDAE			
Glyptocephalus zachirus			<0.1
Parophrys vetulus			<0.1
SCORPAENIDAE			
Sebastes spp.			59.3
STICHAEIDAE			
c.f. *Chirolophus nugator*			<0.1
Lumpenus sagitta		3.9	
UNIDENTIFIED FISH	26.7		
CRUSTACEA	33.3[b]	19.6[b]	3.5[c]
CEPHALOPODA			
Octopus rubescens			0.2
OPHIUROIDEA			
Ophiopteris sp.			<0.1
POLYCHAETA			
Nereis sp.	6.7		0.3
Total individuals	15	103	9,519
H	1.081	1.527	0.894

[a] More than seven genera, including *Artedius*, *Clinocottus*, *Hemilepidotus*, *Jordania*, *Leptocottus*, *Oligocottus*, and *Orthonopias*; for calculation of diet diversity all are grouped as cottids.
[b] Unidentified "shrimp."
[c] Almost entirely (89%) the shrimp *Spirontocaris* sp.

APPENDIX 2. Diet of Brandt's Cormorant at 12 localities (see Methods). Contributions of each prey species by percent of total individuals are shown.

Species	Localities[a] 1	2	3	4	5	6	7	8	9	10	11	12
AMMODYTIDAE												
Ammodytes hexapterus			<0.1									
APOGONIDAE												
Apogon sp.										17.1	30.0	7.0
ATHERINIDAE												
Atherinopsis californiensis			<0.1						1.5			
Atherinops sp.												0.1
Atherinops affinis			<0.1				0.1	3.4	3.0			
Colpichthys regius												2.4
Unidentified atherinid												<0.1[b,c]
BATHYMASTERIDAE												
Rathbunella sp.							0.1					
BATHACHOIDIDAE												
Porichthys notatus	6.7		1.6	3.8	0.1	0.4						
Porichthys analis												0.2
BLENNIIDAE											0.2	
BOTHIDAE												
Citharichthys sordidus			2.4	15.1								
Citharichthys stigmaeus			0.2	1.9					32.8			
Citharichthys spp.					6.8	7.9	5.3				21.6	
Syacium ovale												1.6
Xystreurys liolepis									1.5			
Unidentified bothid		10.0	<0.1[c]									
BROTULIDAE												
Brosmophycis marginata					<0.1							
CARANGIDAE												
Trachurus symmetricus						<0.1	2.5	0.2	4.5			
CLINIDAE												
Gibbonsia sp.							0.1					
Heterostichus rostratus									1.5			
Labrisomus sp.											0.5[c]	
Unidentified clinids											5.4[d]	0.4
CENTROLOPHIDAE												
Ichichthys lockingtoni			0.1									
CLUPEIDAE												
Clupea pallasi	73.3		0.1									
Opisthonema sp.												0.8
COTTIDAE												
Chitonotus pugetensis			<0.1						1.5			
Hemilepidotus spinosus			0.3									
Icelinus cf. *tenuis*			<0.1		<0.1							
Leptocottus armatus			0.5									
Scorpaenichthys marmoratus		4.0										
Unidentified cottid			2.1[c]		0.2[c]	0.1	9.4	0.2				
CYNOGLOSSIDAE												
Symphurus atricauda			<0.1	1.9								
EMBIOTOCIDAE												
Amphisticus sp.			<0.1									
Brachyistius frenatus					0.1	0.3	3.5		9.0			
Cymatogaster aggregata	17.8		1.4		0.4	2.1						
Cymatogaster cf. *gracilis*							4.4	0.2				
Damalichthys vacca			<0.1			<0.1	3.8					
Embiotoca jacksoni			<0.1				0.8	0.2	1.5			
Embiotoca lateralis	2.2					0.1	0.4					
Hyperprosopon argenteum			<0.1			0.6	2.0	0.2				
Hypsurus caryi						<0.1	0.5					
Phanerodon atripes					<0.1	0.2	0.1					
Phanerodon furcatus			0.1		0.1	0.1	0.4		1.5			

APPENDIX 2. Continued.

Species	Localities[a] 1	2	3	4	5	6	7	8	9	10	11	12
Rhacochilus toxotes							0.1					
Zalembius rosaceus			0.1				0.1					
Unidentified embiotocid			0.1[c]		0.1[c]	1.6[c]	4.2[c]					
ENGRAULIDAE												
Engraulis mordax		24.0	2.3	28.3		1.6	0.1	3.4				
GADIDAE												
Microgadus proximus			15.3									
GERREIDAE												
Diapterus sp.										2.0		
Eucinostomus sp.										1.0		0.3
GIRELLIDAE												
Girella cf. *simplicidens*												0.4
Girella nigricans								0.2				
GOBIIDAE												
Acanthogobius flavimanus			<0.1									
Coryphopterus nicholsii			<0.1		0.3	0.1	0.4					
Lepidogobius lepidus			<0.1									
Unidentified gobiid											1.8	0.1
HEXAGRAMMIDAE												
Hexagrammus sp.		2.0	<0.1		0.1							
Oxylebius pictus					<0.1	<0.1	0.5					
KYPHOSIDAE												
Medialuna californiensis				1.9	<0.1	<0.1						
LABRIDAE												
Oxyjulis californica					0.8	0.5	4.0	0.7	31.3			
Pimelometopon pulchrum						<0.1						
Unidentified labrid										13.1	2.6	1.4
MERLUCCIDAE												
Merluccius productus			<0.1									
MYCTOPHIDAE												
Benthosema panamense												1.0
OPHIDIIDAE												
Chilara taylori			3.1		<0.1	0.1						
OPISTOGNATHIDAE												
Opistognathus sp.												<0.1
OSMERIDAE												
Spirinchus sp.			0.1									
Unidentified osmerid		7.0										
PLEURONECTIDAE												
Glyptocephalus zachirus			<0.2									
Iopsetta isolepis			<0.1									
Lyopsetta exilis			<0.1									
Micrometrus pacificus			<0.1									
Parophrys vetulus			1.7									
Pleuronichthys decurrens									1.5			
Pleuronichthys sp.							0.1					
POMACENTRIDAE												
Abudefduf troschelii										3.5	4.6	8.9
Chromis punctipinnis					<0.1	0.3	4.5	88.5	9.0			
Chromis sp. (undescribed)										7.5	2.4	24.4
Pomacentrus spp.												4.2
Unidentified pomacentrid											3.6[c,e]	1.0[c]
POMADASYIDAE												
Haemulopsis sp.												10.3
Orthopristis inornatus												0.4
Orthopristis reddingi										2.0		4.2
Pomadasys cf. *panamensis*												1.8
Xenistius cf. *californiensis*												5.3

APPENDIX 2. Continued.

Species	Localities[a]											
	1	2	3	4	5	6	7	8	9	10	11	12
Unidentified pomadasyid										9.0[f]	4.2	<0.1[c]
SCIAENIDAE												
Elattarchus sp.												<0.1
Genyonemus lineatus			<0.1			0.1						
Paraques viola										1.5		0.6
SCORPAENIDAE												
Scorpaena sp.												<0.1
Scordaenodes xyris												0.3
Sebastes spp.		49.0	68.5	30.2	90.9	85.4	56.8	2.5	1.5			
Sebastes/Pontinus spp.												0.3
SERRANIDAE										43.2	23.0[g]	21.0
SPARIDAE												
Calamus sp.												<0.1
STICHAEIDAE												
Plagiogrammus hopkinsi								0.2				
STROMATEIDAE												
Peprilus simillimus			<0.1									
SYNODONTIDAE												
Synodus sp.												0.2
TRIGLIDAE												
Prionotus sp.												0.1
ZANIOLEPIDIDAE												
Zaniolepis latipinnis			<0.1									
Zaniolepis frenata							0.1					
UNIDENTIFIABLE FISH		10.0[h]										1.8[h]
CEPHALOPODA												
Loligo opalescens			0.2									
Octopus rubescens			<0.1	17.0								
Total individuals	45	?	13,710	53	8,343	9,551	1,703	436	67	199	993	2,007
H	0.800	1.334	1.266	1.656	0.381	0.644	1.743	0.540	1.911	1.673	1.813	2.284

[a] 1 = Vancouver I., 2 = Yaquina Head, 3 = Farallon Is., 4 = Monterey Bay, 5 = Santa Rosa I., 6 = Santa Cruz I., 7 = San Nicolas I., 8 = San Clemente I., 9 = Is. Coronados, 10 = I. San Esteban 11 = I. Sal Si Puedes, 12 = Bahia de los Angeles.
[b] Different from other atherinids identified.
[c] For calculation of diet diversity, this group combined with species in the family (-ies) according to relative abundance.
[d] Probably several species represented.
[e] Could include *Pomacentrus*.
[f] Not *O. reddingi*.
[g] Includes *Diplectrum* sp.
[h] For calculation of diet diversity, this group was disregarded.

APPENDIX 3. Diet of Double-crested Cormorants at several localities (see Methods). Contributions of each prey species by percent of total individuals are shown.

Species	Localities[a]						
	1	2	3	4	5	6	7
ALBULIDAE							
Albula vulpes					0.2	1.2	
AMMODYTIDAE							
Ammodytes hexapterus	20.5						
APOGONIDAE							
Apogon sp.					0.1		
ARIIDAE							
Bagre panamensis						14.4	2.8
Cathorops sp.							55.0
Netuma platypogon							0.9
Sciadeichthys cf. *troscheli*							4.6

APPENDIX 3. Continued.

Species	Localities[a] 1	2	3	4	5	6	7	8	9	10	11	12
ATHERINIDAE												
Atherinopsis californiensis				0.3								
Atherinops affinis				0.2			4.2					
Atherinops sp.									1.0			
Colpichthys regius										0.2		
Leuresthes tenuis							0.3					
Leuresthes sardina										1.3		
BATRACHOIDIDAE												
Porichthys notatus				0.1			3.4					
Porichthys analis									32.5	6.6		0.9
BLENNIIDAE									0.1	1.3		
BOTHIDAE												
Citharichthys sordidus				<0.1								
Citharichthys stigmaeus							0.3					
Citharichthys spp.				0.3[b]						2.4		
Etropus crossotus												10.1
Syacium ovale										0.7		
BROTULIDAE												
Petrotyx cf. *hopkinsi*									0.1	0.1		
CARANGIDAE									0.1			
CLINIDAE										0.1		
CLUPEIDAE												
Clupea pallasi		1.3										
Opisthonema spp.									0.2	11.6		
COTTIDAE												
Leptocottus armatus		2.7		2.4								
Unidentified cottid				0.6[b]								
CYNOGLOSSIDAE												
Symphurus atricauda				0.1								
Symphurus sp.												3.7
EMBIOTOCIDAE												
Brachyistius frenatus				0.1	4.1							
Cymatogaster aggregata		15.5		78.6	12.3		7.1					
Damalichthys vacca							1.1					
Embiotoca jacksoni				0.2								
Embiotoca lateralis		1.3		0.1								
Hyperprosopon argenteum				0.3	0.8							
Hypsurus caryi				<0.1								
Micrometrus spp.				0.4								
Phanerodon furcatus				0.4	2.4		1.1					
Zalembius rosaceus				8.3								
Unidentified embiotocid				4.1[b]	1.6[b]							
ENGRAULIDAE												
Anchoa spp.									4.8[c]	21.2[c]		3.7
Engraulis mordax		0.2		0.3	23.0		15.0					
Engraulis sp. (not *mordax*)												0.9
GADIDAE												
Microgadus proximus				0.9								
GASTEROSTEIDAE												
Gasterosteus aculeatus		0.4										
GERREIDAE												
Eucinostomus spp.									9.7	1.7		
Eucinostomus gracilis							0.3					
GOBIIDAE												
Coryphopterus nicholsi				<0.1								
Lepidogobius lepidus				0.3								
Unidentified gobiid										0.1[c]		0.9

APPENDIX 3. Continued.

Species	Localities[a]						
	1	2	3	4	5	6	7
HEMIRAMPHIDAE							
Hyporamphus sp.					0.1	0.2	
LABRIDAE			9.0		0.1	0.1[c]	
MUGILIDAE							
Mugil sp.					0.2	1.0	1.8
MULLIDAE							
Mulloidichthys dentatus					0.1		
OPHICTHIDAE						0.2	
OPHIDIIDAE							
Chilara taylori		<0.1					
Lepophidium sp.							0.9
OSMERIDAE		<0.1					
PHOLIDAE							
Apodichthys flavidus	23.8						
Pholis laeta	22.8						
PLEURONECTIDAE							
Parophrys vetulus		0.2					
Pleuronichthys spp.						<0.1	
POMACENTRIDAE							
Chromis punctipinnis			0.8				
Chromis spp. (not *punctipinnis*)						2.4	
Eupomacentrus rectifraenum					0.6		
Pomacentrus spp.					1.3		
Unidentified pomacentrid					0.1[b]		
POMADASYIDAE							
Anistotremus sp.						0.1	
Haemulopsis sp.					5.7	1.2	2.8
Orthopristis reddingi					29.5	23.5	
Pomadasys macracanthus							3.7
Pomadasys spp.					1.0	5.5	
Xenistius cf. *californiensis*					3.4	0.2	
Unidentified pomadasyid					0.1[b]	0.1[b]	
SALMONIDAE							
Onchorynchus sp.	0.2						
SCIAENIDAE							
Bairdiella icistia					0.3	0.9	
Cynoscion cf. *reticulatus*					0.1		
Genyonemus lineatus		0.2		65.8			
Larimus sp.					0.1		1.8[d]
Menticirrhus sp.							0.9
Micropogon ectenes						0.1	0.9
Paraques viola					1.4	0.2	
Seriphus politus				0.8			
Stellifer sp.							1.8
Umbrina sp.						0.1	
SCORPAENIDAE							
Sebastes sp.		1.3	44.3				
SERRANIDAE			0.8		2.9	1.5[e]	
SOLEIDAE							
Trinectes fonsecensis							1.8
SPARIDAE						<0.1	
SPHYRAENIDAE							
Sphyraena lucasana						0.1	
STICHAEIDAE							
Lumpenus sagitta	11.5						

APPENDIX 3. Continued.

Species	Localities[a]						
	1	2	3	4	5	6	7
SYNGNATHIDAE							
Syngnathus sp.			0.8	0.5			
SYNODONTIDAE							
Synodus sp.						0.1	0.1
UNKNOWN FISH						0.1	
UNIDENTIFIABLE FISH						1.3[f]	0.4[f]
Total individuals	547	2,818	122	380	909	2,737	109
H	1.799	0.861	1.617	1.325	1.938	2.530	1.812

[a] 1 = Mandarte I., 2 = Farallon Is., 3 = San Miguel I., 4 = I. San Martín, 5 = Bahia de los Angeles, 6 = Bahia Kino, 7 = Bahia de Pabellon.
[b] For calculation of diet diversity, this group included with other species based on relative proportions of each.
[c] At least two species.
[d] Includes *L. acclivis*.
[e] At least two genera.
[f] For calculation of diet diversity, this group was disregarded.