size (in relation to size at maturity) and exploitation rates in the fishery. In a fishery with a small minimum legal size and high exploitation rates, most of the ovigerous females in the population would be small animals laying for the first time.

The incidence of new-shelled ovigerous females in autumn sampling at Arnold's Cove has ranged from 0 to 38.5% of the total ovigerous specimens examined (Table 1). This year-to-year variability, which has also been observed elsewhere in Newfoundland (Ennis 1980), could be accounted for by variation in relative abundance of prerecruit animals caused by annual fluctuation in recruitment and exploitation rate.

TABLE 1.—Percentage of ovigerous lobsters with new shells in autumn sampling at Arnold's Cove, Newfoundland, 1975-82.

Year	No. ovigerous examined	% ovigerous with new shell	Carapace length (mm) Range of ovigerous	Range of new-shelled ovigerous[1]
1975	75	10.7	72-103	73-83
1975[2]	16	12.5	65-92	65-71
1976	31	6.5	73-92	83-90
1976[2]	26	19.2	68-91	68-77
1977	78	38.5	71-101	76-88
1978	12	16.7	71-95	82-83
1979	31	25.8	72-99	72-90
1980	18	0.0	73-99	—
1981	31	6.5	71-101	71-81
1982	27	3.7	75-94	75

[1]These are postmolt carapace lengths.
[2]Diver-caught samples obtained during the same period as the trap-caught samples.

Acknowledgments

I am indebted to P. W. Collins and G. Dawe who, with assistance from other technical staff and casual employees, carried out the field work and data processing associated with this study.

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PARASITES OF OLIVE ROCKFISH, *SEBASTES SERRANOIDES*, (SCORPAENIDAE) OFF CENTRAL CALIFORNIA

The olive rockfish, *Sebastes serranoides*, inhabits reefs from Del Norte County, Calif., to San Benito Island, Baja California, Mexico. Olive rockfish are large (to 64 cm TL), active predators, usually found in the water column, but occasionally hovering over or resting upon rocky substrates. Juveniles are primarily midwater feeders, preying upon zooplankton and small fishes, though some demersal feeding (e.g., isopods, caprellid and gammarid amphipods, etc.) has been noted (Hobson and Chess 1976; Love and Ebeling 1978; Love and Westphal 1981). Adults feed almost entirely on nektonic forms of squid and fish and on substrate-dwelling octopus (Love and Westphal 1981).

Little is known about the parasite fauna of olive rockfish, as previous reports are either descriptions of newly discovered species (Cressey 1969; Moser and Love 1975; Love and Moser 1976; Moser et al. 1976) or surveys of particular parasites throughout a fish community (Turner et al. 1969; Hobson 1971; Dailey et al. 1981). As part of a life-history study, we investigated the parasite population of central California olive rockfish.

Methods

Specimens were collected monthly from April 1975 to February 1976 at a group of shallow-water pinnacles, about 11 km west of Avila Beach, San Luis Obispo Co., Calif., (Fig. 1). These pinnacles, at depths of 20-30 m, are situated 100-300 m offshore from Diablo Cove and North Cove and rise to within 5-10 m of the surface.

Six hundred olive rockfish, ranging from 8.6 to 49.2 cm TL, were collected by hook and line or spear, placed in plastic bags, and frozen for later dissection. After thawing, each specimen was

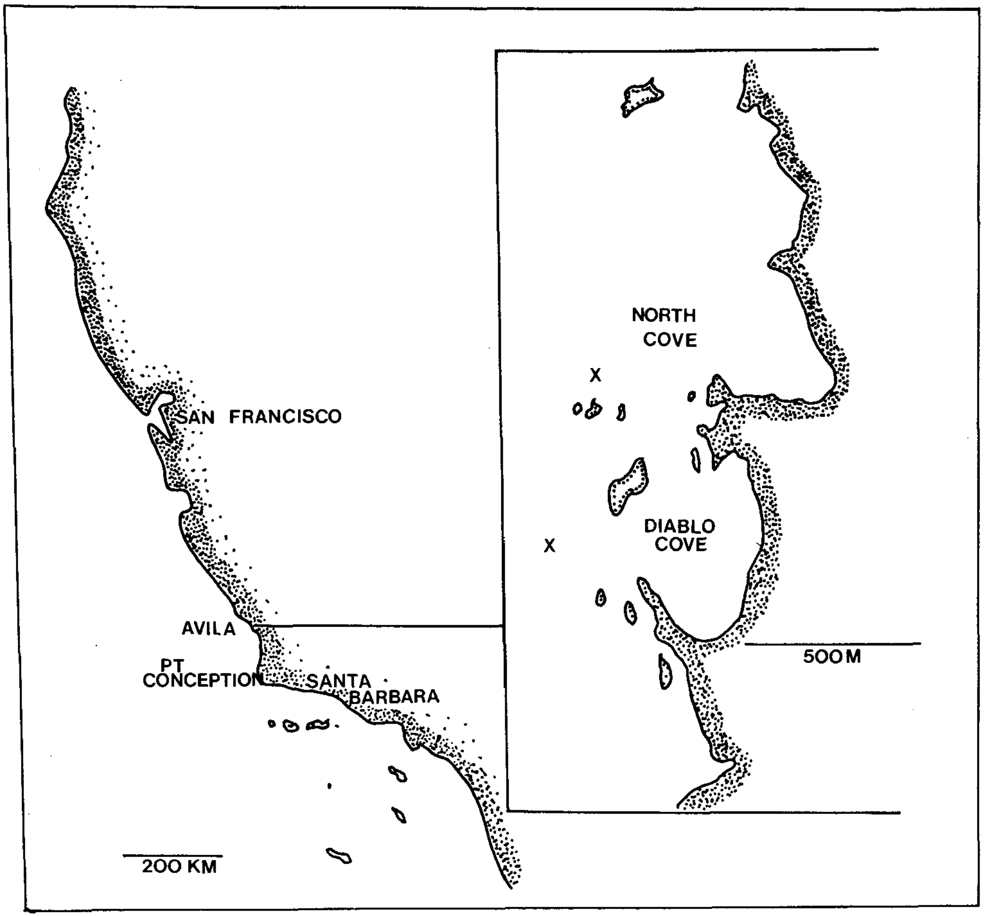

FIGURE 1.—Location of sampling sites (marked with x) for olive rockfish off Diablo Cove, Calif.

measured (total length) to the nearest millimeter and examined for parasites on external surfaces, gills, gill cavities, mouth, mesentery, heart, gallbladder, stomach, intestine, and muscle. Copepods and monogenetic and digenetic trematodes were fixed in alcohol-formaldehyde-acetic acid (AFA). The trematodes were stained with Harris' hematoxylin, cleared with xylene, and mounted. Nematodes were cleared in lactophenol. Protozoans were studied unpreserved after thawing.

Most parasites were identified to the lowest possible taxon. However, the microsporida, copepods of the genera *Caligus* and *Lepeophtheirus*, and larval cestodes, nematodes, and acanthocephalans were not identified to species. Copepods of the genera *Caligus* and *Lepeophtheirus* were only identified to genus, as an earthquake destroyed most of the specimens before they were identified to species.

To facilitate our analysis, we grouped together the relatively uncommon gallbladder myxozoans (= myxosporidans) (*Ceratomyxa sebasta, Leptotheca informis, L. longipes, L. macrospora, Myxidium incurvatum, Zschokkella ilishae*) and the hemiurid trematodes (*Lecithaster gibbosus, Parahemiurus merus, Lecithochirium exodicum,* and *Tubulovesicula lindbergi*).

We analyzed the incidence of infection of all parasites over the entire range of host lengths throughout the year. Differences in prevalence between size classes and between monthly samples were examined using the Kruskal-Wallis test.

Results

For our analyses we divided the specimens into 11 size classes. Table 1 shows the number of specimens taken per month per size class.

TABLE 1.—The number of olive rockfish taken per month per size class, April 1975-February 1976.

Month	Size class (cm TL)									
	5-10	11-15	16-20	21-25	26-30	31-35	36-40	41-45	46+	Total
April	6	6	3	6	8	10	6	7	3	55
May	4	7	4	4	5	8	8	8	4	52
June	5	5	5	8	6	9	5	7	6	56
July	6	5	7	8	6	8	9	8	7	64
Aug.	4	4	7	6	10	8	7	6	5	57
Sept.	5	8	6	9	5	9	9	9	3	63
Oct.	4	7	5	4	8	7	10	5	4	54
Nov.	5	6	5	6	7	8	8	7	3	55
Dec.	4	6	6	5	7	11	8	8	5	60
Jan.	2	3	5	6	4	6	6	7	5	44
Feb.	2	1	6	4	5	8	6	4	4	40
Total	47	58	59	66	71	92	82	76	49	600

Thirty-six parasite species were recovered from olive rockfish (Table 2). Five species were found in <1% of the individuals examined. These incidental parasites were an unidentified microsporidan and the copepods *Neobrachiella robusta, Chondracanthus pinguis, Naobranchia occidentalis,* and *Sarcotaces arcticus*. Found in <10% of the hosts were *Davisia reginae, Kudoa clupeidae, Leptotheca longipes,* and *L. macrospora* (Myxozoa); *Trochopus marginata* (Monogenea); *Aporocotyle macfarlani, Lecithaster gibbosus, Lecithochirium exodicum, Parahemiurus merus,* and *Tubulovesicula lindbergi* (Digenea); *Anisakis* sp. and *Phocanema* sp. (Nematoda); *Caligus* sp. and *Clavella parva* (Copepoda); and Rhabinorhynchidae gen. sp. (Acanthocephala).

Larval cestodes were the most commonly encountered parasites, infecting 98% of all individuals >20 cm in length. Larval *Contracaecum* sp. were found in 62% and cysticanths of immature *Corynosoma* sp. in 18% of fishes >20 cm.

Of parasites which use *Sebastes serranoides* as a final host, *Microcotyle sebastis* had the highest prevalence, occurring on more than 90% of hosts >20 cm. It was most prevalent on the filaments of the first gill arch (Table 3), declining in number through successive arches ($\chi^2 = 108.1, P < 0.001$). No significant differences in infection intensities were noted between left and right arches.

Other commonly encountered ectoparasites were *Holobomolochus spinulus, Neobenedenia girellae,* and *Lepeophtheirus* sp. Adult metazoan endoparasites were not abundant, though three, *Deretrema cholaeum, Opechona sebastodis,* and *Hysterothylacium aduncum*, were often found in larger fish.

Three myxozoans, *Henneguya sebasta, Leptotheca informis,* and *Zschokkella ilishae*, were found in more than 10% of hosts. *Henneguya sebasta* was found in 93% of hosts >35 cm. Nine percent of *H. sebasta* infections were sufficiently severe to virtually occlude the bulbous arteriosus. Although no histological sections were made, no evidence of gross pathogenic effects were noted, as these heavily infected individuals were of an age and weight indistinguishable statistically (analysis of variance) from lightly or non-infected individuals.

TABLE 2.—Parasites recovered from olive rockfish, *Sebastes serranoides*, off Diablo Cove, Calif. *denotes first host records.

Parasite	Location
Protozoa (Myxozoa)	
Ceratomyxa sebasta	Gallbladder
Davisia reginae	Urinary bladder
Henneguya sebasta	Bulbus arteriosus, gallbladder (rarely)
**Kudoa clupeidae*	Muscle
Leptotheca informis	Gallbladder
Leptotheca longipes	Gallbladder
Leptotheca macrospora	Gallbladder
Myxidium incurvatum	Gallbladder
Zschokkella ilishae	Gallbladder
*Protozoa (Microsporida)	Urinary bladder
Monogenea	
**Microcotyle sebastis*	Gills
**Neobenedenia girellae*	Skin, mouth
**Trochopus marginata*	Gills
Digenea	
**Aporocotyle macfarlani*	Afferent branchial arteries
**Deretrema cholaeum*	Gallbladder
**Lecithaster gibbosus*	Stomach
**Lecithochirium exodicum*	Stomach
**Opechona sebastodis*	Intestine
**Parahemiurus merus*	Stomach
**Podocotyle* sp.	Stomach
**Tubulovesicula lindbergi*	Stomach
Cestoda	
*Tetraphyllidea (immature)	Viscera
Nematoda	
Anisakis sp. (immature)	Viscera
**Contracaecum* sp. (immature)	Viscera
**Hysterothylacium* (=*Thynnascaris*) *aduncum*	Stomach, intestine
Phocanema sp. (immature)	Muscle
Copepoda	
**Neobrachiella robusta*	Gills
Caligus sp.	Skin, gills
**Chondracanthus pinguis*	Gills
**Clavella parva*	Dorsal and anal fin rays
Holobomolochus spinulus	Gills, inner surface of gill opercula
**Lepeophtheirus* sp.	Skin, gills
**Naobranchia occidentalis*	Gills
**Sarcotaces arcticus*	Body cavity near anus
Acanthocephala	
**Corynosoma* sp. (immature)	Viscera
**Echinorhynchus gadi*	Intestine
*Rhabdinorhynchidae gen. sp.	Intestine

TABLE 3.—Position and number of *Microcotyle sebastis* on 32 olive rockfish, *Sebastes serranoides*, off Diablo Cove, Calif.

Arch number	Arch position		Total
	Left	Right	
1	114	124	238
2	60	63	123
3	29	37	66

We found numerous cases of multiple species myxozoan infections in the gallbladder, particularly in individuals >35 cm. Twenty-two percent of all infections were comprised of two species, 5.1% of three, and 1.2% of four. The occurrence of myxozoans in *Deretrema cholaeum*-infected gallbladders occurred less frequently than expected ($\chi^2 = 123.3, P < 0.0001$).

The species of parasites infecting olive rockfish by host length and age is shown in Table 4. *Sebastes serranoides* harbors a maximum number of parasite species between 31 and 40 cm or 4 and 10 yr of age [compared with 3-6 yr in *S. alutus* and *S. caurinus* (Sekerak 1975)]. Of the five species of parasites found in the smallest size class, four exhibited direct life cycles, whereas in fish of 20 cm (1-2 yr old) 6 of 11 species had indirect life cycles. In the largest class (41-50 cm), slightly less than half (15 of 34) of the species had indirect life cycles. By 20 cm, representatives of all the parasite groups, with the exception of microsporida, were found in olive rockfish. The prevalence rates of six parasite species and one parasite group increased significantly with increasing host length (Fig. 2). Seven species or species groups showed significant annual changes in prevalence (Fig. 3).

Discussion

Of the seven parasite species showing increasing prevalence with increasing host length, six (*Lepeophtheirus* sp., *Neobenedenia girellae*, *Microcotyle sebastis*, *Holobomolochus spinulus*, *Henneguya sebasta*, and the gallbladder myxozoans) had direct life cycles and one (*Hysterothylacium aduncum*) had an indirect cycle. A change in diet to-

TABLE 4.—Parasite species infecting five size classes of olive rockfish off Diablo Cove, Calif. See Table 1 for number of specimens per size class.

Host length cm TL (age in years)				
5-10 (0)	11-20 (1-2)	21-30 (1-4)	31-40 (4-10)	41-50 (7-20)
	Acanthocephala	Acanthocephala	Acanthocephala	Acanthocephala
	Corynosoma sp.	*Corynosoma* sp.	*Corynosoma* sp.	*Corynosoma* sp.
		Rhabdinorhynchidae gen. sp.	Rhabdinorhynchidae gen. sp.	Rhabdinorhynchidae gen. sp.
Cestoda	Cestoda	Cestoda	Cestoda	Cestoda
Tetraphyllidea	Tetraphyllidea	Tetraphyllidea	Tetraphyllidea	Tetraphyllidea
Copepoda	Copepoda	Copepoda	Copepoda	Copepoda
N. robusta	*H. spinulus*	*Caligus* sp.	*Caligus* sp.	*Caligus* sp.
C. parva	*Lepeophtheirus* sp.	*H. spinulus*	*C. pinguis*	*C. pinguis*
N. occidentalis		*Lepeophtheirus* sp.	*H. spinulus*	*H. spinulus*
		S. arcticus	*Lepeophtheirus* sp.	*Lepeophtheirus* sp.
			N. occidentalis	*N. occidentalis*
			S. arcticus	*S. arcticus*
	Digenea	Digenea	Digenea	Digenea
	D. cholaeum	*D. cholaeum*	*A. macfarlani*	*A. macfarlani*
	O. sebastodis	*L. gibbosus*	*D. cholaeum*	*D. cholaeum*
		L. exodicum	*L. gibbosus*	*L. gibbosus*
		O. sebastodis	*L. exodicum*	*L. exodicum*
		P. merus	*O. sebastodis*	*O. sebastodis*
		Podocotyle sp.	*P. merus*	*P. merus*
		T. lindbergi	*Podocotyle* sp.	*Podocotyle* sp.
			T. lindbergi	*T. lindbergi*
Monogenea	Monogenea	Monogenea	Monogenea	Monogenea
M. sebastis	*M. sebastis*	*M. sebastis*	*M. sebastis*	*M. sebastis*
	N. girellae	*N. girellae*	*N. girellae*	*N. girellae*
		T. marginata	*T. marginata*	*T. marginata*
	Nematoda	Nematoda	Nematoda	Nematoda
	Contracaecum sp.	*Anisakis* sp.	*Anisakis* sp.	*Anisakis* sp.
	H. aduncum	*Contracaecum* sp.	*Contracaecum* sp.	*Contracaecum* sp.
		H. aduncum	*H. aduncum*	*H. aduncum*
			Phocanema sp.	*Phocanema* sp.
	Protozoa (Myxozoa)	Protozoa (Myxozoa)	Protozoa (Myxozoa)	Protozoa (Myxozoa)
	H. sebasta	*C. sebasta*	*C. sebasta*	*C. sebasta*
		H. sebasta	*D. reginae*	*D. reginae*
		K. clupeidae	*H. sebasta*	*H. sebasta*
		L. informis	*K. clupeidae*	*K. clupeidae*
		L. longipes	*L. informis*	*L. informis*
		L. macrospora	*L. longipes*	*L. macrospora*
		M. incurvatum	*L. macrospora*	*L. sebasta*
		Z. ilishae	*L. sebasta*	*M. incurvatum*
			M. incurvatum	*Z. ilishae*
			Z. ilishae	
		Protozoa (Microsporida)	Protozoa (Microsporida)	Protozoa (Microsporida)
Total number of specimens:				
5	11	29	35	34

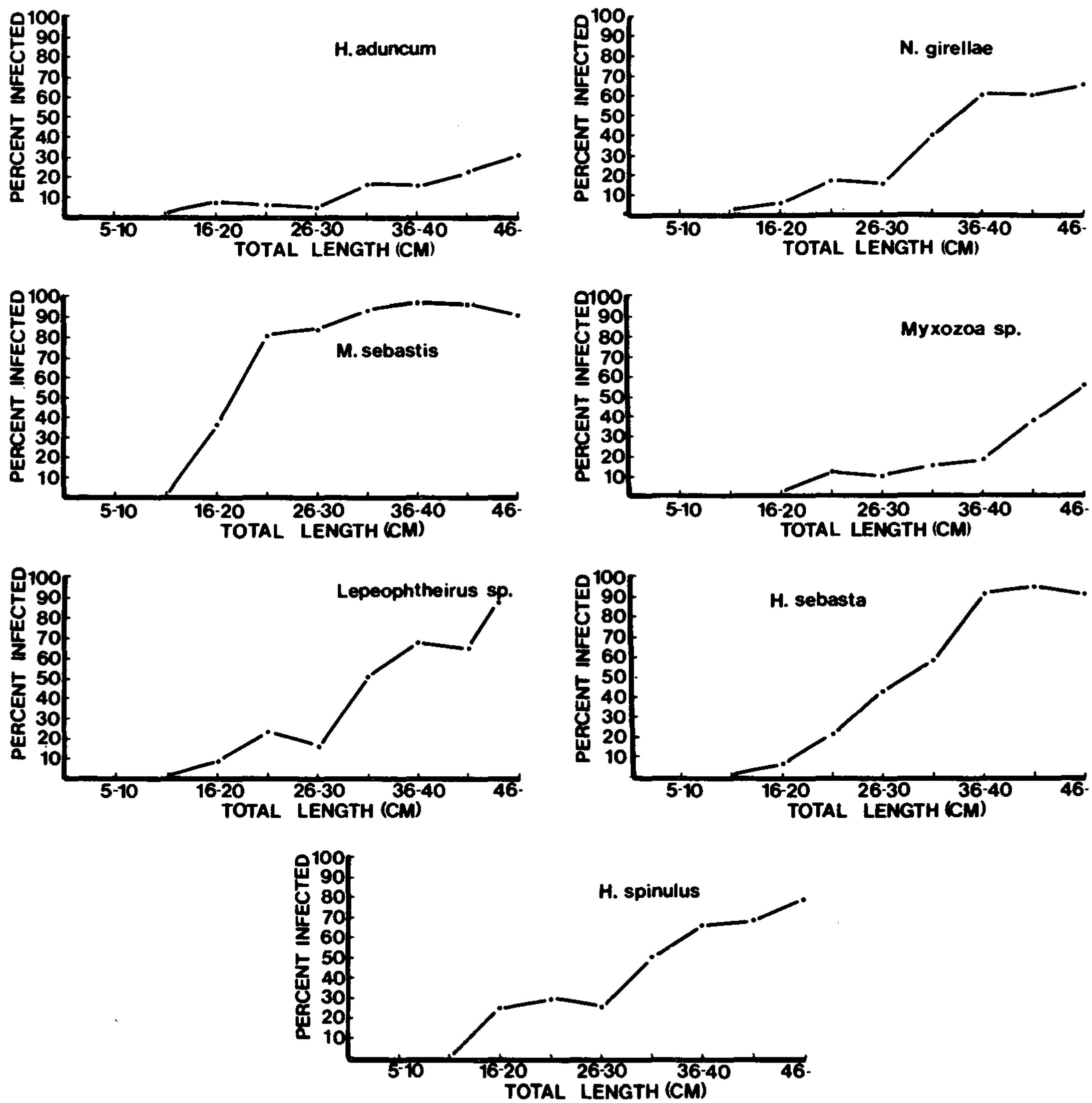

FIGURE 2.—The relationships between host length and percent prevalence of infection by seven parasite species from olive rockfish taken off Diablo Cove, Calif. All relationships show significant difference at $P \leq 0.05$. See Table 3 for numbers of fish examined in each length interval; see Table 1 for the number of specimens per size class.

ward fish and away from zooplankton (Love and Westphal 1981) probably accounts for the increase in *Hysterothylacium aduncum* infections, as fish are thought to be intermediate hosts for this species (Margolis 1970). The prevalence of *Clavella parva* was the opposite—it was found only in hosts <10 cm in length. *Clavella parva* attaches to dorsal, anal, and caudal fin rays. Perhaps structural barriers (such as ray diameter or surface characteristics) or increased water flow over the fins in larger fish prevent infection. Similar infection patterns were noted in *Sebastes alutus* and *S. caurinus* by Sekerak (1975).

Among species with seasonal patterns of infection, winter maximum infections were exhibited by *Lepeophtheirus* sp., *Holobomolochus spinulus*, the gallbladder myxozoans, and *Deretrema cholaeum*. The first three forms listed have direct life cycles. Olive rockfish are winter and early spring spawners (December-March) with internal fertilization occurring from November to February. It is possible that these parasites time their

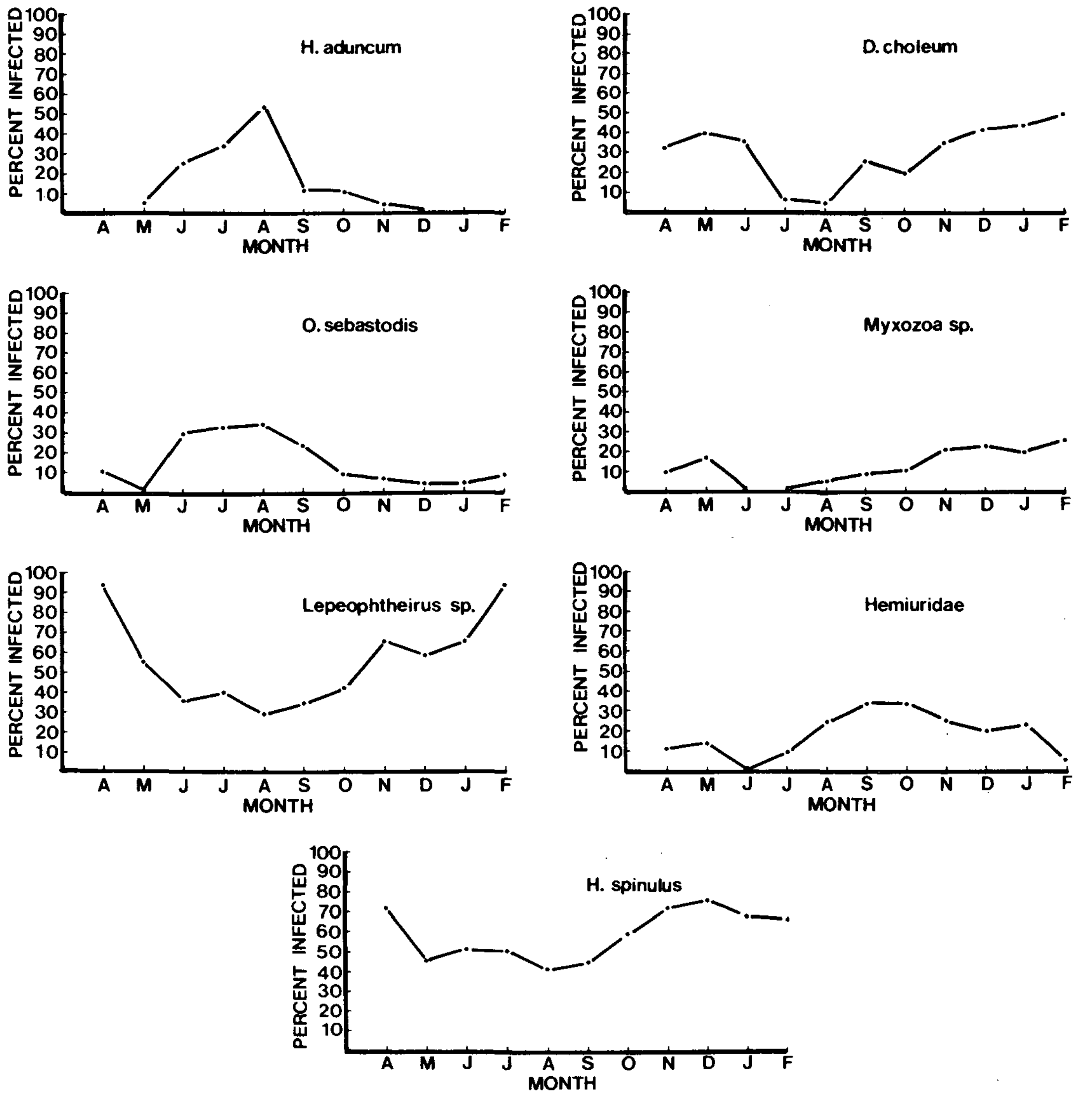

FIGURE 3.—The relationships between month of capture and percent prevalence of infection by seven parasite species from olive rockfish taken off Diablo Cove, Calif. All relationships show significant differences at $P \leq 0.05$. See Table 1 for the number of specimens per month.

movements and reproduction to coincide with that period when their hosts may be at closest proximity with each other. This phenomenon was observed between the Monogenea, *Dactylogyrus vastator* and *Mazocraes alosae*, and their respective hosts, *Cyprinus carpio* and *Alosa sapidissima* (Kennedy 1975).

Parasites with maximum prevalence during other periods all had indirect life cycles. The hemiurid trematode infections peaked in autumn, *Opechona sebastodis* in summer, and *Hysterothylacium aduncum* was most abundant in April and August. Seasonality among hemiurids has been reported by Shotter (1973) in whiting, *Odontogadus merlangus*, of the Irish Sea and in staghorn sculpin, *Leptocottus armatus*, from Oregon by Burreson and Olson (1974). In both cases infections were greatest in late summer or early fall.

The infection patterns we observed may reflect differences in the oceanographic conditions off central California. Water conditions in this region may be divided into two periods (Bakun 1973), "upwelling" (March-August) and "oceanic" (September-February). Upwelling periods are characterized by an increase in the flow of nutrient-rich bottom water to the surface and increased plankton abundance. Olive rockfish food habits change with these seasons (Love and Westphal 1981). Zooplankton (particularly pelagic tunicates and euphausids), squids, and juvenile rockfish are eaten in greater quantity during the upwelling season, due to increased availability.

The secondary intermediate hosts for hemiurids and *Opechona sebastodis* are planktonic (Shotter 1973; Yamaguti 1971), and the prevalence increase may be due to greater seasonal predation on the planktonic intermediate host. Similarly, as fish are possible intermediate hosts of *Hysterothylacium aduncum*, its infection pattern may reflect the rockfish's heavy predation on juvenile rockfish during the upwelling period.

All of the parasite species infecting olive rockfish infect at least some other rockfish species. The genus *Sebastes* has exhibited an explosive radiation in the northeast Pacific (Kabata 1970). This rapid speciation has occurred relatively recently, probably during and after the Miocene[1]. Despite extreme morphological and behavioral differences between species, there is little species specificity among rockfish parasites, perhaps because of the rapidity of the host speciation events. Eighty-nine adult metazoan parasites have been reported from rockfishes between Alaska and California (Love and Moser 1983). Of these, 30 species have been found to infect only *Sebastes* spp. and 10 of the 89 species were unique to one host species.

Some of this specificity may be a function of host behavior or habitat preference rather than physiological differences (Kennedy 1975) between rockfish hosts. Holmes (1971) found that a rockfish's proximity to rocky reefs influenced the prevalence of the digenetic trematodes *Psettarium sebastodorum* and *Aporocotyle macfarlani*. *Aporocotyle macfarlani* was found in species associated with inshore reefs, *P. sebastodorum* in those hosts living away from rocks or in deeper waters. Olive rockfish, limited to relatively shallow reefs, occasionally harbored *A. macfarlani* but was not infected with *P. sebastodorum*.

Some parasites, particularly ectoparasites, are widespread among rockfishes. For example, *Microcotyle sebastis* has been reported from 22 species, *Naobranchia occidentalis* from 13, *Neobranchiella robusta* from 21, and *Chondracanthus pinguis* from 19. These and other parasites exhibit an extensive latitudinal range, considerably longer than some of their hosts. Further surveys of those species only lightly studied (such as *Sebastes eos, S. melanostomus, S. mystinus, S. rastrelliger*, and *S. semicinctus*) will show that some of those parasites infect nearly all rockfish species.

[1]W. Eschmeyer, California Academy of Science, Golden State Park, San Francisco, CA, pers. commun. 1982.

Acknowledgments

We thank Mike Moser and Larry Jensen for their assistance in parasite identification. Dave Behrens, Richard Bray, Craig Fusaro, Robert Henderson, Lew Halderson, Ralph Larson, Dave Laur, Gerry Robinson, and Jerry Wellington assisted in collecting specimens. We are also indebted to Waheedah Muhammad for typing the final manuscript.

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SENSITIVITY OF THE POPULATION GROWTH RATE TO CHANGES IN SINGLE LIFE HISTORY PARAMETERS: ITS APPLICATION TO *MYA ARENARIA* (MOLLUSCA:PELECYPODA)

The question of sensitivity analyses in demographic studies was first addressed by Lewontin (1965), and since that time, Hamilton (1966), Demetrius (1969), Emlen (1970), Goodman (1971), Keyfitz (1971), and Mertz (1971) have made contributions in the area. More recently, Caswell (1978) has given general formulae for the sensitivity of the population growth rate (λ) derived from a Leslie model, to changes in single life history parameters written as formulae involving eigenvectors of the Leslie matrix. The application of such analyses to the study of the population dynamics of commercially important species can provide useful information to those interested in resource management.

The work presented here describes the sensitivity of the population growth rate to changes in the settlement rate (Brousseau et al. 1982) and in the age-specific fecundity and survivorship rates of the soft-shell clam, *Mya arenaria*, using a modified Leslie matrix model and an extension of the sensitivity formulae derived by Caswell (1978). Predictions concerning the effect that changes in these life history parameters will have on λ and the implications of these results to the management of this species are discussed.

Results

Leslie Model

The population of females is divided into n age classes. The Leslie matrix, M, has the following form:

$$M = \begin{bmatrix} a_1 & a_2 & a_3 & \dots & a_{n-1} & a_n \\ r_s b_1 & 0 & 0 & \dots & 0 & 0 \\ 0 & b_2 & 0 & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & 0 & & b_{n-1} & 0 \end{bmatrix} \quad (1)$$

Here, a_i is the mean number of female eggs produced annually by a female in class i (age $i - 1$ to i); assuming a one-to-one sex ratio, a_i is one-half the total egg production. The parameter b_i is the probability of a clam in class i surviving to class 2, 3, ..., $n - 1$. The survivorship from age class 1 to age class 2 is divided into 2 factors, r_s and b_1. The factor r_s is the settlement rate or the probability that an egg will survive the planktonic larval stage and develop into a clam with a 2 mm shell length (0-2 mo of age); b_1 is the probability that a clam with a 2 mm shell length will survive the remainder of the year (about 10 mo). If x is a column vector with n components such that x_i is the number of females in age class i immediately following spawning, then Mx represents the population 1 yr from now.

For benthic marine invertebrates possessing planktotrophic larval stages, the events surrounding metamorphosis and settlement are extremely