BULLETIN OF MARINE SCIENCE, 63(3): 523–530, 1998

DIET AND FEEDING BEHAVIOR OF THE DEEP-WATER SEA STAR *RATHBUNASTER CALIFORNICUS* (FISHER) IN THE MONTEREY SUBMARINE CANYON

Lynn M. L. Lauerman

ABSTRACT

Diet was determined for 98 specimens of *Rathbunaster californicus* (Fisher), a deep-water sea star, collected with a Remotely Operated Vehicle (ROV) between 380 and 650 m depth within the Monterey Submarine Canyon, California. Gut content analysis revealed at least seven phyla among the prey items, with crustaceans (especially benthic-dwelling caprellid amphipods) predominating. The presence of large decapod shrimps, hyperiid amphipods, other midwater crustaceans, siphonophore parts, and a tomopterid polychaete in stomach contents indicated that *R. californicus* can catch highly mobile, midwater animals swimming close to the substratum. Such active predation was seen directly via the ROV's video system, which showed *R. californicus* catching euphausids, sergestids, and a myctophid fish. In the laboratory, the sea stars engulfed dead food items such as squid and smelt and used their pedicellariae to catch mobile prey such as brine shrimp. These data show that *R. californicus* in Monterey Bay is an opportunistic predator and scavenger and is one of few sea stars reported to be capable of catching midwater prey.

Sea stars are conspicuous and abundant members of many marine communities, inhabiting all oceans from intertidal to abyssal depths. Sea star predation often is important in structuring intertidal and subtidal marine communities (Menge, 1982; Dayton et al., 1974), thus understanding diet and feeding behavior of sea stars can be important to interpreting the role of these animals in community organization. Feeding habits of many shallow-water species have been well studied, but little is known about diet and feeding of deep-water sea stars. Until recently, it was difficult to make the in situ observations and careful collections needed to study feeding dynamics of deep-living sea stars in their communities. However, the development of submersibles and remotely operated vehicles (ROVs) has greatly facilitated such work.

Qualitative visual surveys conducted by the Monterey Bay Aquarium Research Institute's (MBARI) ROV VENTANA indicate that the many-rayed sea star *Rathbunaster californicus* (Fisher; Order Forcipulatida) is one of the most conspicuous and abundant megafaunal organisms in some areas of the Monterey Submarine Canyon, California. This sea star ranges from southern Alaska to southern California (Austin, 1985) and is found between 60 and 1000 m in Monterey Bay (pers. observ.). The many arms of *R. californicus* bear long tube feet with suction cups, straight pedicellariae, and spines surrounded by retractile wreaths of crossed pedicellariae. All of these structures probably are used for feeding (Jangoux, 1982). Fisher (1928) observed several captive *R. californicus* catching small crabs and shrimp with crossed pedicellariae and tube feet, and Carey (1972) found sediment and echinoid and crustacean fragments in the stomach of one of two *R. californicus* specimens trawled off Oregon.

Very little is known about the natural history of *R. californicus,* partly because its 8–22 long flexible arms autotomize readily. Trawled specimens generally are retrieved as a mass of arms and discs unsuitable for quantitative or laboratory study. Moreover, in

Monterey Bay, *R. californicus* often inhabits rough terrain where trawling is not feasible. VENTANA can maneuver easily in this terrain and it was used to collect specimens and to video tape close-up in situ feeding events. The purpose of this study was to determine the diet and feeding behavior of *R. californicus* in the Monterey Submarine Canyon.

MATERIALS AND METHODS

Between June 1990 and October 1991, 98 specimens of *R. californicus* were collected for stomach content analysis from two deep-water sites in the Monterey Submarine Canyon (C4-C5 at ~36°42′N, 121°59′W; Soquel at ~36°47′, 122°2′) using MBARI's ROV VENTANA (Etchemendy and Davis, 1991). All ROV dives but one were made during the mid-afternoon; one dive occurred at night. All dives were recorded and the video tapes are archived at MBARI in Moss Landing, California.

To collect sea stars, the ROV pilot used real-time video, transmitted via fiber optic cable to the surface ship, to maneuver the ROV's manipulator arm over the top of an individual sea star. Either a mechanical jaw or a suction device mounted on the arm lifted the sea star gently by its disc and deposited it into a hydraulically opening and closing sample drawer (76 × 43 × 23 cm). Most specimens collected by these methods were fully intact and few arms were lost. Specimens collected during each dive were recovered together in the volume of ambient temperature sea water contained in the drawer. After recovering the ROV, specimens were placed in individual jars. Concentrated formalin was injected into each stomach to stop digestion of food items and the whole animal was fixed in 10% buffered formalin for at least 10 d. Specimens were transferred to 70% ethanol for long-term storage.

All potential food items found in the storage jar were transferred to a jar reserved for incidentally collected material. These items may have been regurgitated during collection, transit, or fixation or may have fallen off the arms. Food items either were picked out of the stomach folds through the mouth opening on the oral surface or through incisions on the aboral surface. The stomach folds and disc then were washed with water. Any food items retrieved in this wash were stored in the jar of incidental material. All food items were identified to the lowest possible taxonomic level.

A list of food items was made for all dissected stomachs from each site. Counting individual food items was impossible because many were in fragments, thus volumetric data are not available. Instead, presence/absence was used to compare diet between the two sites. The percentage of *R. californicus* containing each food category was calculated for stomach contents and for incidental material. Food items were plotted against frequency of occurrence (presence) to compare graphically stomach contents and incidental items within each site and between sites. To determine whether diets were different between the two sites, a Mann-Whitney U-Test and a percent similarity index (PSI) were used.

Feeding behavior of *R. californicus* was determined from chance in situ observations recorded by VENTANA's video camera at numerous benthic sites between September 1988 and December 1991. With limited dive time, however, long-term observations of individual animals rarely were made and detailed data on how long the feeding process took are not available. As part of other research, captured sea stars were kept alive in aquaria at various times between March and December 1991. Dead smelt and squid were fed to *R. californicus* kept in aquaria at the California Department of Fish and Game facility at Granite Canyon, California, at Moss Landing Marine Laboratories, and at the Monterey Bay Aquarium. In addition, live brine shrimp were fed to *R. californicus* kept at the Monterey Bay Aquarium. Reaction to prey items and methods of handling prey were noted to describe feeding behavior.

RESULTS

Forty-eight specimens of *R. californicus* were collected between 425 and 600 m during seven dives at the C4-C5 site (June 1990–October 1991). On average, they had 17 arms (SD = 1.8; range 13–21) and aboral disc diameters of 2.8 cm (SD = 0.3; range 2–3.5 cm). Fifty specimens were collected between 380 and 450 m during three dives at the Soquel site (July 1991–October 1991; one night dive). Mean number of arms of these specimens was 16 (SD = 2.0; range 9–19) and mean aboral disc diameter was 2.5 cm (SD = 0.4; range 1.7–3.2 cm). The sea stars were collected from numerous substrate types, including rock outcrops, cobble, and soft sediment plains.

Of the sea stars collected at the C4-C5 site, 21% had empty stomachs (trace amounts of sediment and detritus), 67% contained a moderate amount of prey (small clumps of material picked out of stomach folds), and 12% had large amounts of prey in their stomachs (large clumps of material packed into stomach cavity). Of the sea stars collected at the Soquel site, 26% had empty stomachs, 70% were moderately full, and only 4% contained large amounts of prey. At both sites, the diet was highly varied and contained members of at least seven phyla (Table 1). However, neither the composition of stomach contents nor the composition of incidental material (87% and 88% similar, respectively) were significantly different between the two sites (Mann-Whitney U-Test; $P < 0.05$).

Overall, *R. californicus* appeared to be primarily an opportunistic predator and scavenger (Fig. 1). At both sites, benthic-dwelling caprellid amphipods were the most frequently observed whole organisms in *R. californicus* stomachs. Most stomachs also contained sediment and whole crustaceans or crustacean parts. Fish parts, mollusc remains, whole crustaceans, crustacean parts, and sediment were found in similar percentages in stomachs and incidental material. Polychaete parts, foraminifera, and fecal pellets were found more frequently in incidental material than in stomach contents.

The presence of animals usually associated with the water column, such as large decapod shrimps, hyperiid amphipods, other midwater crustaceans, siphonophore parts, and a tomopterid polychaete, in gut contents indicated that *R. californicus* may be able to catch live animals swimming just above the substratum. Sea stars were observed in situ catching swimming organisms such as euphausids, sergestids, and in one case, a myctophid fish. The attraction of midwater animals to the ROV's lights may have biased the gut content data of ROV-collected sea stars, but such collections show that the sea stars are capable of using this food source should the opportunity arise.

In situ, most *R. californicus* sat flat on the substrate without their arm tips raised. The wreaths of crossed pedicellariea crowning the spines were conspicuous and fully extended. When swarms of krill or sergestids appeared, often attracted by the ROV's lights, the sea stars curled the tips of their many arms upward. When prey items bumped into the sea stars, pedicellariae grabbed the prey and the sea stars' arm tips curled further upward towards the disk. The tube feet on the upturned arm tips became active and the disk arched upward, looking inflated. It took several minutes to transport prey from pedicellariae to tube feet, underneath the animals, and out of the camera's view. No large aggregations of sea stars were observed, although two sea stars were found associated with the remains of a gelatinous organism, tentatively identified as a salp. Another sea star was found associated with part of a dead fish, presumably cut into pieces by VENTANA's thrusters.

In the laboratory, all food items offered to *R. californicus* were eaten (Table 1). The sea stars used their pedicellariae to catch mobile prey such as brine shrimp (G. Van Dykhuizen,

Table 1. Diet of *Rathbunaster californicus* from the Monterey Submarine Canyon. ** indicates observations made in the laboratory and * indicates in situ feeding observations. All other food items were found in stomach contents. In situ food items of known origin are designated (M) for midwater (living in water above sediment) and (B) for benthic (living on or in the sediment). Those items that could be benthic or midwater are marked with (?).

Vertebrates	**Echinoderms**
Herring —dead**	Ophiuroid parts —vertebral arm ossicles (B)
Smelt —dead**	Echinoid parts (*Allocentrotus fragilis*) (B)
Anchovy —dead**	Miscellaneous spines (B)
Myctophid* (M)	
Unidentified fish* (M)	**Polychaetes**
Fish scales (M)	Maldanidae (B)
Fish vertebrae (M)	Spionidae (B)
	Worm tubes (B)
Molluscs	Tomopteridae (M)
Squid (*Loligo opalescens*) —dead**	Setae (?)
Gastropods (B)	Miscellaneous polychaete parts (?)
Small bivalves (B)	
Shell fragments (B)	**Nematoda**
	Unidentified (B)
Crustaceans	
Brine shrimp (*Artemia* sp.)**	**Foraminifera**
Krill (*Euphausia* sp.)*, in stomach (M)	3 calcareous types (?)
Sergestids*, in stomach (M)	
Sergestid antennae (M)	**Miscellaneous**
Hyperiid amphipods (M)	Salp?* (M)
Caprellid amphipods (B)	Siphonophore part? (M)
Caprellid eggs (B)	Chaetognath parts? (M)
Ostracods (?)	Sponge spicules (B)
Isopods (?)	Sediment (sand & mud) (B)
Gammarid amphipods (?)	Detritus (?)
Other whole decapods (?)	Miscellaneous hard parts (?)
Miscellaneous unidentified crustaceans (?)	Fecal pellets (?)
Crustacean antennae (?)	Gelatinous masses (?)
Crustacean parts (?)	
Red masses (crustacean parts) (?)	

pers. comm.). When fed large items such as dead smelt or pieces of squid, *R. californicus* did not evert its stomach, but engulfed the entire food item.

Discussion and Conclusions

In Monterey Bay, *R. californicus* is an opportunistic predator and scavenger with the ability to catch mobile swimming prey. The composition of both stomach contents and incidental material was not significantly different between the two collection sites in Monterey Bay, probably because the common prey types were widely distributed within the canyon. Based on the observed opportunistic feeding strategy, the diet of *R. californicus* in any location probably would reflect availability of prey.

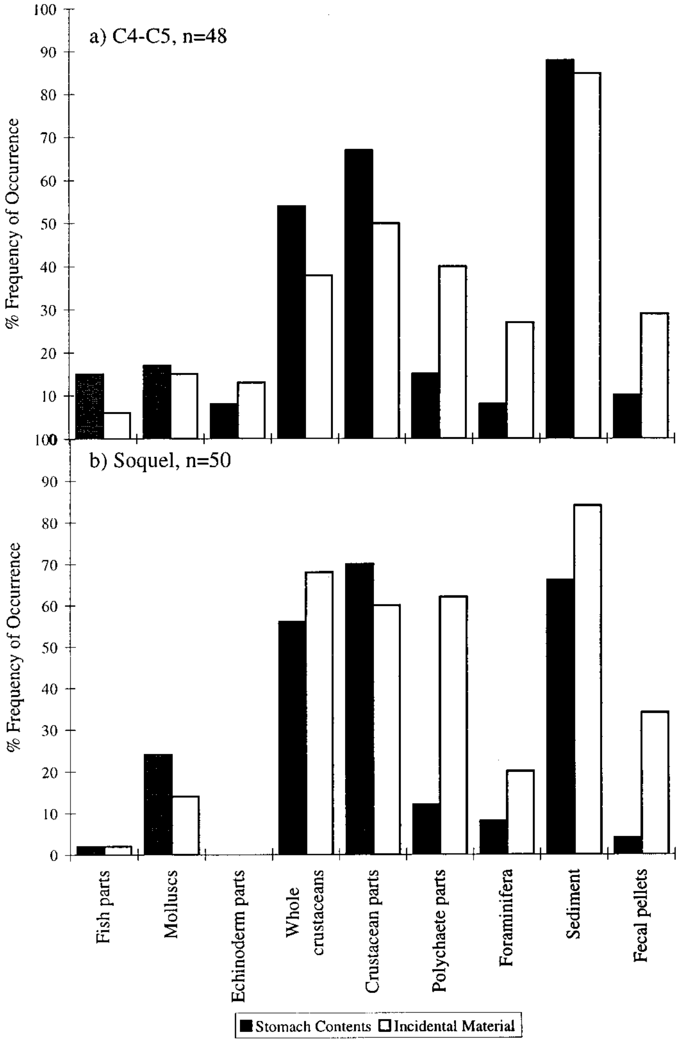

Figure 1. Percent of *Rathbunaster californicus* in which each category of food was found. Solid bars represent material actually found in the stomach. Open bars represent potential food items found in the storage jar, or "incidental" material.

Most *R. californicus* had empty or only partially full stomachs (88% at C4-C5 and 96% at Soquel). However, egestion of food from the stomach during transit from the sea floor to the surface may account for some of the empty stomachs. Unfortunately, because all specimens collected on a dive were deposited together into one drawer, the prevalence of egestion could not be assessed. The sediment and detritus collected along with the animals could not be distinguished from potentially regurgitated food. The small percentage of specimens with full stomachs may indicate that this sea star does not readily find or ingest large quantities of food. In Monterey Bay, this sea star may be food-limited or may not require much food for maintenance. *R. californicus* can approach the size of *Pycnopodia helianthoides* (another forcipulate sea star with arm radius ≥40 cm, Morris et al., 1980) when fed ad libitum in the laboratory (to 30 cm, G. Van Dykhuizen, pers. comm.), but specimens this large were never found in the field (max. arm radius in this study was 10.4 cm (n = 50); in literature 15.5 cm (Fisher, 1928)).

Distinguishing actual food items from items ingested incidentally during feeding is a problem encountered in many diet studies. The most abundant items, benthic-dwelling caprellid amphipods, were found in much greater abundance inside *R. californicus* stomachs than in incidental material and are considered to be actual prey. However, caprellids usually are found clinging to other organisms (Jessen, 1969; Brusca and Brusca, 1990) and may have been ingested in association with other food items. Polychaete parts, foraminifera, and fecal pellets were more frequent in incidental material than in the stomachs and may be actual prey or items ingested incidentally with other prey. Sediment was abundant both in stomachs and in incidental material. While it was impossible to tell whether ingestion of sediment naturally occurs or if it was an artifact of sampling, many sea stars do ingest sediment and the associated detritus, microbes, and meiofauna can be a food resource (Jangoux, 1982).

The environment where these sea stars were collected consists of many microhabitats (e.g., sediment plains surrounded by rocky outcrops or areas of cobble) and *R. californicus* inhabits all of these. Diet composition of an individual might reflect the habitat and substrate where it was captured. On a given dive, however, animals were collected from different habitat types and deposited into the single large sample drawer. Upon recovery individual sea stars could not be assigned to a specific substrate, thus the correlation between diet and habitat type was not analyzed.

Facultative necrophagy as a dietary supplement has been reported among Antarctic sea stars, and Arnaud (1970) hypothesized that deep-living sea stars also would have this tendency. Jangoux (1982) reported that some sea stars are facultative scavengers even though none seem to use this as a primary means of foraging. *R. californicus* scavenged remains of fish and midwater gelatinous organisms and responded quickly to food in the laboratory. The ability to respond rapidly to large food falls would allow this species to take advantage of unpredictable food resources (Smith, 1985).

Benthic crustaceans were the most abundant prey item in *R. californicus* stomach contents, but swimming prey items also were commonly found. These prey items could have been freshly dead and scavenged from the bottom, ingested during collection when VENTANA's lights were on, or eaten during transit when prey were trapped in the water enclosed by the sample drawer. The presence of midwater prey items in *R. californicus* guts may reflect temporal trends. Some prey items, such as sergestids and myctophids, are vertical migrators and may be more prevalent along the canyon walls during the day. However, the relationship between diel vertical migrations and pelagic prey in the gut was not addressed in this study because all but ten *R. californicus* specimens were collected during the day. Diet also could be related to collection date, but because samples were collected sporadically and with highly variable sample sizes on different dates, the correlation between gut content and time of year was not analyzed.

Many crustaceans and fish are attracted to or show erratic movements when illuminated by the ROV's lights and this may have biased the in situ observations. At times, euphausids and sergestids swarmed around the ROV during benthic surveys. However, midwater organisms may routinely dwell close to the sea floor or canyon walls. Stancyk et al. (1998) discovered the ophiuroid *Ophiura sarsii* preying on euphausids, squid, and myctophid fish during submersible dives off Japan and North Carolina. Most predation events were in progress when encountered, so they probably were not artifacts of the submersibles or their lights. Whether naturally occurring or an artifact, *R. californicus* is capable of catching swimming organisms with its pedicellariae, tube feet, and arms. When presented with the opportunity, either in situ or in the laboratory, it responded by catching mobile prey.

The ability to catch highly mobile prey has been reported for other forcipulate asteroids such as *Stylasterias forreri* (Robilliard, 1971; Chia and Amerongen, 1975), *Labidiaster annulatus* (e.g., Dearborn et al., 1991), and *Leptasterias tenera* (Hendler and Franz, 1982). *S. forreri* also is found in deep water in the Monterey Submarine Canyon (pers. observ.) and *L. annulatus* occurs between the intertidal zone and 554 m in the Antarctic (Dearborn et al., 1991). Robilliard (1971) hypothesized that feeding by chance encounter of pedicellariae and mobile prey items would take little expenditure of energy, could provide a large net energy gain, and still allow intake of other food sources. Information on such benthopelagic coupling is scarce, but these findings suggest that this may be a common mode of feeding, at least for the Forcipulatida and perhaps especially for deep-dwelling sea stars. The ability to catch highly mobile prey also has been reported in some species of ophiuroids (e.g., Hendler, 1982a,b; Morin, 1988; Stancyk et al., 1998) and echinoids (Nestler and Harris, 1994; L. Basch, pers. comm.), indicating that this feeding method may be more prevalent than previously thought in the Echinodermata.

In the deep waters of Monterey Bay, the scavenging and predatory lifestyle of *R. californicus* results in a varied diet reflecting opportunistic feeding. Like its close relatives, this species can capture highly mobile swimming prey, thus utilizing a food resource not available to many other benthic organisms. *R. californicus* may use the watercolumn just above the bottom as a rich feeding ground to supplement benthic food sources.

Acknowledgments

I would like to thank C. Baxter, G. Cailliet, J. Nybakken, B. Robison, G. Matsumoto, G. Van Dykhuizen and the many MBARI and MBA staff that were involved in this study. The MBARI ROV pilots deserve special thanks for their ingenuity in collecting samples. N. Jacobsen and K. Schlining were invaluable in retrieving database and video records. Editorial comments by L. Basch, S. Beaulieu, J. Drazen, N. Holland, D. Pawson, and K. Smith improved this manuscript. This research was supported by MBARI, Moss Landing Marine Laboratories, the Monterey Bay Aquarium, and the California Department of Fish and Game at Granite Canyon.

Literature Cited

Arnaud, P. M. 1970. Frequency and ecological significance of necrophagy among the benthic species of Antarctic coastal waters. Pages 259–266 *in* M.W. Holdgate, ed. Antarctic Ecology, vol. 1. Academic Press, London.

Austin, W. C. 1985. An annotated checklist of marine invertebrates in the cold temperate Northeast Pacific, vol. 1. Khoyatan Marine Laboratory, Cowichan Bay, British Columbia.

Brusca, R. C. and G. J. Brusca 1990. Invertebrates. Sinauer Associates, Inc., Sunderland, Massachusetts.

Carey, A. G. Jr. 1972. Food sources of sublittoral, bathyal and abyssal asteroids in the northeast Pacific Ocean. Ophelia 10: 35–47.

Chia, F.-S. and H. Amerongen. 1975. On the prey-catching pedicellariae of a starfish, *Stylasterias forreri* (de Loriol). Can. J. Zool. 53: 748–755.

Dayton, P. K., G. A. Robilliard, R. T. Paine and L. B. Dayton. 1974. Biological accommodation in the benthic community at McMurdo Sound, Antarctica. Ecol. Monogr. 44: 105–128.

Dearborn, J. H., K. C. Edwards and D. B. Fratt. 1991. Diet, feeding behavior, and surface morphology of the multi-armed Antarctic sea star *Labidiaster annulatus* (Echinodermata: Asteroidea). Mar. Ecol. Prog. Ser. 77: 65–84.

Etchemendy, S. and D. Davis. 1991. Designing an ROV for oceanographic research. Sea Tech. 32: 21–24.

Fisher, W.K. 1928. Asteroidea of North Pacific and Adjacent Waters: Part 2. Forcipulata. Bull. U.S. Nat'l. Mus. 76: 1-245.

Hendler, G. 1982a. The feeding biology of *Ophioderma brevispinum* (Ophiuroidea: Echinodermata). Pages 21–27 *in* J.M. Lawrence, ed. Echinoderms: Proc. International Conference, Tampa Bay. A.A. Balkema, Rotterdam.

_________. 1982b. Slow flicks show star tricks: elapsed-time analysis of basketstar (*Astrophyton muricatum*) feeding behavior. Bull. Mar. Sci. 32: 909–918.

Hendler, G. and D. R. Franz. 1982. The biology of a brooding seastar, *Leptasterias tenera*, in Block Island Sound. Biol. Bull. 162: 273–289.

Jangoux, M. 1982. Food and feeding mechanisms: Asteroidea. Pages 117–159 *in* M. Jangoux and J. M. Lawrence, eds. Echinoderm nutrition. A. A. Balkema, Rotterdam.

Jessen, M. P. 1969. The ecology and taxonomy of the caprellidae (Order: Amphipoda; Suborder: Caprellidea) of the Coos Bay, Oregon, area. Ph.D. Dissertation, Univ. Minnesota.

Menge, B. A. 1982. Effects of feeding on the environment: Asteroids. Pages 521–551 *in* M. Jangoux and J. M. Lawrence, eds. Echinoderm nutrition. A. A. Balkema, Rotterdam.

Morin, J. G. 1988. Piscivorous behavior and activity patterns in the tropical ophiuroid *Ophiarachna incrassata* (Ophiuroidea: Ophiodermatidae). Pages 401–417 *in* R. D. Burke, P. V. Mladenov, P. Lambert and R. L. Parsley, eds. Echinoderm biology. A. A. Balkema, Rotterdam.

Morris, R. H., D. P. Abbott and E. C. Haderlie. 1980. Pages 128–129 *in* Intertidal invertebrates of California. Stanford Univ. Press, Stanford, California.

Nestler, E. C. and L. G. Harris. 1994. The importance of omnivory *in Strongylocentrotus droebachiensis* (Müller) in the Gulf of Maine. Pages 813–818 *in* D. Bruno, A. Guille, J.-P. Féral and M. Roux, eds. Echinoderms through time. A. A. Balkema, Rotterdam.

Robilliard, G. A. 1971. Feeding behavior and prey capture in an asteroid, *Stylasterias forreri*. Syesis 4: 191–195.

Smith, C. R. 1985. Food for the deep sea: utilization, dispersal, and flux of nekton falls at the Santa Catalina Basin floor. Deep Sea Res. 32: 417–442.

Stancyk, S. E., T. Fujita and C. Muir. 1998. Predation behavior on swimming organisms by *Ophiura sarsii*. Pages 425–429 *in* R. Mooi and M. Telford, eds. Proc. 9th Int'l. Echinoderms Conference, San Francisco, California. August 5–9, 1996. A. A. Balkema, Rotterdam.

DATE SUBMITTED: March 21, 1997. DATE ACCEPTED: February 12, 1998.

ADRESSES: *Moss Landing Marine Laboratories, P.O. Box 450, Moss Landing, California 95039-0450 and Monterey Bay Aquarium Research Institute, MBARI, 7700 Sandholdt Road, P.O. Box 628, Moss Landing, California 95039-0628.* CURRENTLY AT: *Marine Biology Research Division — 0202, Scripps Institution of Oceanography, La Jolla, California 92093, phone: 619-534-4858, fax: 619-534-7313, email: lml@ucsd.edu.*