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The City University of New York, Ph.D., 1973
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A FIELD STUDY OF THE SEA SNAKE
PELAMIS PLATURUS (LINNAEUS)
IN THE GULF OF PANAMA

by

CHAIM KROPACH

A dissertation submitted to the Graduate
Faculty in Biology in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy, The City University
of New York.

1972

This manuscript has been read and accepted for the Executive Committee in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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INTRODUCTION

The sea snake family, Hydrophiidae, is of great interest because of its special adaptations to marine life, and the fact that its member species exhibit the entire transition from terrestrial to completely pelagic life. However, in spite of the large number of species in the Hydrophiidae, relatively little is known about this specialized ophidian group.

Pelamis Daudin 1803 is a monotypic genus and is the most specialized of the sea snakes. It has made the complete transition to marine life and is truly pelagic. The species _Pelamis_ _platurus_ (Linnaeus) 1766 (Plate 1) is the most widely distributed and most pelagic of the hydrophiids. It is found in the tropical and subtropical waters of the Indo-Pacific Ocean and has colonized the waters of western America. For a serpent which has the widest geographical range of all marine and terrestrial snakes, _Pelamis_ has been neglected by herpetologists for much too long.

Although sea snakes were known to Aristotle (Book II, Vol. 6), contributions to the knowledge of their biology started to appear only in the nineteenth century. But from writers such as G. Fernandez de Ovideo y Valdes in 1519 and Ravanau de Lussan in 1693 (Taylor, 1953) as well as Coleridge (1798) it is known that sailors were familiar with sea snakes long before scientists paid attention to them. Early treatments of hydrophiid biology either gave _Pelamis_ a brief mention (Hopley, 1882; Boulenger, 1890; Rogers, 1903) or did not mention it at all (Cantor, 1841; M'Kenzie, 1820; Rogers, 1904). These pioneer studies, frequently by people for whom herpetology was a second profession, were often of great value. An example is the study by Strauch (1874) in which the geographic range of Pelamis was described: this range is almost identical to the one known to us a century later, in spite of the many additional records for the species. A monograph on the sea snakes was published in 1926 by Malcolm Smith, and it remains the major work on this group to the present day.

Widely known to fishermen and natives of the Indo-Pacific region, Pelamis has attracted the attention of scientists in recent years, mainly with the increasing interest in marine research. Some recently published accounts deal with observations on Pelamis in captivity (Shaw, 1962; Zeiller, 1969; Pickwell, 1971); others deal with temperature physiology (Graham *et al.*, 1971), salt balance (Dunson *et al.*, 1971), and cephalic glands (Burns and Pickwell, 1972). Biochemical-toxological aspects of hydrophiid venoms have been treated by many authors and summarized by Barme (1968), by Halstead (1970), and in several recent papers by Tu *et al.* (1970; others). The ecology of Pelamis has been little studied, although some field observations (Paulson, 1967), general ecological notes (Volsøe, 1939, 1956), and food habits (Klawe, 1964) have been reported.

The dearth of information on this interesting species justified a long-term study. I undertook this, knowing well that only preliminary information would be provided in the course of a year, and I view this report as preliminary. Field studies that have been carried out on terrestrial snakes have lasted 7-15 years, even though they were made in limited areas on known populations; the study of a pelagic animal involves a multitude of problems which render the gathering of data even more difficult.

The objectives of this study were: 1) To obtain population data on *Pelamis platurus*, such as population structure, breeding season, seasonal fluctuation in abundance in the study area, and movement of snakes. 2) To study the food habits of *Pelamis*. 3) To identify the predators of *Pelamis*, to investigate the snakes' anti-predator strategy, and to determine the population-limiting factors operating on *Pelamis* in the Gulf of Panama. 4) To be able, at the end of this preliminary study, to define the niche of *Pelamis*.

This thesis is based primarily on my field study in the Gulf of Panama, from August 1969 to September 1970. In order to include as much of the available information on this species as possible, the thesis is supplemented by reports from the literature, whenever relevant. The zoogeographic data on *Pelamis* and the oceanographic aspects of the discussion are based primarily on the literature. The study was conducted at the Smithsonian Tropical Research Institute (STRI) Marine Laboratory in Balboa, Canal Zone.

Plate 1. The sea snake Pelamis platurus (Linnaeus).

MATERIAL AND METHODS

I. Distribution of Pelamis platurus within the Gulf of Panama

The work was confined to the northern part of the Gulf of Panama, including the Archipelago de Las Perlas. Only rarely were more distant areas surveyed near Piña nad near Coiba and the Secas Islands, outside the Gulf. Field trips were made in the study area (Fig. 1) during the period August 1969 through September 1970, whenever a boat was available. Additional trips were made in October 1970 and January 1971.

Whenever snakes were observed, the location was determined by triangulation with a compass. U.S. Hydrographic Office charts were used to determine positions within the Gulf.

II. Collecting and field observations

Collecting and observations were made during daylight from a variety of vessels, but most commonly from a 16-foot Boston Whaler, equipped with an 85 HP outboard motor. The animals were caught with a dip net at the ocean surface and were placed in large buckets with up to one hundred snakes in each. Observations were made, depending on the circumstances, while the engine was run at low speed (5 mi/hr or less), or with the engine turned off. The snakes generally did not appear to be disturbed by the noise or activity around them, and I assumed that this activity did not affect the observations.

Collecting at night in open sea was done only under exceptional circumstances when a large vessel was available. Night stations were occasionally made in the Pearl Islands. In these cases, a powerful night light drawn from a twelve-volt battery was used to test the widely accepted contention that *Pelamis* is photopostive. Observations of *Pelamis* underwater were made directly, with the aid of SCUBA, to a depth of 60 feet.

III. Group size and density of *Pelamis platurus*

The amount of time spent searching for snakes during each cruise was recorded. The number of sea snakes in large aggregations was estimated by collecting and counting the snakes along short segments of an aggregation and extrapolating to get an estimate for the entire group. The relative density of the snakes was measured in terms of numbers sighted in one hour's searching time.

IV. Sampling

Population samples were collected regularly and fixed in 10% formalin solution. Care was taken to insure that, as much as possible, samples would be random. This was done by preserving a predetermined number of snakes from a large group, for example the first 50 snakes encountered, or all the snakes encountered during a given period. No apparent differences in ability to escape capture were noticed among the different size classes of snakes, and it was assumed that the collected snakes were good samples of the groups observed at the ocean surface. Sampling, however, was not complete for the entire year because of long intervals between field trips.

V. Marking

The snakes were usually marked in the laboratory and released on the following day at the area of capture. Small groups of snakes were marked and released on location. Snakes were never held in the laboratory longer than overnight before release.

Marking was done by notching the snakes' tails at the margins according to "codes" in which the color patterns of the tails were utilized. Usually three notches, but sometimes only two or as many as four, were made (on one snake six notches were made). This method provides for a limited number of codes, but the number could be increased by using differently-shaped notches such as V-shaped and U-shaped notches in various combinations.

The marking technique usually used in field studies on snakes (Blanchard and Finster, 1933) could not be applied to Pelamis because of the absence of ventral plates. Other methods, such as removal of scales and the use of "electric pencil" (after Weary, 1969) did not give satisfactory results.

Each notch was two to four scales deep. Bleeding after notching was slight or none. The wounds of snakes observed in the laboratory healed rapidly, leaving clearly visible notches within 16-21 days. The outline of the notches were not distorted by scar tissue, and the shape (U or V) was clearly maintained. Although snakes in captivity commonly incurred fungal infections in the cephalic region, their notch wounds never became infected.

The large number of snakes involved and the limited number of codes made the individual marking of snakes impossible. Therefore, all the snakes which had been caught in a given area at a given time and were later released together were marked with one group-code. In marking, a distinction was made between snakes more and less than 40 cm total length, and they were marked differently.

VI. Maintenance of the snakes in the laboratory

In the laboratory the snakes were placed in a large indoor tank, 9.0 x 6.6 meters by 2.4 meters deep (Plate 2). Pelamis exhibited a tendency to hit or rub their heads against the rough walls of the tank and tended to develop infections where the skin was rubbed off. To prevent this, the walls of the tank were lined with polyethylene sheets stretched on wooden frames. The frames were suspended 7-8 cm from the walls of the tank, providing both a smooth surface and cushioning for the snakes when they bumped against the walls.

Water was pumped into the tank directly from the ocean every 7-10 days, replacing about 10-15% of the water. At intervals of about 10 weeks the tank was cleaned and the entire water volume changed. The floor was routinely cleaned with a vacuum pump every 7-10 days.

The snakes were fed a variety of small fish seined locally. Live fish were placed in the tank with the snakes. More commonly, when live fish were not available, the snakes were fed with dead fish held in a forceps and shaken near the snake's head until the snake took it. An ultraviolet light source was placed at one end of the tank as suggested by Zeiller (1969) to help maintain good health.

Some snakes survived for an entire year under these conditions. At Queens College, N.Y., the snakes were kept in a 100-gallon tank filled with artificial sea water (supplied by Dayno Sales Co., Lynn, Mass.), or in smaller tanks of 10-gallon capacity. The large tank was provided with a filtering system. The smaller tanks were cleaned by siphoning water and precipitates from the bottom. Several snakes were kept in filtered fresh water for long periods.

VII. Modifying the structural environment of Pelamis in the tank

In order to study the reactions of Pelamis to their structural environment, two features were constructed: a simulated drift line and a rock pile. The simulated drift line was prepared from wood washed onto the shore. The line was four meters long, and the pieces of wood, tied together with a cord, varied in length from 15 to 100 cm.

The rock pile simulated the rocks of a shallow underwater shelf, and was constructed in the tank about 3.5 meters from one corner; it was about 1.2 meters high. The rocks were originally a dark color; at a later time they were painted to appear spotted black and white, and even later were painted entirely white.

VIII. Predation studies

Marine predators which were utilized for this study were caught from boats by trawling. Sharks were caught with a hook and line at stations.

In the predation experiments Pelamis was offered to marine predators which had undergone periods of starvation. The prey was offered in several forms: whole snakes, skinned snakes, pieces of snakes, pieces of skinned snakes, and skin or skin segments. Pelamis was also offered disguised within squid. As a control, fish were offered to the predators after they had refused Pelamis. In most experiments fish were also offered at first in order to create feeding excitement among the predators. The predators were also offered eels, Pelamis painted black or black and red, and small fish enveloped in Pelamis skin.

Most of the experiments, conceived by Dr. Ira Rubinoff of STRI, involved comparison of the reactions of Pacific and Atlantic predators. In these experiments, the Atlantic predators became the controls for the Pacific predators, since both groups were kept under identical conditions. The results of these experiments have been reported elsewhere (Rubinoff and Kropach, 1970). Only observations which have not been published are reported here.

IX. Shedding schedules

Data on the average frequency of shedding was obtained by collecting sloughed skins from the tank and averaging for the total number of snakes present in the tank. In addition, data on the shedding frequency of individual snakes were collected at Queens College, N. Y., where snakes were kept under conditions which allowed the identification of the individuals contributing the sloughs.

X. Weather measurements at sea

Four weather parameters were measured in the field: wind direction, wind speed, air temperature, and water surface temperature. Wind speed was measured in miles per hour with a hand anemometer. Water surface temperature and air temperature were measured with a quick-reading Schultheis thermometer. The bucket method was used for taking surface water temperatures, and readings were made to 0.1°C.

In order to detect local surface currents, floats were cast on the sea surface and the direction of their movement noted. However, no way of measuring current speed was available other than rough estimates of the rate of movement of these floats along distances which could be estimated relatively accurately. The floats were either corks from fishing nets, sealed glass or plastic containers, or pieces of cardboard, and could be observed from a distance.

Weather records were also obtained from the Panama Canal Company, which used the following equipment: water temperature was measured with a Weather Measure T601 thermograph; air temperature was measured with a standard U.S. Weather Service thermometer; and wind direction and speed were measured with a wind vane and anemometer manufactured by Green Instruments, Inc., and recorded on a 3-pen quadruple register.

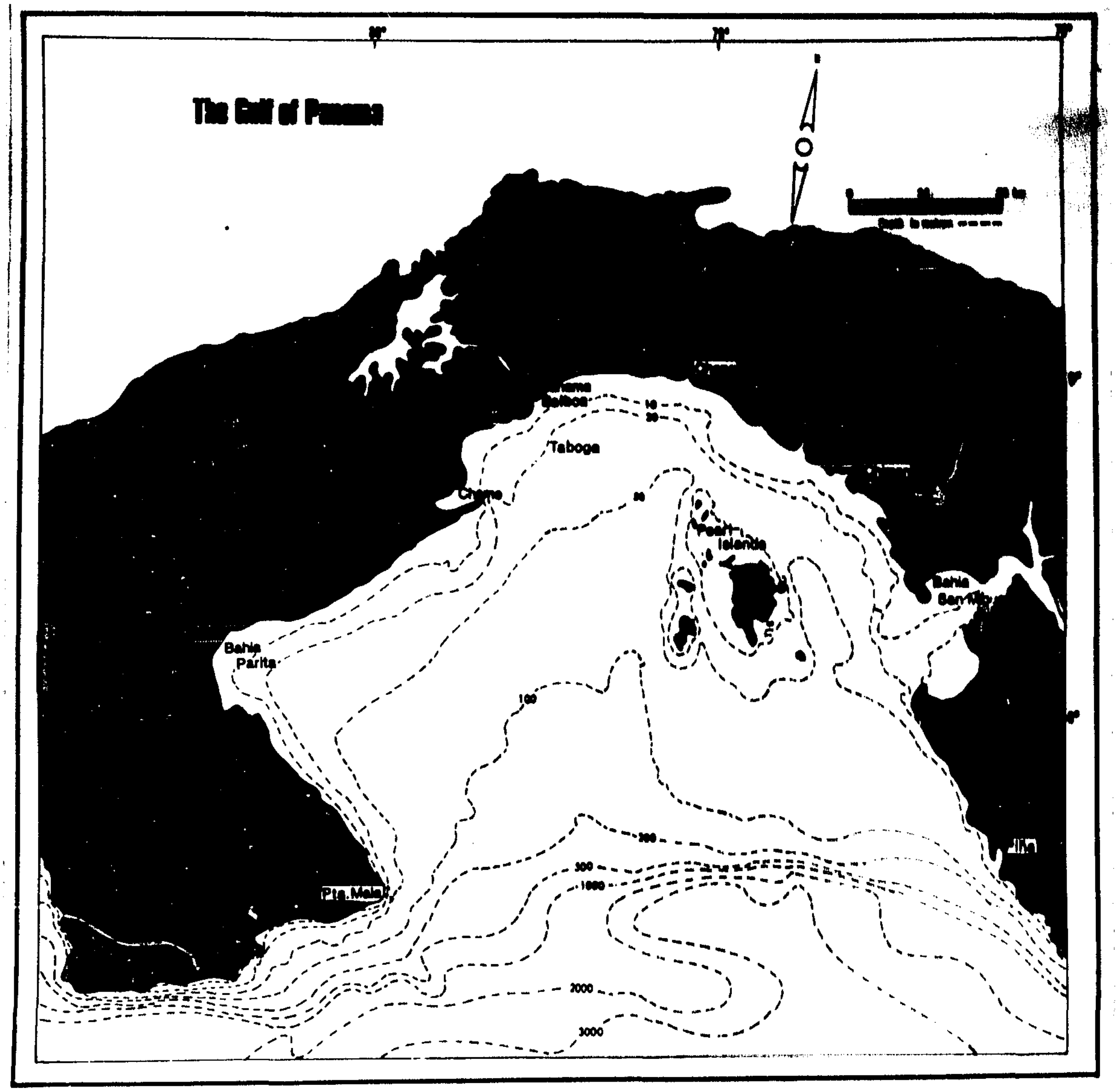

Fig. 1. The study area.

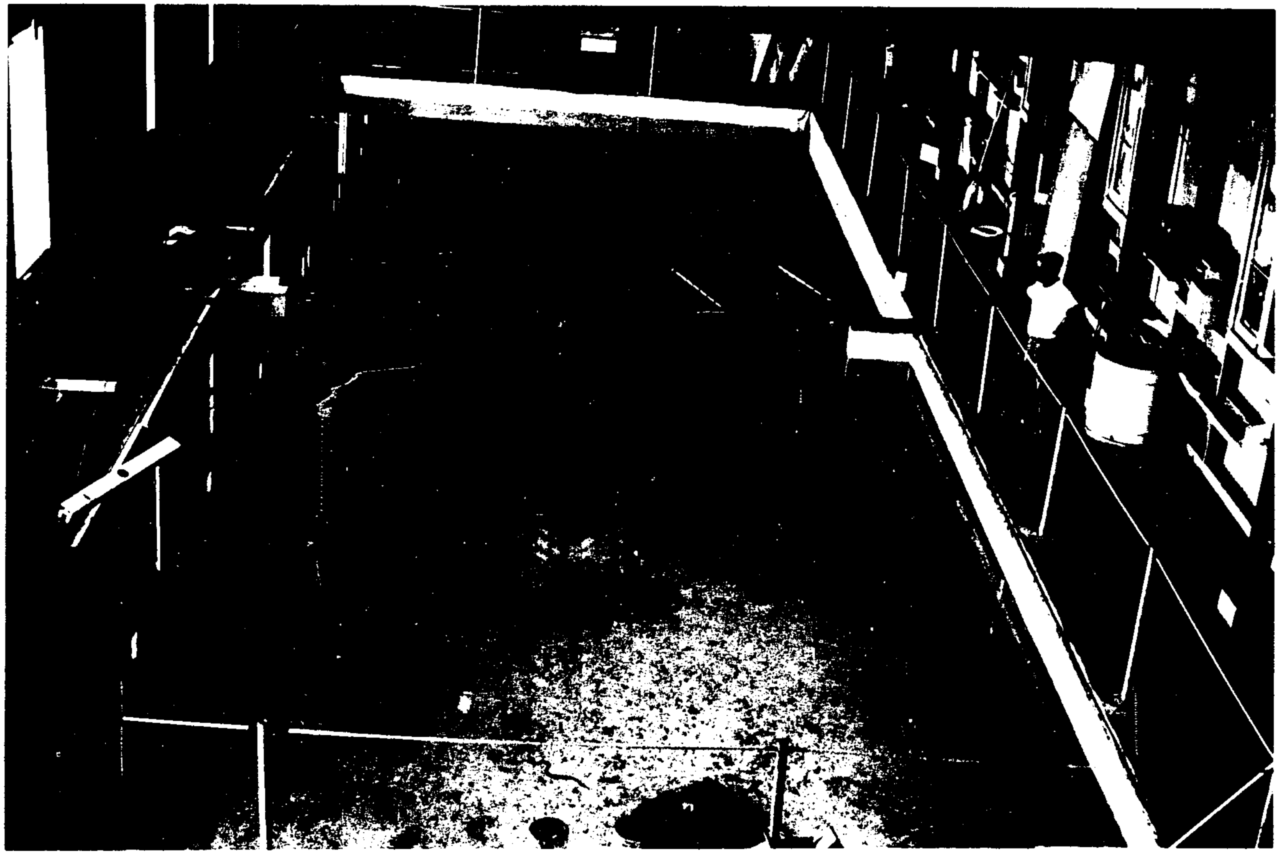

Plate 2. An indoor tank where *Pelamis* were kept.

TAXONOMY

I. The status of the group

The status of the sea snakes is hotly debated. Although there is no fossil record for the group they are known to be related to the elapid snakes and, thus, they were historically placed with them in the Family Colubridae, Section Proteroglypha (Boulenger, 1896).

The close relationship of the hydrophiids and the elapids is not disputed, the former being distinguishable mainly by their ecological adaptations to marine life. The few morphological characters which distinguish the hydrophiids are minor in comparison with the general elapid characters which are retained, particularly in their hard anatomy (Romer, 1956; McDowell, 1972). Johnson (1956), in his study of snake vertebrae, also pointed out the close relationship of the Elapidae and Hydrophiidae, as Schmidt (1949) had done in his "evolutionary tree" of the snakes. Studies of the blood chemistry of reptiles (Dessauer, 1970) and morphology of the pituitary gland (H. Saint-Girons, 1970) also demonstrated the close affinity between the elapids and the hydrophiids.

Smith (1926) gave this group a family status, in which he recognized two subfamilies, Laticaudinae and Hydrophiinae. Smith's classification implies (but does not explicitly state) a dual origin for the sea snakes, both lines derived from the Elapidae. Dowling (1959) and Underwood (1967) considered sea snakes a subfamily of the Elapidae. McDowell (1969, 1972), who worked on the head bone and muscle anatomy of sea snakes, maintained their subfamily status in the Elapidae, and suggested a triple origin for the hydrophiids: one for the <u>Aipysurus</u>

group (equal to Smith's Laticaudinae excluding Laticauda), another for the Hydrophis group, on the line of the more primitive Hydrelaps, and a third origin for Laticauda, which he placed on a line separate from all other hydrophiids. (All three lines are from elapid snakes.)

I maintain the view that classification should reflect phylogeny. As long as the phylogeny of sea snakes remains unknown their status will be debated. All sea snakes can be included in a family of their own or as a subfamily within the Elapidae, depending on one's definition of the family rank. If there had been only one species of sea snakes, few would object to its classification in the Elapidae as a "very specialized member species." The fact that many species have become so specialized should not influence one's thinking. If a group as diverse as the Colubridae has a family status, consistency would require or at least justify the inclusion of the sea snakes in the Elapidae.

II. The status of the species

The classification of sea snakes into species is a difficult task because of their relative scarcity in museum collections and the great variability within the individual species. Thus the number of species in this group varies from one authority to another.

Boulenger (1896) recognized 55 species of sea snakes in 10 genera. Becke (1909), in a popular work, set the species number at "nearly one hundred," and Wall (1909) reduced it to 35 species in 11 genera. At present 50 species are recognized in 16 genera (Smith, 1926, 1931), but the number may decrease when more is known about each species, its geographic range, and the intra-specific variations. McDowell (1972) eliminated some species in his reclassification of the group. Recently, statistical techniques were applied to sea snake classification (Voris, 1971), but the results of this study were not published.

Pelamis platurus (Linnaeus) has undergone a long history of changes in status and name (Smith, 1926). Although markedly different from all other sea snakes in its color pattern, *Pelamis* well illustrates the taxonomic problems all hydrophiids share. This species exhibits such great variability in patterns that the possibility of its representing more than one species has been raised (Taylor, 1950). At present *Pelamis platurus* retains the status given to it in Smith's monograph as the representive of a monotypic genus.

DESCRIPTION OF THE ANIMAL

Pelamis platurus is a relatively small snake, reaching a total length of 733 mm for the male and 834 mm for the female. The species exhibits several morphological adaptations for pelagic life (see chapter 8, on movement) which are present to some degree in other hydrophiine snakes. These are:

1) Narrow head and body; elongate snout. The body is laterally compressed. 2) The body is covered with small, juxtaposed scales.

3) Ventral plates are absent. The ventrals are about the size of the dorsal and lateral scales. 4) The ventral part of the body is often compressed to form a keel. 5) The tail is flat (hence, platurus - "flat-tailed"). 6) The presence of membranous valves at the external nares (Smith, 1926; Parsons, 1970.) 7) The rostral shield is modified to provide complete closure of the mouth (Smith, 1926, 1931). 8) The single lung extends to the base of the tail. The trachea-lung, anterior to the lung proper, is functional in respiration (see below).

9) The vertebrae are elongate and have longer neural and haemal spines than in other snakes, and the occipital condyle is reduced (Johnson, 1955; Romer, 1956). The tuberculiform process of the costal head is weak (Hofstetter and Gasc, 1969). 10) Pelamis is ovoviviparous and thus free of the need to come on land to lay eggs. This I consider the most imporatant single adaptation for pelagic life.

It is interesting to note that some of the morphological adaptations seen in Pelamis and other hydrophiines are present in aquatic fresh-water snakes. In both the Homalopsinae (fresh-water colubrid snakes) and the Acrochordidae (a small family of fish-eating snakes which live in estuaries and enter the sea) there are species whose rostral shield is modified for complete closure of the mouth, although in a different way than in Pelamis (Smith, 1931). The tuberculiform process of the costal head is weak in some hydrophiines and in the two species of the Acrochordidae, and the hypapophyses are well developed on all the trunk vertebrae (Hofstetter and Gasc, 1969). The acrochordids also lack the ventral plates and have juxtaposed scales; on land they progress very slowly and with difficulty; they have valvular nostrils which are placed in raised positions on the dorsal surface of the snout; and they are live bearers (Schmidt, 1949; Schmidt and Inger, 1967). One acrochordid, Chersydrus grannulatus, also has a raised keel on the mid-ventral line (Schmidt and Inger, 1967) and a trachea-lung (Beddard, 1904).

Volsøe (1939) thought that an increased fat content helped Pelamis to achieve buoyancy. I did not find support for this in my observations. It also does not seem logical because buoyancy achieved in this manner would be static, and a diving animal such as Pelamis would need means for dynamic control of its flotation. Fat contents in Pelamis, as in other reptiles, are more likely correlated with the nutritive and reproductive state of the animals.

Vertebral column

In addition to the modifications listed above, which can be explained as adaptations for locomotion in an aquatic medium, the following information was obtained from X-ray plates (Dr. Max K. Hecht, pers. comm.): in Pelamis there is no significant difference between the sexes with respect to total number of vertebrae; in the male this number ranged from 180 to 197, in the female from 181 to 196, but the males have a greater number of vertebrae in the tail, 34 to 45 in comparison with 30 to 40 in the females (see also last chapter, on the population). No difference was noted in the total number of vertebrae between the young and adults (based on 127 adults and 46 young), although such a difference had been noted in some terrestrial reptile species (Inger, 1943).

Scutellation

The most apparent features of Pelamis are, as mentioned above, the lack of ventral plates and the juxtaposed arrangement of the small scales. The latter are hexagonal, almost quadrangular, or slightly rounded, and midventrally are divided by a longitudinal sulcus (Fig. 2). The mid-ventral sulci sometimes unite to form a long groove marking the mid-ventral line. Another general feature is the thickening of the snake towards the midbody, where the greatest number of scale rows, 49-67, is found (Smith, 1926). The number of ventral scales ranges from 264 to 406 (Smith, 1926). Some of the scales on the posterior half of Pelamis bear small tubercules, 1-3 on each. These are more prominent on males than on females, but their presence or absence cannot be used as a secondary sex character. Their presence is not noted on all Pelamis, and is usually more notable on old individuals. The tubercules give the skin of adult Pelamis a rough texture, but the snakes' appearance is never spinous (in contrast with that of Lapemis hardwicki, another sea-snake species).

The head scales are large and easily distinguishable (Fig. 2). Scale numbers vary, and often (approximately 30%) are not bilaterally symmetrical. As with the vertebral number, no difference between young and adults was found with respect to scale counts (see chapter on the population). Smith (1926) examined 47 individuals (22 young), and found the following: upper labials, 7-8; lower labials, 10-11; preoculars, 1-2; postoculars, 2-3; anterior temporals, 2-3. Smith also found that the fourth and fifth upper labials "were usually separated from the eye by suboculars." Minton (1966) found in ten individuals the following: upper labials, 6-8; lower labials, 9-13; preocular, 1; postoculars, 2-3; anterior temporals, 2-3. In four snakes the fourth upper labial contacted the eye; in six snakes a subocular separated the eye from the fourth upper labial.

This testimony to the variations in scutellation was confirmed by my counts, made on 151 adults (77 males, 74 females) and 105 young (53 males, 52 females). Scale numbers, based on these 256 snakes, were: upper labials, 6-10 (6 on only one specimen); lower labials, 9-14, the first five much larger than the others. The mental scale is rarely divided (in one specimen only). Preoculars, 1-2; postoculars, 2-4 (4 on one specimen only); suboculars, 0-2; anterior temporals, 2-4. Because of the position of the nares true internasals or loreals are absent. Great variability is seen in the scales contacting the eyes: in 49.4% of the 256 specimens examined, the upper labials were separated from the eye by a subocular scale (rarely by two); in 37.1% of the observations the fourth upper labial alone contacted the eye; in 4.8% both the fourth and fifth upper labials contacted the eye; in 2.2% the fifth upper labial alone touched the eye; in 6.2% an upper labial (fourth or fifth) and a subocular contacted the eye; and in one specimen the fourth, fifth, and sixth upper labials touched the eye.

The differences in scutellation between my sample and published data (Smith, 1926; Minton, 1966) are not necessarily due to differences between the populations from which the samples were taken (Smith's data are from a mixed sample), but may be due to sample size differences. Similar data on Pelamis from other parts of the species' range are not yet available for comparison.

Hemipenis

The hemipenis is slightly bilobated and is spinous except at the base. The sulcus spermaticus is forked near the tip of the hemipenis; its lips are smooth (non-spinous) and fleshy (Fig. 2).

Cephalic glands

Early work on sea snake glands was done by Kathariner in 1900 (Parsons, 1970), who concluded that Pelamis does not possess a nasal gland. The same conclusion was reached by Schmidt-Nielsen and Fange (1958), Dunson and Taub (1970), and Taub and Dunson (1970). The latter also concluded that Pelamis lacks the Harderian gland, and reported the discovery of a new gland which they named the natrial gland because of the salt secretion attributed to it.

In contrast with these views, Burns and Pickwell (1972) reported that Pelamis possesses both nasal and Harderian glands, but that the nasal gland is poorly developed. No evidence for the existence of a natrial gland was found in their study. They stated that "marine snakes do not possess glands not found in land snakes." Dunson et al. (1971) also published a corrected version of salt secretion in Pelamis, stating that the salt gland is the posterior sublingual gland.

The glands present in Pelamis and other sea snakes are the oral glands (anterior and posterior sublingual, labial, and venom glands), nasal, and Harderian glands (Burns and Pickwell, 1972).

Other work on the anatomy of the cephalic region, not involving the glands, was reported by H. Saint-Girons (1970). According to this report, the morphology of the hypophysis in sea snakes is generally unchanged except for the postereodorsal position of the neural lobe (H. Saint-Girons, 1970).

The viscera

The internal organs and their arrangement within the body cavity are essentially as in other snakes which I have encountered (with the exception of the lung). Of the paired organs, the ones on the right side of Pelamis are anterior to those on the left. The lengths of the major organs and their distances from the snout are listed below (Table 1) in terms of "snout-vent units" (SVU). I define a SVU as 1/100 of the snout-vent length. The use of SVU facilitates the comparison of snakes of different sizes. The values given in Table 1 are based on measurements taken from 27 males and 26 females adult Pelamis. Adult snakes were used to reduce the complications caused by changes in body proportions due to allometry, but I assume that some effects of allometry remained even among these specimens because they were not of equal lengths. Where sex is not specified there was no difference between males and females with respect to that measurement.

Table 1. The major organs and their arrangement within the body.

organ	length, SVU	standard error	distance from snout to anterior end of the organ, SVU	standard error
heart	2.69	.065	24.41	.223
liver	14.36	.284	28.68	.266
trachea-lung			8.16	.306
stomach			41.17	.467
gall bladder, in males			52.13	.381
in females			49.06	.320
right ovary			49.52	.335
left ovary			60.71	.523
right testis			59.35	.811
left testis			68.34	.395
right kidney	11.29	.217	71.0	.287
left kidney	10.66	.224	74.98	.323

The lung

The lung of Pelamis is a specialized structure, different in several ways from that of most snakes. It is a single lung, membranous rather than spongy, which extends through the entire length of the body to the vent. In comparison with Pelamis, lung length in terrestrial snakes is in the order of 12-14 SVU (12 in Thamnophis elegans, 14 in Spilotes pullatus which I examined). In Laticauda colubrina, a sea snake which possesses several characters transitional between land snakes and other hydrophiine snakes, the lung was measured to be 76 SVU (2 specimens examined). In Hydrophis cyanocinctus, a hydrophiine, the lung extends, as in Pelamis, to the vent.

Another difference between Pelamis and terrestrial snakes is found in the distance between the snout and the lung: in terrestrial snakes this distance is much larger than in Pelamis (16-22 SVU in comparison with about 8 SVU in Pelamis). Thus the dead space in the respiratory system of Pelamis is proportionally smaller than that of land serpents.

The anterior section of the lung, the trachea-lung, is found in other hydrophiines and in some fresh-water snakes (Beddard, 1904). It is a functional section of the lung which increases respiratory efficiency by further reducing the dead space. This section of the lung ends near the heart. The posterior part of the lung has become modified, according to Beddard (1904), to serve as a swim bladder. The respiratory part of the lung has transverse folds which allow expansion during inspiration. The posterior part is characterized by transverse muscular bands which help in constriction of this section and expelling of air (Beddard, 1904).

Coloration

The basic coloration of Pelamis platurus is black dorsum and yellow venter (very rare exceptions are all yellow). Laterally it may be yellow or brown, with or without black spots, stripes, or bars. The tail is variably spotted with black and yellow in a pattern which appears to be different from snake to snake (although the shapes of the black spots are repeated throughout the population). This snake is very distinct in its coloration (Plate 1) and can be distinguished from all other sea-snake species with no difficulty. Many variations of the basic pattern can be found in a single population (chapter 12).

Fig. 2. External characters of *Pelamis platurus*.

A. Left to right: ventral, lateral, and dorsal view of the head.

B. Body scales: left - dorsal; right - ventral (appro. 6x).

C. Hemipenis: left - ventral, right - lateral view.

Key: A. Scales: 1) rostral
2) mental
3) nasal
4) prefrontal
5) supraocular
6) frontal
7) parietal
8) lower labials
9) chin shields
10) upper labials
11) preoculars
12) postoculars
13) temporals
B. 14) scale tubercules
15) mid-ventral sulci
C. 16) sulcus spermaticus

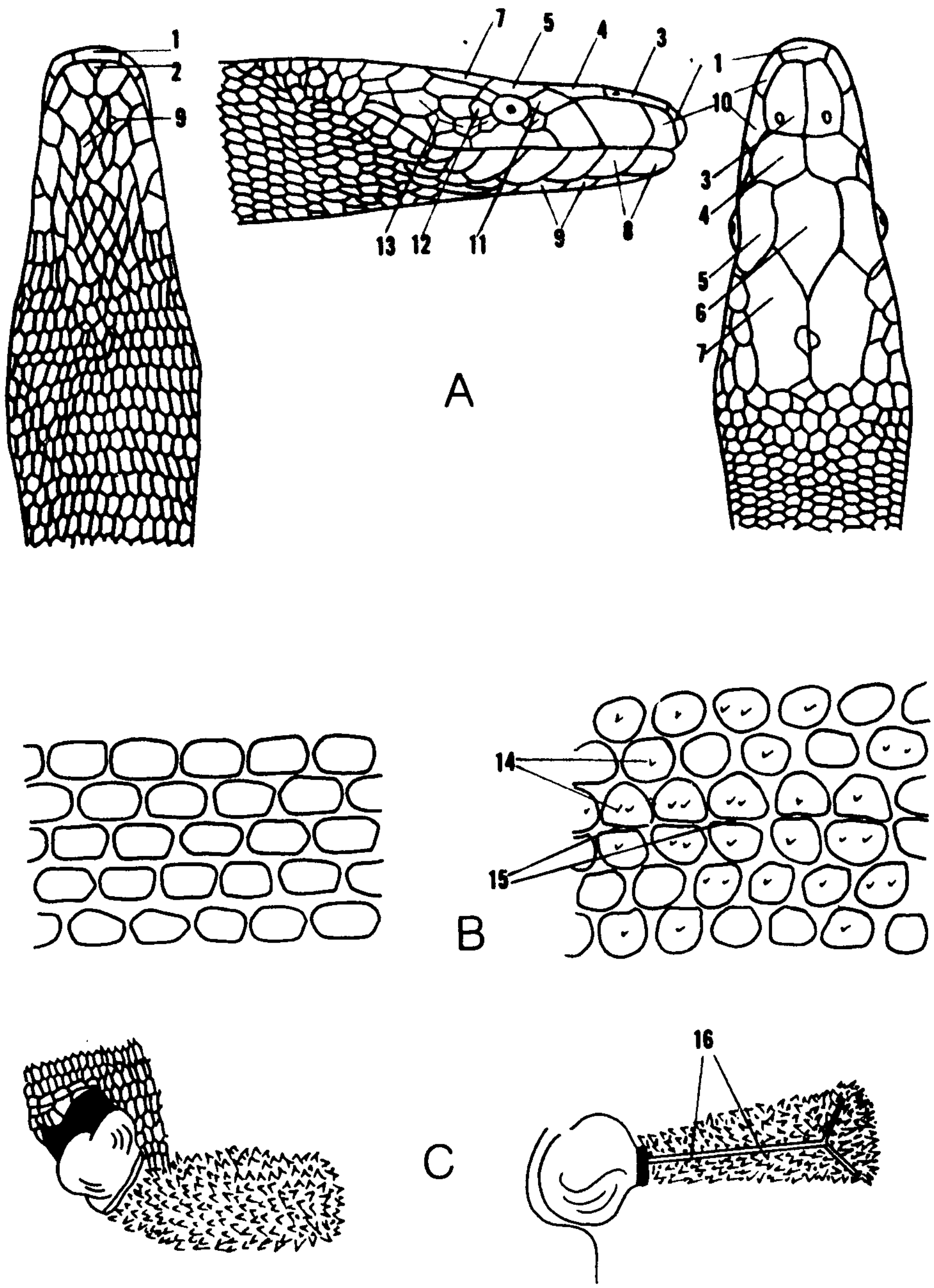

FIG. 2. External characters

DISTRIBUTION

I. World distribution

According to Smith (1926) the two subgroups of the Hydrophiidae have distinct geographic origins: the Laticaudinae is of Australian origin and the Hydrophiinae is an Indo-Maylayan group. The present distribution of the hydrophiids leaves little doubt that their place of origin was somewhere in the Indo-Maylayan region, although an attempt to pinpoint this place would be very difficult. From this region they spread to Japan in the north, Australia in the south, and the Persian Gulf in the west.

Pelamis platurus is the only hydrophiid which has extended its range beyond the boundaries of this Indo-Australian zone,thus achieving the widest range of all serpents. Other sea snakes are restricted to shallow coastal waters (Herre, 1942; Shuntov, 1971), a reason usually put forward to explain their more limited range (but one which does not fully account for their absence from the coastal waters of East Africa.) *Pelamis*, however, has been recorded from sites hundreds of miles offshore, in deep oceanic waters (Smith, 1926; Deraniyagala, 1955; Tweedie, 1961; William Perrin, Bureau of Commercial Fisheries, La Jolla, California, pers. comm.) Two specimens in the possession of Dr. Max K. Hecht were taken by the *Anton Bruun* northeast of Madagascar, more than a thousand miles off the nearest continental region. The range of *Pelamis* extends in the Indian Ocean to Madagascar and the coasts of East and South Africa, and in the Pacific Ocean to Hawaii, the Galapagos Islands, and the western coast of America (Fig. 3).

Guibé (1958) also reported the occurrence of Enhydrina, another hydrophiine sea snake, in Madagascar, and Volsøe (1956) reported its occurrence in East African waters. These records are an outstanding exception to what is known about Enhydrina and they perhaps require further conformation. Mertens reported in 1934 that Enhydrina occurs in Madagascar, but this was questioned by Volsøe (1939). Thus Pelamis still remains the only hydrophiid snake outside the Indo-Australian region.*

Pelamis is absent from the Atlantic Ocean and the Mediterranean, but Shuntov (1963), in his distribution map, reported its presence in the Caribbean Sea. The source of this range extension is not known, and it is not confirmed by specimens. Similarly, the map of Bartholomew et al. (1911) showing hydrophiids as occurring in the mid-Atlantic off West Africa is believed to be erroneous.

Graham et al. (1971) have noted that the latitudinal distribution limits of Pelamis coincide with the 18°C. surface isotherms. They pointed out that the northernmost (Southern Siberia, Gulf of California, and outer coast of Baja California) and southernmost (South Tasmania) extensions of Pelamis are achieved due to warm currents, and probably occur in the summer months. Maki (1931) stated that "Pelamis inhabit a sea warmer than 12°C," but this temperature seems too low for Pelamis. Cold currents limit the range of Pelamis in the southern Eastern Pacific (Humboldt Current) and South Africa (Benguela Current), and this prevents Pelamis from entering the Atlantic. The longitudinal limits are set by the continents, but may be extended by the activities of

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*The snake reported from Madagascar by a ship's captain in 1842 is kept at at the British Museum of Natural History, but its real collection site is not known with certainty.

man, such as sea-level canal which is proposed for Panama (Rubinoff and Kropach, 1970; Graham et al., 1971).

Herre (1942) believed that the "principal factor governing the distribution of sea snakes is the depth of the water," and that deep waters acted as a barrier to many sea snakes and have "efficiently separated most Asiatic and Australian species." This was also implied by Shuntov (1971). The main reason for this is that the species Herre studied were bottom feeders. The distribution of Pelamis, however, appears to be independent of water depth, since specimens are known from the surface of deep oceanic waters. Moreover, their feeding habits free them from the need to reach the ocean bottom.

Table 1 lists localities from which Pelamis has been reported. Some of these are obviously records of "accidentals" such as the record from Posyet Bay, south of Vladivostok (Strauch, 1874), from which Pelamis has not been reported again.

One must distinguish between locality records and the actual range of the species (Grobman, 1950), which is considered here to be the geographic area where populations of the species exist during some part of the year. This definition can accomodate terrestrial reptiles which in many areas are not active throughout the entire year. While this distinction is made between true species range and the wider distribution reached by strays, it is recognized that strays may serve as potential colonizers, and thus may ultimately expand the true species range.

An example of the distinction made above is the distribution of Pelamis in the Eastern Pacific. Here the northernmost range is Bahia Banderas in Mexico (George V. Pickwell, Navy Undersea Research Center, San Diego, California, pers. comm.), but records of capture are available from even more northern localities. Similarly, records of Pelamis from southern Australia (Glauert, 1950) and Tasmania (Lord, 1920) and other places are likely to be strays.

From the information available at present, it appears that the distribution of Pelamis is determined by water temperature and by currents. The relationship of these snakes to surface currents is discussed in connection with aggregations (chapter 7) and with movement (chapter 8). It will suffice to state here that enough evidence has been accumulated to justify stating that currents play an important role in the distribution of Pelamis.

On the basis of such evidence, colonization of the Eastern Pacific by Pelamis could by hypothesized to have taken place by means of the Equatorial Countercurrent of the Pacific Ocean. This current is known for its steadiness and speed, and averages 50 cm/sec (1.8 km/hr), except for March and April, when the speed drops to 20 cm/sec (0.7 km/hr) or less (Neumann and Pierson, 1966).

The marine fauna of the Panamic Region (Central American Eastern Pacific) is distinct from that of the Indo-Pacific, and only a few Indo-Pacific shore forms reached America (Ekman, 1953). This indicates that other species were able to cross the Pacific Ocean. The fact that currents provide a means of transportation for organisms was recognized by Sverdrup et al. (1942), who wrote (p. 858): "When combined with temperature and other factors, [water movements] may control the limits of propagative and sterile distribution of both pelagic and benthic life."

Neill (1964), in discussing the problems of the distribution of

Pelamis, said that Pelamis "could not have crossed the open ocean," although he recognized its ability to "follow surface currents." He then suggested that Pelamis must have colonized the Eastern Pacific during a past warm climate, when the snake could have migrated through the shallow waters south of the Bering Bridge (at the same time that land reptiles made their way across the bridge proper.) Then the snake continued southward and colonized the shallow marine waters of western America.

Ample evidence that Pelamis occurs in deep mid-ocean waters and close to isolated islands contradicts Neill's hypothesis. But the main argument against it is, perhaps, the absence of Pelamis in the Caribbean Sea, indicating a late colonization of the Eastern Pacific, sometime within the past 3-4 million years, after the formation of the Central American land connection in the Pliocene. The Bering Bridge is believed to have existed in the late Eocene, some 50 million years prior to that event.

The hypothesis which considers the Equatorial Countercurrent to be an important factor in the distribution of Pelamis is based on evidence from more localized currents. Its appeal lies in the fact that it can be subjected to experimental testing. The possibility that human activities caused the transfer of sea snakes to Central America has been ruled out (Taylor, 1953), but from Klemmer (1962) it is learned that transport by human activities should always be considered. Klemmer writes: "...It is still not known how a 75 cm Laticauda colubrina found its way to the streets of Magdeburg and was run over by a bicycle."

Some questions regarding the distribution of Pelamis remain. For example, no records are known from the area of Mauritius, where water temperatures are close to optimal (20-28°C).* Conflicting reports on its presence in the Red Sea raise another question. The hydrographic situation in the Red Sea, with warm surface currents entering it over the "sill" (Thompson, 1939a, 1939b; Neumann and McGill, 1962), should allow the entrance of Pelamis from the Gulf of Aden. While it has been claimed that indeed Pelamis does occur in the Red Sea (Smith, 1943; Deraniyagala, 1955; Loveridge, 1957; Corkill and Cochrane, 1965), no specimens from there are known (Flower, 1933). Inquiries with biologists and oceanographers who are familiar with this area also indicate that Pelamis is not known to occur in the Red Sea (pers. comm. from L. Fishelson, J. Hoofien, and D. Por in Israel, and C. Newman, University of Miami, Miami, Florida). Pickwell (1972) explained the absence of Pelamis from the Red Sea by the high salinity which limits its food species, but this is not a sufficient explanation because Pelamis is a general feeder which is not dependent on a specific food source (chapter 10).

This question may be resolved when and if sea snakes are found in the Red Sea, or when more information on the hydrography of the region becomes available, and explains their absence there. Meanwhile, references to specimens from this area, as well as to those in the Atlantic Ocean (Bartholomew et al., 1911; Shuntov, 1963), may be explained by the following quotation from Flower, 1933 (p. 825): "The so-called 'sea snake' from the Gulf of Suez is a fish, a Muraenid eel..." A. Loveridge is quoted in this context by Flower: "An interesting minute-eyed

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*Dr. Max Hecht saw Pelamis in a museum in Mauritius. The specimen was presumed to have been collected in Mauritius waters.

Muraenid, *Moringua abbreviata*, has been mistaken for a 'seasnake' at Pemba on the East African coast."

It is likely that eels have been mistaken for sea snakes in other places, too. In Panama, native fishermen spoke of "dangerous sea snakes" and "non-dangerous sea snakes." In some Caribbean Islands off Panama the natives regularly refer to eels as "culebras" (snakes). Some Indian Ocean eels, such as *Rhinomuraena ambonensis* and *Moringua bicolor*, when observed in the field, would challenge the expert. It is important, then, that only localities from which specimens were collected and identified be considered as "records." The ease with which some eels can be mistaken for snakes forces one to be conservative on the subject.

II. Distribution in the Eastern Pacific

Pelamis platurus is the only hydrophiid wich has extended its range to the Eastern Pacific; it is found from Ecuador to the Gulf of California. Taylor's reference (1951) to *Pelamis* from Chile is interesting, but it is not supported by others or by records from Peru. It is questionable that *Pelamis* could live in the cold coastal waters of Peru and Chile, which do not exceed 22°C and may be as cold as 15°C (Sverdrup *et al.*, 1942).

Villa (1962) reported the presence of the sea snake *Laticauda colubrina* off Nicaragua, but the report, based on two lost specimens, has not been confirmed by additional records and is questionable for several reasons: *Laticauda* lay their eggs on land and are not fully independent oceanic animals; their distribution is said to be restricted to shallow waters (Herre, 1942; Shuntov, 1971); and their anatomy is less advanced than that of the Hydrophiinae (Hydrophis or Pelamis) for locomotion in the sea - not having achieved the lateral compression so typical of the latter. They are the least likely species to have crossed the Pacific Ocean, but, had they done so, their habit of coming on land would have made them more easily detectable than other species, and more specimens would have been recorded.

Several investigators have tried to determine the northernmost locality in the Eastern Pacific from which Pelamis has been recorded. At present this seems to be San Felipe, in the Gulf of California (Pickwell, pers. comm.) Cope (1887) had reported them from Guaymas, and Shaw (1961) reported the famous "tequila specimen" from Los Angeles Bay, approximately 30°N Lat., 114° W Long. All these must be accidentals, swept by the warm summer longshore currents which flow into the Gulf (Fig. 8).

Along the outer coast of Baja California, however, the situation for Pelamis is quite different; here the cold California Current exerts its influence and prevents Pelamis from reaching farther north. The northernmost reliable record of Pelamis on the open ocean side is at Cabo San Lucas, at the tip of Baja California (Pickwell, pers comm.) The origin of the record from around Guadalupe Island, at 29° N Lat., 118.5° W Long. (Halstead, 1970) is not known, but this is a cold water area, and the record is questionable.* The northernmost Eastern Pacific true range for Pelamis is Bahia Banderas, Mexico. Here I observed specimens during the Alpha Helix Expedition, 1970, and gravid

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*On November 24 and 25, 1972 the Orange Coast Daily Pilot of San Clemente, California, reported that one Pelamis was washed onto a San Clemente beach. Whether the snake arrived naturally or was transported by man is not known.

females and juveniles have been collected there regularly by Pickwell.

The presence of Pelamis between Ecuador and Central Mexico was known to early explorers (Taylor, 1953), and has been repeatedly confirmed in the literature. I have seen and collected these snakes, from Mexico to Panama, during the Alpha Helix Expedition, 1970, and received reports of their appearance along the coast of Colombia. In Panama the snakes are known from the outer coast of Chiriquí, Bahía Honda, Coiba, the Secas Islands, and Darien (Table 2), and are common in the Gulf of Panama.

III. Distribution in the Gulf of Panama

The notion that Pelamis is a deep-water species which does not come close to shore is widespread both among the lay public and biologists. It was commonly used in the sea-level canal controversy by those who claim that sea snakes will not be able to reach the Caribbean Sea when the new canal is constructed (e.g. Miami Herald, 5 June 1970). Often Pelamis is referred to as a "blue-water species," again meaning a species which inhabits deep waters only.

The sampling program in the Gulf of Panama revealed a more complicated picture. The distribution of Pelamis in the Bay is patchy and unpredictable with respect to locality. Snakes in large numbers can be observed in a large variety of places and depths in the northern section of the Bay. These aggregations are met with the year around and are not seasonal. They occur sometimes in shallow waters (10 m or less) among the Pearl Islands or close to the mainland. Three such aggregations were extremely close to shore - one several hundred yards from Panama City, one at the Pacific entrance to the canal, beyond the first canal buoys, and one at the Pacific entrance anchorage area. The fact that snakes are often washed up on local beaches also indicates that they occur near the mainland.

These aggregations are correlated with slick lines, a common feature of Panama Bay, and have been discussed separately (chapter 7). Upwellings and cooling of water during the dry season may (and are expected to) influence the distribution of Pelamis in the Bay. This, however, was not observed during the 1970 dry season when the water temperature dropped only slightly, to a minimum of 23°C., in comparison with 28°C. for the rest of the year. Some of the largest aggregations were observed during this season. The situation may be different when the water temperature drops to 18°C or even to 16°C, as it does in some seasons. Duellman (1961) concluded that in Michoacán, Mexico, the abundance of Pelamis depended on the season. There was no evidence for such seasonal variations in the Gulf of Panama.

IV. Summary

A distinction is made (in agreement with Grobman, 1950) between the species range and the wider geographical distribution as depicted by locality records (Table 2). The range is considered to include all localities where populations are known to exist some part of the year. Usually a wider distribution is recorded for this species because of strays which are carried by currents to localities outside of the species range, and probably also because of misidentification of muraenid, moringuid, and ophichtid eels.

It is reasonable to assume that currents play an important role in the distribution of Pelamis and in the colonization of new, suitable areas by stray snakes. In the Gulf of Panama, the distribution of Pelamis does not appear to be influenced by depth or season, but by physical features of the ocean. Full discussion of these features appears in chapter 7.

TABLE 2. The geographic distribution of *Pelamis platurus*.

Number on map	Locality	Source
1	Posyet Bay, 42° 39' N, 130° 47' E.	Strauch, 1874 (Probably accidental)
2	Korea	Shannon, 1956
3	Sea of Japan and Japan	Goris, 1965
4	Ryukyu Islands Amami	Herre, 1942 Mishima, 1965; Halstead, 1970
5	Okinawa	Okada, 1938
6	China and Yellow Sea	Pope, 1935; Brown (U.S. Navy), 1968
7	China Sea Taiwan	Smith, 1926 Maki, 1931; Wang and Wang, 1956; Kuntz, 1963
	Botel Tobago (Hungtow)	Wang, 1962
8	Hong Kong	Romer, 1954
9	Philippine Sea	Brown (U.S. Navy), 1968
10	Philippines	Herre, 1942; Romer, 1954
11	Sulu Sea	Brown (U.S. Navy), 1968
12	South China Sea	Shuntov, 1966
13	Vietnam "Indo-China" Gulf of Tonkin	Barme, 1963, 1968 Bourret, 1935 Shuntov, 1962
14	Gulf of Siam Thailand	Strauch, 1874 Suvatti, 1950; Taylor, 1965
15	Malaysia (Singapore)	Tweedie, 1961
16	N.W. Malaya and the Strait of Malacca	Reid and Lim, 1957
17	Burma	Barme, 1968
18	Bay of Bengal	Strauch, 1874
19	Andaman	Lanza, 1954

TABLE 2. Cont.

Number on map	Locality	Source
20	Madras S.E. India	Strauch, 1874 Halstead, 1970
21	Ceylon	Wall, 1921; Taylor, 1950; Deraniyagala, 1960
22	Trivandrum	Smith, 1926
	Indonesia:	Haas, 1950
23	Sumatra	Barme, 1968
24	Cocos (Keeling) Island	Gibson-Hill, 1950
25	Java	Strauch, 1874
26	Borneo Celebes Sea	Strauch, 1874; Haile, 1958 Brown (U.S. Navy), 1968
27	Celebes Moluccas Sea	Strauch, 1874 Brown, (U.S. Navy), 1968
28	Banda Sea	" " "
29	Flores, Timor Sea	" " "
30	Arafura Sea	" " "
	Australia:	Kinghorn, 1956
31	Darwin	Barrett, 1950
32	Perth	Glauert, 1950
33	Denmark (Foul Bay)	Glauert, 1950
34	Tasmania	Lord, 1920, 1924; Scott, 1932
35	Tasmanian Sea	Brown (U.S. Navy), 1968
36	Sydney	Cogger, 1959
37	Cairns	Hosmer, 1958

TABLE 2. Cont.

Number on map	Locality	Source
38	Coral Sea	Cogger, 1959
39	York Peninsula	Smith, 1926
40	Gulf of Carpentaria	Brown (U.S. Navy), 1968
41	New Guinea	Smith, 1926; Loveridge, 1948
42	Solomon Islands Rennell Island	Smith, 1926; Tanner, 1951 Volsøe, 1958
43	New Caledonia	Gail and Rageau, 1958
	New Zealand:	
44	Kermadec Islands Taranaki Coast Dargaville	Cheeseman, 1887 Phillips, 1941; McCann, 1966 Cheeseman, 1907
45	Mahia Peninsula	Phillips, 1941
46	26° 34' S, 180° 57' W.	Smith, 1926
47	Samoa, Marshall, and Caroline Islands	Becke, 1909
	Melanesia and Polynesia	Barme, 1968
48	Tahiti	Strauch, 1874
49	Hawaii	Oliver and Shaw, 1953
50	Clipperton Island	Sachet, 1962
51	Galapagos Island	Krefft, 1953
52	Ecuador Coast	Boulenger, 1890; Orces, 1948; Peters, 1960; Klawe, 1964
53	Colombia	Daniel, 1955
	Panama:	Grocott and Sadler, 1958
54	Gulf of Panama	Cope, 1887; Smith, 1935; Smith, 1958

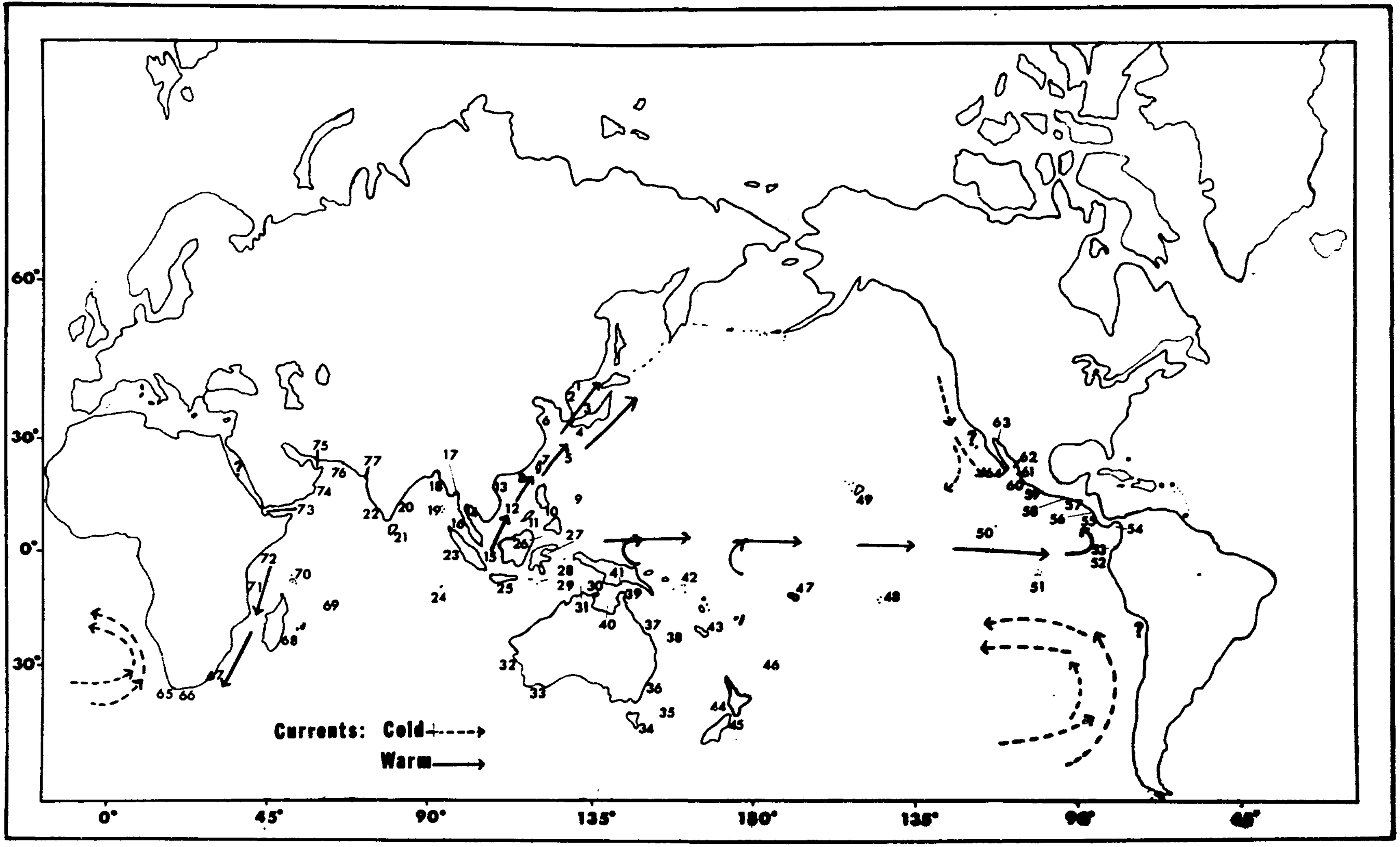
TABLE 2. Cont.

Number on map	Locality	Source
55	Chiriquí Coast	Ambrose, 1956
	Bahía Honda	Myers, 1945
56	Costa Rica	Strauch, 1874; Cope, 1887; Taylor, 1951
57	Nicaragua	Villa, 1962
58	Guatemala	Rodas, 1938
	Mexico:	
59	Chiapas	Toro and Smith, 1956
	Salina Cruz, Oaxaca	Smith, 1926
60	Michoacán	Duellman, 1961
61	Tres Marías	Zweifel, 1960
	Puerto Vallarta, Jalisco	Zweifel, 1960
	Banderas Bay	Pickwell, 1971
62	Sinaloa	Hardy and McDiarmid, 1969
	Lower Gulf of California	Ditmars, 1931
	Guaymas	Cope, 1887
63	Los Angeles Bay	Shaw, 1961
	San Felipe	Pickwell, pers. comm. (northernmost record in Eastern Pacific)
	Outer coast of Baja California:	
	Uncertain records	Hubbs, 1960
64	Cabo de Lucas	Pickwell, pers. comm.
	South Africa:	FitzSimons, 1912
65	Cape of Good Hope	FitzSimons, 1912; Rose, 1962
	False Bay	FitzSimons, 1912; Visser, 1967
66	Port Elizabeth and Algoa Bay	FitzSimons, 1912; Visser, 1967
67	Durban	FitzSimons, 1912

TABLE 2. Cont.

Number on map	Locality	Source
68	Madagascar	Smith, 1926; Guibe, 1958
69	7° 20' N, 64° 40' E.	Hecht, pers. comm. (approximate water depth: 4500 meters)
70	Seychelles	Smith, 1926
	East African Coast	Frade and Manacas, 1955; Volsøe, 1956
71	Tanzania	Loveridge, 1957, 1959; Isemonger, 1962
72	Kenya	Isemonger, 1962
73	Arabian Peninsula, S.E. of Aden	Corkill and Cochrane, 1965
	Obok, entrance to Red Sea	Boulenger, 1897
74	"Arabian Sea"	Halstead, 1970
75	Gulf of Oman and Strait of Hormuz	Volsøe, 1939
76	West Pakistan	Minton, 1962, 1966
77	Bombay	Smith, 1926
78	Maldive Islands	Phillips, 1958
?	Chile	Taylor, 1951
?	Outer coast of Baja California, about 29°N, 118°W	Halstead, 1970 (see footnote on p. 35)
?	Red Sea	Smith, 1943; McCann, 1966
	North of Gidda	Deraniyagala, 1955; Corkill and Cochrane, 1965 (highly questionable, see discussion on p. 33).

FIG. 3. **Pelamis distribution**



THE STUDY AREA

The Gulf of Panama is located on the Pacific side of the Isthmus of Panama, where Central America assumes a general east-west direction. The boundaries of the Gulf to the west, east, and north are formed by the coast line of the Isthmus. To the south, the Gulf entrance is marked by the 200 meter isobath and approximately by the line connecting Cape Mala with Punta Piña, at 7°26'46" (Fig. 1). It is about 200 km wide at this point, while the inland depth of the circular Gulf is approximately 170 km, thus occupying about 28,850 km^2 (Smayda, 1966).

The Gulf is shallow, and its floor takes about 200 km to gradually reach the depth of 200 meters. Then there is a sudden drop to 3000 meters in the next 10-50 km. The gradual slope of the Gulf is disrupted only by some volcanic islands, most of which are grouped in the "Archipelago de las Perlas," and by two submarine valleys which extend northward on either side of the islands (Fig. 1). The importance of these valleys, especially the larger one west of the Perlas, is discussed in the chapter on the ecology of the Gulf.

Hundreds of streams and rivers make up an extensive drainage system which empties into the Gulf of Panama. In the eastern part of the Isthmus the continental divide is very close to the Caribbean shore, and the Pacific drainage area is huge, covering most of eastern Panama. The effect of this drainage system is to greatly dilute the Gulf during the rainy season. The three most important drainage points are the Chepo River, San Miguel Bay, and Parita Bay (Fig 1). The latter two are prominent coastal features. Another important coastal feature is the Bay of Chame and Punta Chame in the northern part of the Gulf.

"Panama Bay" and "Gulf of Panama" are used here synonymously in reference to the area defined above. Although the term "Bay of Panama" is sometimes used for the northernmost section of the Gulf (Bennet, 1965), there is no geographical feature which defines this area (not even depth - the isobaths generally form arcs parallel to the coastline of the Gulf), and this term is not used here in this sense.

THE ECOLOGY OF THE GULF OF PANAMA

I. General

The hydrography and ecological conditions of the Gulf of Panama have been well studied through the efforts of the Inter-American Tropical Tuna Commission. The Gulf and its adjacent areas provide some of the most productive fisheries in the world, and play an important role in the economics of several countries.

Among the commercially important products of this area are the yellowfin and skipjack tuna, Thunnus albacares and Katsuwonus (Euthynnus) pelamis, and other scombrids. Other food fish are the dolphin, Coryphaena hippurus, and various snappers, Lutjanus spp. The chief food of the tuna is the anchoveta, Cetengraulis mysticetus, which is also processed industrially for oil and meal. Several species of shrimp, mostly of the genus Penaeus, are harvested in the Gulf and provide the basis for the economy of the coastal villages. The results of the Commission's studies are summarized by Schaefer et al. (1958), Forsbergh,(1963, 1969), and Smayda (1966).

The main ecological feature of the Gulf of Panama is its distinct seasonality with the upwelling of cold, more saline, nutrient-rich water during the period January-April, which corresponds to the dry season. Upwelling, in turn, is a result of two geographical features of the Isthmus and the Gulf. The first is the relatively low profile of the Isthmus, which allows the passage of the northerly trade winds from the Caribbean side to the Pacific side.

The second feature is the wide expanse of the Gulf, which extends as a shallow shelf for about 200 km. This shallow area (average depth 60 meters, maximum about 200 meters) holds warm water which is relatively nutrient-impoverished and low-saline throughout most of the year (May-December) with little mixing of more fertile deep-ocean water. The strong, persistent northerly winds which blow during the dry season cause a seaward flow of the shallow water of Panama Bay and deep, cold, nutrient-rich, high-saline waters flow into the Bay. The floor of the shallow Gulf of Panama is broken by a submarine valley which projects toward the Chepo River. Smayda (1963) stated that "this valley is important in guiding the incursion of offshore waters during upwelling." Recent studies have shown that both the intensity of upwelling and its circulation are highly influenced by the bottom topography of the Gulf (Smayda, 1966).

These upwellings were first recognized by Fleming in 1935, and since then have been studied more or less continuously (Forsbergh, 1963). The result of an upwelling in the Gulf of Panama is a displacement of up to 78m of water in the upper part of the Gulf water mass. For more than half of Panama Bay this means a displacement of the entire water column.

The phenomenon of upwelling has a marked effect on the biology of the Gulf of Panama. The nutrient-rich offshore waters which enter the Gulf cause an influx of phyto- and zooplankton. Upwellings also stir up the bottom and raise nutrients from bottom sediments (Smayda, 1966). The anchoveta, Cetengraulis mysticetus, appears to have adjusted its life cycle so that it benefits from this seasonal enrichment; it spawns before the beginning of the upwelling season (September-December) and reaches its population peak around April. Yellowfin and skipjack tuna also migrate into the Gulf of Panama when their food is most abundant, around April-May (Forsbergh, 1969). Marine birds such as cormorants flock in the Gulf in large numbers.

During upwellings water temperatures in the Gulf drop appreciably, sometimes to levels 10°C below those of the rainy season. Because of the submarine valleys, the upwellings and their effects are most pronounced in the inner, northern regions of the Gulf of Panama, those which are outlined by the 50-meter isobath (Smayda, 1966).

In the rainy season the opposite trends dominate the Gulf: southerly winds prevent the mixing of Gulf water with offshore nutrient-rich waters; water temperature is higher than in the dry season; runoff causes greater dilution in salinity and nutrient contents; increased turbidity and greater cloud cover combine to decrease the depth of the euphotic zone, and thus appreciably decrease productivity; plankton biomass is about half that of the dry season (Smayda, 1966).

This marked seasonality greatly influences the fauna in the Gulf in terms of productivity, food abundance, and growth of populations. As is mentioned in the discussion of the distribution of *Pelamis*, the changes in water temperature can be expected to act as the most important factor in determining the presence of sea snakes in the Gulf.

II. Weather records of the year

The degree of upwelling in the Gulf of Panama varies from year to year and within a single season, depending on the persistence and speed of the northerly winds. Some upwellings may occur even in the middle of the rainy season, if there are sufficient winds from the north (Schaefer *et al.*, 1958; Smayda, 1966).

The year during which this study was conducted had only a mild upwelling and water temperatures in the Gulf dropped only slightly; the lowest measured at sea was 23°C. The complete weather records for the year were obtained from the Meteorological and Hydrographic Branch of the Panama Canal Company. Wind measurements were taken at a station in Balboa Heights; air and water surface temperatures for the Gulf of Panama were taken in Balboa at the Pacific entrance of the Panama Canal. The weather data for the year are represented in Fig. 4.

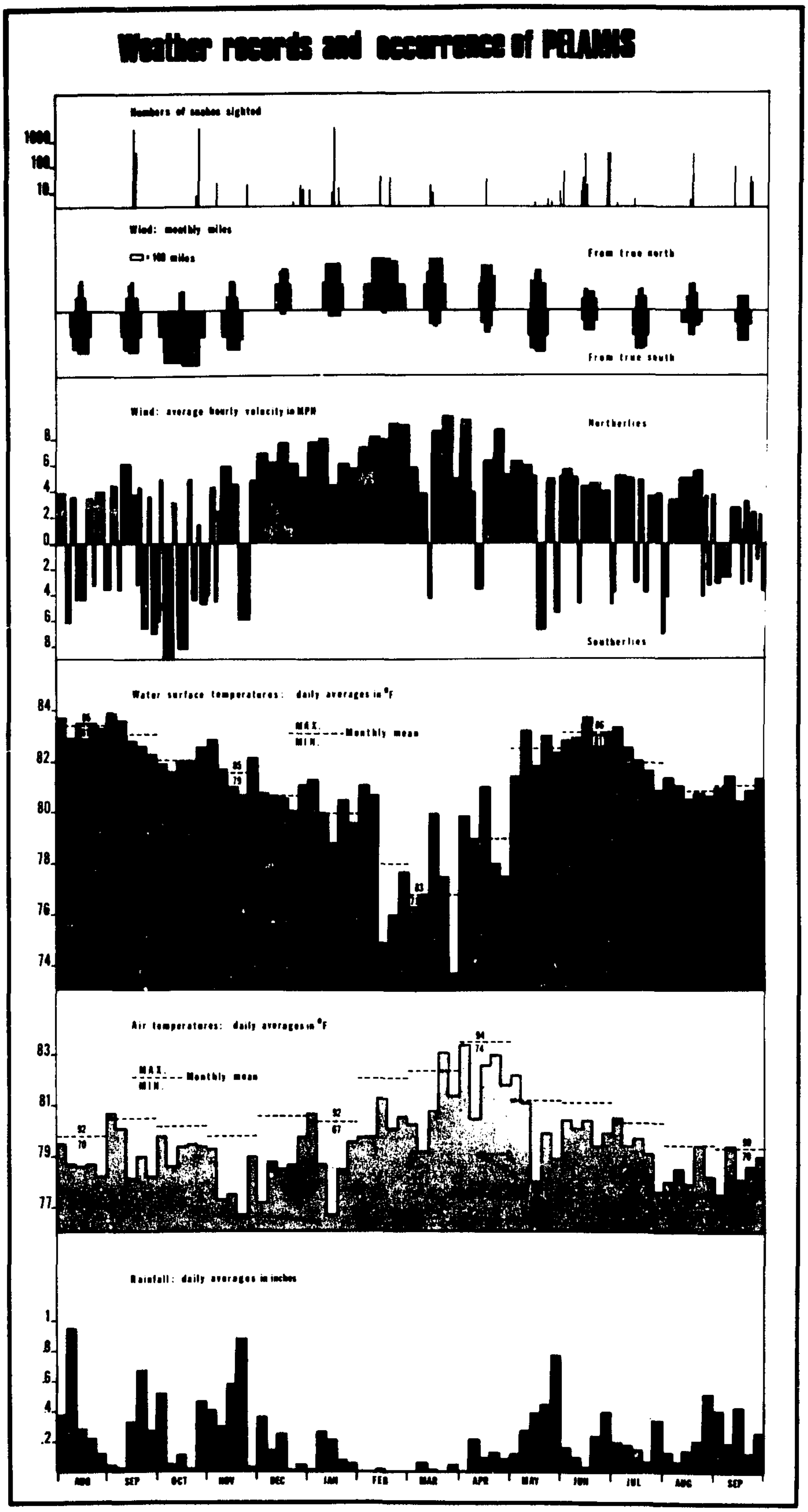
Monthly averages of some data such as rainfall tend to obscure some of the information. Therefore all weather records are represented in terms of daily averages for non-overlapping periods of six days. Days on which large numbers of sea snakes were observed are also marked on Fig. 4.

III. Summary

The Gulf of Panama experiences distinct seasonality due to upwellings. Upwellings increase the productivity of the Gulf, and enhance biological activity. The organisms living in the Gulf have to adjust to this seasonality, mainly to the fluctuations in temperature and salinity. Organisms which require stability, such as corals, are poorly represented in the Gulf.

The extent of the upwelling may vary from year to year and within a season, depending directly on the strength and persistence of the northerly winds. The fact that upwellings are induced by northerly winds has been clearly demonstrated (Schaefer et al, 1958; Forsbergh, 1963). The 1970 dry season was not marked by strong upwelling, but some typical dry season faunal phenomena such as the appearance of large flocks of cormorants were observed.

Fig. 4.


Weather records and occurrence of PELAMIS
Numbers of snakes sighted
1000
100
10
Wind: monthly miles
▭ = 100 miles
From true north
From true south
Wind: average hourly velocity in MPH
Northerlies
Southerlies
8
6
4
2
0
2
4
6
8
Water surface temperatures: daily averages in °F
MAX.
Monthly mean
MIN.
84
82
80
78
76
74
86
85
79
83
86
Air temperatures: daily averages in °F
MAX.
Monthly mean
MIN.
83
81
79
77
92
70
92
67
94
74
90
70
Rainfall: daily averages in inches
1
.8
.6
.4
.2
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP

THE SPATIAL DISTRIBUTION OF PELAMIS PLATURUS IN THE GULF OF PANAMA

(Definition of the niche of Pelamis)

I. Preliminary observations

A 4-day preliminary survey of the northern section of the Gulf of Panama, including the Pearl Islands, was conducted from the vessel "Aida Rita" at an early stage in the study. At the survey's conclusion a plan was developed to conduct all future search for sea snakes along prescribed courses, so that all observations from the same localities could be compared over a span of time.

The finding of a large aggregation of sea snakes, associated with a drift line, on the next field trip (a month later and, fortunately, still at an early point in the study) led to a change of plans for studying the spatial distribution of Pelamis in the Gulf. The aggregation was so striking in its magnitude, and the drift line along which it occured so impressive with its faunal concentration, that it seemed worthwhile to channel my limited field time into exploring this phenomenon of snake aggregations along special oceanic surface features. As the study proceeded, it became clear that drift lines and slicks (see below) play an important role in the biology of Pelamis and other marine organisms (see section III), and that an understanding of this phenomenon is critical in the study of any marine ecological problem involving pelagic fauna. Therefore, a more detailed discussion of slicks seems warranted.

II. Slicks as surface phenomena

A. Description

An important feature of the ocean surface is the occurrence of slicks, which are smooth, narrow, long lines on the surface. Slicks have been known to men traveling on the high seas for a long time. Captain James Cook, in the account of his first voyage around the world (1773) wrote: "On the ninth of December 1768 we observed the sea to be covered with broad streaks of a yellowish colour, several of them a mile long, and three or four hundred yards wide." Often various floating objects, vegetation, and debris are accumulated along slicks, hence the commonly used term "drift-lines". Slicks vary in width from 2-3 feet to several hundred feet, and may be many miles long. They occur either singly or in groups of parallel or nearly parallel lines, sometimes interconnected with a network of smaller lines.

The duration of slicks varies from several hours to days, but under special conditions lines may persist for many months, or even permanently (Welander, 1963). In most slicks, a sudden change in wind direction and speed may cause their disruption, sometimes accompanied by the dispersal of the debris floating on them. Slick lines may move and change their position by several miles in the course of a day.

A slick may take on any of three characteristic appearances: a smooth line with little or no foam, a line of foam and scum, or a line with floating objects in varying amounts such as logs and vegetation washed in from rivers, seaweeds, and jetsam from passing ships (Plate 3). These three types are often seen as alternating segments along a single line, and therefore no distinction among them is made here.

The slicks appear smooth and shiny due to the organic surface films from which they are made. These organic films consist mostly of oils and organophosphates derived from marine organisms, particularly diatoms (Dietz and LaFond, 1950; Sutcliffe et al., 1963). These films have a smoothing effect on the surface ripples because, due to their lower surface tension, they tend to damp small surface waves. Thus, when the films are distributed unevenly on the surface, and a breeze is blowing, they appear as smooth, shiny patches on a rippled sea (Dietz and LaFond, 1950). It is therefore clear that slicks are particularly pronounced during light winds.

When winds are strong or when it rains, the slicks may disappear due to the disruption of the films, but they may still be detectable due to the floating debris which retains the line form. If there is no wind and the sea is perfectly calm, slicks cannot be distinguished because the entire ocean surface is glass-smooth and has a slick-like appearance. But again, if foam or debris has accumulated on the slick line, its location and direction can be easily observed. When the organic films are highly compact they stabilize bubbles and thus form foam (Ewing, 1950a) which may appear in bands or wide sheets.

B. Slick formation

Several mechanisms have been offered as explanations for slick formation. One, first proposed by Langmuir in 1938, was that they result from wind-induced water circulation. Langmuir observed streaks of floating seaweed in the Atlantic Ocean and noted the change in their direction as wind direction changed. Years of observations and experiments in Lake George, New York, confirmed his earlier conclusions that such streaks are caused by wind-induced water circulation. According to his model, alternate right and left helical vortices are formed in the water with their longitudinal axes in the wind direction. Lines or streaks appear on the surface where right and left (clockwise and counterclockwise) vortices meet, causing the convergence of surface currents which flow in a direction perpendicular to that of the wind. Divergence of the vortices at the surface occurs midway between adjacent lines. The direction of the lines or streaks is the same as that of the wind.

This kind of water movement is often called "Langmuir circulation," and the lines formed are termed wind slicks (Welander, 1963; McLeish,1968), or wind rows (Faller et al, 1964). Langmuir also recognized the possibility of slick formation due to other mechanisms.

Numerous subsequent observations and experiments with improved oceanographic tools supported Langmuir's views (Woodcock, 1944; Welander, 1963; Faller et al, 1964). McLeish (1968), however, attributed the generation of slicks to turbulence in water rather than to wind, but he also recognized the fact that floating materials tend to accumulate on convergences of horizontal currents. He also pointed out that the main cause for turbulence is wind, and thus retained the term wind-slicks. His proposed theory is basically that wind-induced water movements not of the "Langmuir-circulation type" are responsible for slick formation. Similarly, Faller (1969), after a series of laboratory experiments, concluded that Langmuir circulations are formed by the action of surface waves, which are usually produced by wind.

Scott et al. (1969) proposed six different mechanisms to explain the origin of Langmuir circulations and their associated slicks. They felt that for each of these they had sufficient evidence, and they concluded that each of the various mechanisms may cause such circulations under a different set of conditions. The three mechanisms which were best supported by their evidence were shearing instability, which is wind-induced, and two mechanisms which require the action of surface films.

Recently, elaborate experiments at sea near Bermuda and in the Great Lakes (Assaf et al., 1971; R. Gerard, Lamont-Doherty Geological Observatory, pers. comm.) have clearly confirmed that surface lines (slicks, streaks, wind rows, drift lines, etc.) are formed by wind-induced Langmuir circulations. The experimenters used dye bombs and floating cards to track the flow of currents. Their measurements and observations, made simultaneously from a research vessel and an aircraft, were documented by aerial photography showing the gradual formation of drift-card lines along wind-induced current convergences.

The theory of eind-induced circulation has been criticized mainly because slicks are often observed when wind stress is relaxed or when there is no wind at all (Diet and LaFond, 1950; Owen, 1966). Owen suggested that parallel surface lines were formed by thermal energy exchange across the sea surface, the so-called "thermohaline effect." But this mechanism has a local effect, and cannot explain the large scale surface circulations. Dietz and LaFond (1950) were the first to point out that slicks were made of organic films, and that they are more prominent in near-shore, productive areas. They considered the existence of organic films as the most important factor in the formation of slicks. The only role the wind plays, according to their view, is that of stirring the water surface, thus generating ripples which make slicks more easily discernible. But at the end they are forced to address themselves to the question of what causes the uneven distribution of the organic surface films in the first place. They admit that films are made more compact at zones of convergence which are formed by wind-induced Langmuir circulation.

A completely different mechanism for slick formation is proposed by Ewing (1950a, 1950b), who noted that slicks form, under certain conditions, in relation to internal waves and are independent of wind direction. Internal-wave slicks form when winds are absent or light, that is, of a speed not greater than 3.4 m/sec. Ewing recognized that other mechanisms for slick formation were possible, and that at wind speeds greater than 3.4 m/sec., wind-induced circulation begins to dominate, and the slicks start to be oriented in the wind direction.

The exact causes for internal waves have not yet been firmly established (LaFond, 1962), but many possible causes are considered. Usually, internal waves form between water layers of different densities, but they also occur as results of oceanic fronts (see below), tidal periods, bottom topography effects, variation in atmospheric pressure, and strong winds (LaFond, 1962).

Internal-wave slicks have their long axes parallel to the troughs of the internal waves (Ewing, 1950a, 1950b), or above the line halfway between a crest and a trough (LaFond, 1962; Neumann and Pierson, 1966; Fig. 5). These slicks, like wind slicks, are made of surface films made more compact by horizontal convergences. The zone above a wave crest is a zone of divergence (extension of film), and approximately above a trough is a zone of convergence (compaction). Slicks can occur in deep waters due to large-amplitude internal waves (Perry and Schimke, 1965).

Another common feature relevant to this discussion is the oceanic frontal zone. This is the vertical boundary between two water masses of different densities. When intersecting the sea surface, this boundary is called a "front" (Cromwell and Reid, 1965). Although their appearance is generally different from that of slicks, fronts are zones of large-scale convergences, or "giant drift lines," and in this they share some of the properties of slicks. Fronts are termed, according to the properties characterizing the water masses involved, "saline fronts" or "thermal fronts" (Amos et al., 1972), but in some fronts the density differences are due to both salinity and thermal factors. Beebe (1926) described a clearly visible thermal front between cold ocean water and hot water resulting from a volcanic eruption near the Galapagos Islands.

Some fronts, such as the Polar Front, the Arctic Convergence, the Kuroshio-Oyashio Front and others, are permanent oceanic features of certain regions (Katz, 1969; Amos et al., 1972), in that they occur seasonally and are of long duration. Typically these occur where ocean currents change their directions, or where large river deltas empty into the ocean after heavy rains. Of these, the Sargasso Sea Front was well studied by several workers (Voorhis and Hersey, 1964; Katz, 1969), and is claimed to be a permanent one (Backus et al., 1969).

Fronts are visible as narrow lines of turbulent water, usually with foam and floating debris. The turbulence may be accompanied by a hissing or roaring sound (Cromwell and Reid, 1956; Amos et al., 1972). The length of a front may reach hundreds of kilometers (Katz, 1969; Amos et al., 1972), or even 1000 km (Thorpe, 1972). Its width may vary from several meters to several hundred meters.

C. Summary

With the development of more advanced and precise oceanographic tools, more factors are discovered to be involved in complex surface phenomena, sometimes obscuring the causative ones. Discussions of these phenomena occupy a substantial volume of the oceanographic literature, but are restricted here to the necessary minimum.

Basically, all types of slicks, drift lines, and fronts share one essential feature: they mark the convergences of horizontal surface currents moving in opposite directions. Neumann (1968) called these zones of convergence "singularities" to indicate their zero horizontal movement, but actually many times they are observed to move (Perry and Schimke, 1965; Amos et al., 1972; pers. obs.) Their biological significance is discussed in section IV.

Plate 3. Ocean slicks.

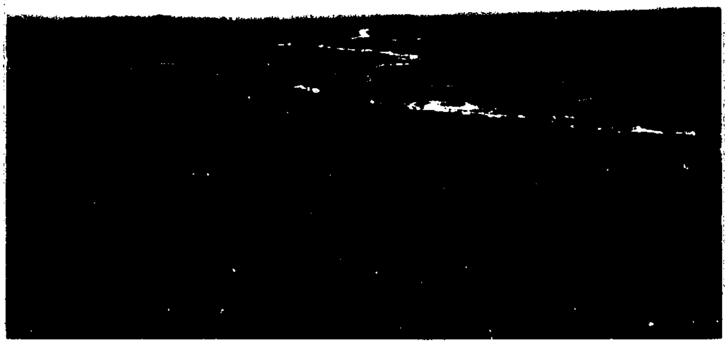
A. A typical drift line - rich with wood and scattered foam.

B. Compacted foam and flotsam.

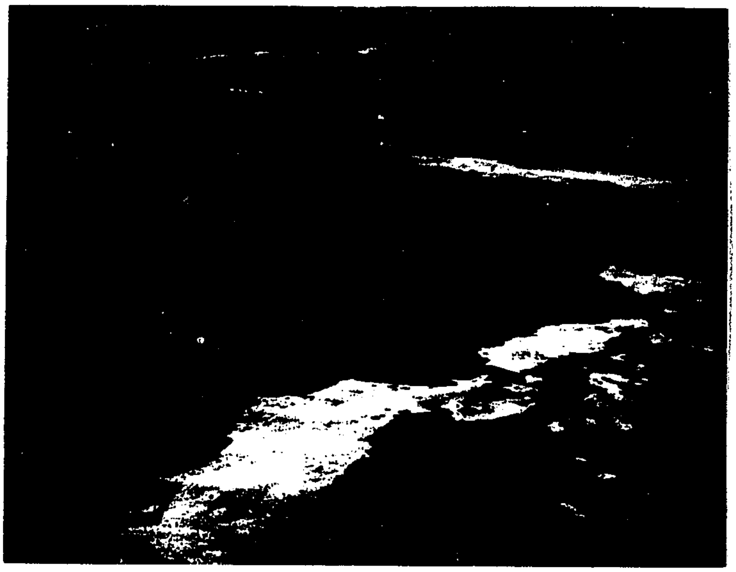
C. Narrow slick line with foam compacted into sheets.

A.

B.



C.



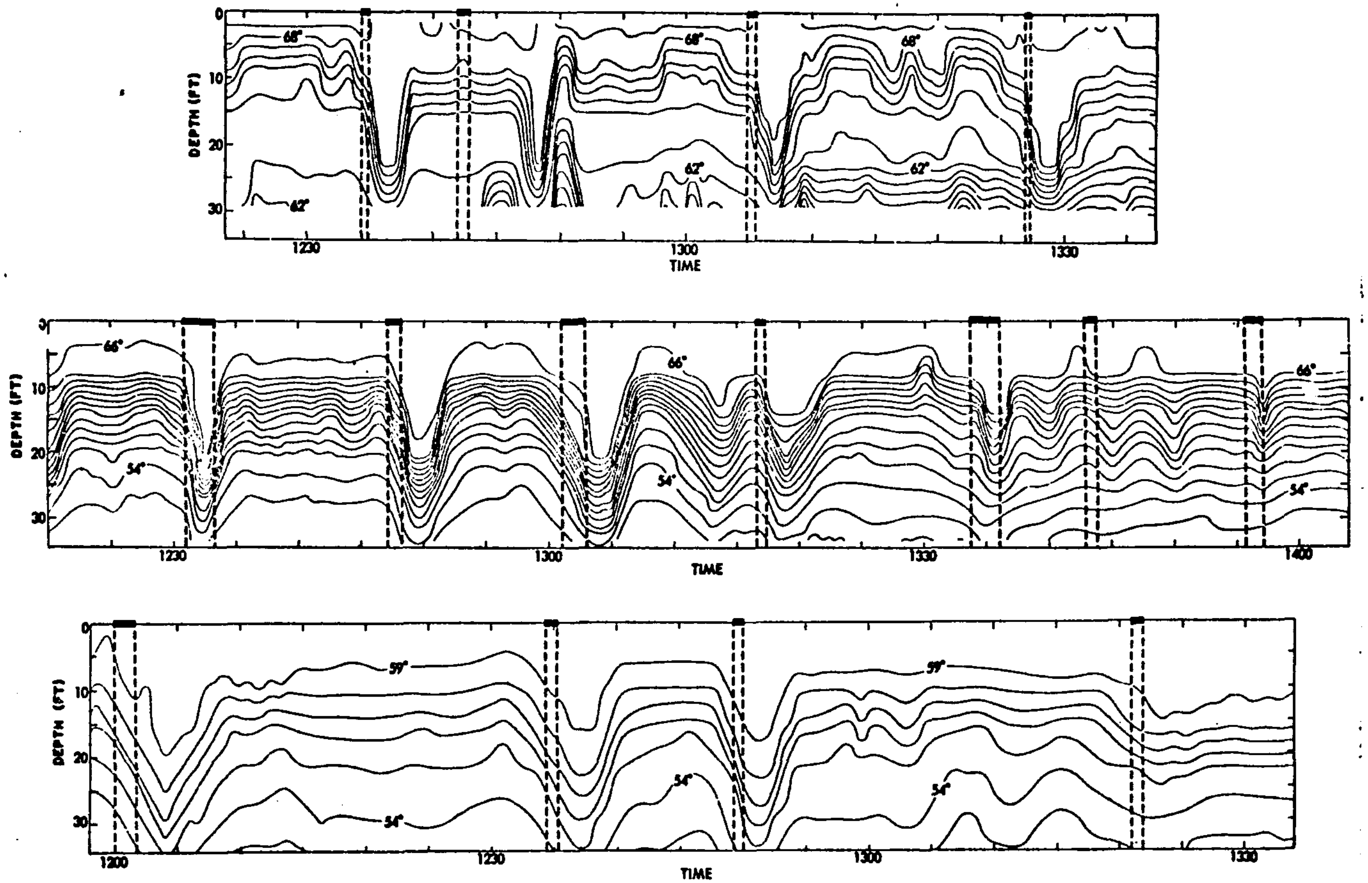


Fig. 5. Observed relation between internal waves and sea-surface slicks. The internal waves are revealed by the temperature structure. From LaFond, 1962. (p. 746)

III. Sea snakes and slicks

A. Field observations

Pelamis is often found in groups along surface lines of all types (slicks, slicks with foam and debris, and large drift lines). These groups were called aggregations, after Allee (1931). The aggregations ranged in size from several individuals to thousands of snakes, and they varied in density. Search for sea snakes in non-slick waters was continued, but revealed only solitary individuals. Table 3 summarizes this spatial distribution of *Pelamis* in the Gulf of Panama. Although careful search for snakes was conducted along slicks when they were encountered, total searching time on non-slick areas was much greater.

The aggregations on slicks included adults and juveniles. All the population samples were taken from such groups. It is not known how long it takes for these aggregations to build up, but on several occasions they appeared overnight. When slicks or drift lines were disrupted the snakes disappeared, presumably by diving.

Table 3 and Figure 4 show that aggregations of *Pelamis* were not seasonal. Their appearance in the Gulf of Panama was not associated with any weather phenomenon, although the most prominent drift lines usually occurred after heavy rains when debris washed out from rivers and eventually converged along slicks. Aggregations, however, occurred regularly along slicks without drifting objects, and thus were not associated with any particular weather. The spaces between successive aggregations are mostly the result of gaps between field trips (Fig. 4).

My observations in the Gulf of Panama showed that floating objects

Table 3. Numbers of *Pelamis* sighted on slicks and in non-slick areas. See text for details.

Month	No. of groups on slicks	Estimated No. of individuals on slicks	Density on slicks, minimum – maximum	No. sighted not on slicks, and searching time
August	0	—	—	24, in 4 days
September	3	several thousand	21 - 130	2, in 3 days
October	2	several thousand	36 - 150	3, in 3 days
November	3	219	54 - 168	3, in 1 day
December	4	67	26 - 40	12, in 8 days
January	3	several hundred	14 - 180	0
February	5	130	20 - 52	0
March	3	50	12 - 25	1, in 7 hours
April	1	50	50	0
May	6	100	4 - 50	0
June	10	several hundred	10 - 120	2, in 3 days
July	1	8	8	11, in 3 days
August	2	several hundred	5 - 148	1, in 5 hours
Total	43	many thousands		59

placed on either side of the slick were swept into its center, where commonly there was a line of foam marking the zone of convergence. The rate of movement to the slick center varied widely from about 3 cm/sec to 25 cm/sec, indicating that surface currents were converging at the line, and that great variations in the speeds of these currents were the rule. Motion of the surface layers towards the slick have similarly been observed by experimenting with dye (Welander, 1963). Often the boat was carried to the line and remained there. When the line changed its position, the boat, flotsam, and fauna remained on the line and moved with it.

Although Dietz and LaFond (1950) found the waters of slicks to be warmer than those of the surroundings, my own repeated measurements of surface temperatures on either side of and within slicks showed no clear trend. These measurements were made whenever possible, regardless of whether snakes were found. In most of these measurements there were no appreciable temperature differences between the two converging currents or between them and the slick.

On only three occasions was the slick found to be warmer than the waters beside it, by 0.1°C or 0.2°C. Twice the slick was found to be cooler than the water on one side, by 0.2°C and 0.6°C. Finally, on two occasions larger temperature differences between the two sides were measured, one of 1.0°C and the other of 3.0°C. Field notes taken on both occasions described typical oceanic fronts, although of a small scale. In the front or "current rip" described by Beebe (1926), the temperature difference between the two sides was 4°C.

No apparent correlation between the existence of a temperature gradient (or temperature discontinuity) and the presence of snakes could be established. The front with a 3°C difference had no snakes on it, but on the one with a 1°C difference approximately 50 snakes were sighted. Snakes were noted on slicks with temperatures of 0.1°C and 0.2°C above and 0.6°C below surrounding waters, but some slicks of 0.2°C above adjacent waters had no snakes on them, and one of the largest aggregations encountered was on a slick where no thermal differences could be detected.

Knowledge of the activites of Pelamis while the snakes are on a slick is important for the understanding of the snakes' adaptations to this aspect of their physical and biological environment. Observations on their behavior were made from a boat whenever aggregations were encountered, and on several occasions individual snakes were followed for extended periods of up to thirty minutes. Of particular interest were such problems as what snakes were doing while aggregated on a slick, what possible advantages they derived from coming to a slick, what social interactions, if any, took place among snakes while grouped together, and what interactions took place with other species on the slick.

Snakes were usually seen to lie motionless on the surface. Little active movement was observed on the surface, but the snakes' capability of vigorous and rapid swimming was demonstrated during dives. Feeding was observed often at the surface or 1-2 feet below the surface. Occasionally snakes were seen to go through sequences of knotting. All these activities will be discussed separately later. Snakes were not seen to shed at sea, but a large number of sloughed skins were seen in some of the aggregations. Contrary to expectations, no matings were witnessed in any of the aggregations. Even when plenty of driftwood was present, not once was a snake seen to bask on a floating log, or to hide under flotsam. The only time that a snake was seen on driftwood it was struggling frantically to get off, probably having been trapped on it somehow.

No social interaction among snakes was apparent. Interaction with other species was restricted to feeding. Predation on Pelamis was never observed in spite of the presence of potential predators along slicks. The problems of predation and parasitism on Pelamis are discussed separately.

Other organisms observed on slicks represented a considerable sample of the local fauna. There were dense concentrations of planktonic organisms, medusae, and fishes of all sizes (lobotids, balistids, pomacentrids, scombrids, coryphaenids). Porpoises, sea turtles, sharks, and rays were also commonly observed along slicks. Eleven whale sharks were once observed to feed along a slick, and a manta ray was watched while it fed along another for two hours. Marine birds such as boobies (Sula leucogaster), phalaropes (Lobipes lobatus), gulls, and terns in large numbers were seen to feed on slicks. Local fishermen also converge on slicks which they consider good fishing grounds, especially for dolphins (Coryphaena) and scombrids. Overall, slicks appear to be zones of dense faunal concentration.

B. Reaction of sea snakes to their structural environment

To test whether Pelamis is attracted to driftwood, a simulated drift line was prepared and floated in the tank in which about 100 snakes were kept. During the several weeks that the line was in the tank the snakes were never seen to pay any attention to the wood.

When they were placed on pieces of wood they wriggled their bodies vigorously until they managed to slide off the wood.

To examine the snakes' reaction to a reef-type substrate, a rock pile was constructed in the tank. The snakes never showed any interest in this substrate, which was presented in dark, mottled, and white colors. They did not rub against it or try to hide among the rocks. When hiding places were available in the tank (in the form of cement blocks, rocks, or folded paastic sheets), several snakes became trapped there and drowned.

IV. Discussion

A. Nature of the aggregations

The term aggregation was used for the groupings of <u>Pelamis</u> because it is noncommital and does not imply interaction among the snakes. Allee (1931) proposed that this term be used for groups which cannot clearly be defined as social. He stated: "There is in the term itself a strong suggestion that the groupings involved are not closely integrated..." The nature of the aggregation, according to the classification discussed by Allee, may be 1) accidental association, 2) secondary, 3) symphagic, 4) synaporic, and 5) heterotypical. These terms, in order, mean 1) grouping without mutual benefit to individual members, 2) aggregations resulting from coming together of individuals rather than the remaining together of progeny, 3) groupings about food supply (fish in this case), 4) groupings caused by an external agent (i.e. current), and 5) associations of various species. Allee correctly pointed out that these are not clear-cut situations. The loose, general term "aggregation" seems to be satisfactory.

Pelamis derives several advantages from converging on slicks. First, this facilitates the search for food, which consists of small fish (Klawe, 1964; pers. obs.) On slicks the chance of encountering a school of fish is greatly increased, and snakes were seen to feed there on a variety of fishes (Hunter and Mitchell, 1967; pers. obs.) Many snakes caught on slicks had their stomachs packed with food, while none of the 24 snakes caught away from slicks had any food in them.

Secondly, an aggregation facilitates the finding of a mate, simply by virtue of having many snakes concentrated in a small area. The fact that _many_ shed skins were seen on slicks may suggest that _Pelamis_ rubs against floating objects to facilitate shedding. This, however, is not supported by observations in the field or in the laboratory, and may be explained in other ways (the average shedding schedule of _Pelamis_ is such that about 5% of the snakes in an aggregation may be shedding their skins in one day; see chapter 11).

The disadvantages of coming to slicks may be several. The first is increased competition from other snakes and other marine organisms. Secondly, slicks probably provide a situation in which ectoparasites can find _Pelamis_ easily and settle on them. The third theoretical disadvantage is the presence of potential predators along the slick. This is minimized by the apparent antipredator adaptations of _Pelamis_ which are discussed separately. The advantages offered to _Pelamis_ aggregating on slicks obviously outweigh the possible disadvantages listed above.

Other reptile aggregations not social in nature are known. Examples are the hibernation dens of rattlesnakes and of _Storeria dekayi_ and _Thamnophis_ (Noble, 1936), overnight aggregations in the banded gecko, Coleonyx (Greenberg, 1943), and diurnal aggregations in the gekkonid lizard Tarentola annularis (Hoofien, 1962). All of these aggregations were not social in nature, and were formed as the animals were seeking shelter for the season, for the night, or from the desert heat.

Sea-snake aggregations have been known for a long time (Cantor, 1841; Verrill, 1937; Shaw, 1961). A huge aggregation of Astrotia stokesii in the Indian Ocean was described by Lowe (1932). None of these, however, was reported as occurring along a slick. Beebe (1926) saw Pelamis on a front in deep ocean on his way to the Galapagos Islands, and Amos et al. (1972) reported seeing snakes, probably Hydrophis, on a front in the Indian Ocean. Several authors have described seeing Pelamis in conditions which indicate slicks, but they were apparently not aware of this (Klauber, 1935; Myers, 1945; Paulson, 1967). It also must be noted that slicks and drift lines are much harder to detect in the open ocean than in near-shore areas or bays, where productivity is higher (Dietz and LaFond, 1950), and where flotsam is more readily available. Mid-ocean aggregations along converging currents may therefore be seen with little or none of the accompnaying "markers" such as foam or flotsam. Aggregations of Pelamis in the Gulf of Panama and along Costa Rica were briefly described at the end of the field work phase of this study (Kropach, 1971a), and were confirmed later by Dunson and Ehlert (1971).

B. Mechanisms of aggregation formation

Several mechanisms for aggregation formation can be considered. The snakes may detect slicks from afar and swim to them; they may find slicks while randomly searching for food; they may be attracted to floating objects as are many fish (Hunter and Mitchell, 1967), or they may be carried passively by the converging surface currents.

No evidence for the first possibility is available, but from what is known of reptilian biology, the ability to detect slicks from long distances is ruled out. Considering the short time it took for some of the large aggregations to build up, and the relatively weak swimming abilities of Pelamis, the possibility of snake grouping through random search for food is also ruled out. Attraction to floating objects is ruled out on the basis of field and laboratory observations in which Pelamis showed no interest in floating wood.

The possibility that the snakes are brought together by converging surface currents is accepted not because it is the remaining one from the list above, but because it is the only one for which evidence is available. Pelamis was observed being carried by surface currents in the Gulf of Panama, even though active swimming took place at times. When snakes were placed in turbulent water they were at the mercy of the medium, and several times during the year snakes were found washed ashore.

Reports of Pelamis being carried by currents and being washed ashore are widespread (see section on population-limiting factors). Several authors have pointed out the close association of Pelamis with currents. Neill (1964) wrote that Pelamis "follows surface currents," and Glauert (1950) explained the presence of Pelamis in southern Australia by "southern water movement." Shuntov (1966) noted that the snakes were not able actively to move out of areas where currents rotated, and that in the Northern Australian shelf currents were important in determining sea snakes' distribution (Shuntov, 1971).

Volsøe (1939) wrote that Pelamis were washed from the Gulf of Oman to the strait of Hormuz by tidal waves, and Deraniyagala (1955) called this species a "current indicator." In view of the numerous reports of sea snake aggregations, of sighting snakes along flotsam, and of Pelamis being influenced by currents, it is astonishing that the relation of these snakes with surface convergences went unnoticed until this study began. The zoogeographic significance of this relation is discussed in chapter 4 and in the next section.

C. The biological significnace of oceanic convergences

While most oceanographers treated surface phenomena such as slicks from a purely physical point of view, Japanese, Indian, and Panamanian fishermen have followed the lines with the knowledge that there they would harvest fish in greater amounts than elsewhere (Uda, 1938; Barkley, 1968). Biological observations on surface convergences were first made by Beebe who followed a large drift line for 2½ days on the Arcturus expedition (Beebe, 1926). He described the great faunal concentration along the line which represented a considerable sample of the pelagic fauna. His account is fascinating, but what he described is not unusual. The "current rip" on which he reported was similar to those observed during this study in the Gulf of Panama.

More recent studies show that organic molecules are accumulated along convergences (Dietz and LaFond, 1950; Sutcliffe et al., 1963). Plankton and weakly swimming organisms such as Pelamis are carried by currents to slicks or fronts (Bainbridge, 1957) in the same manner that land-based flotsam is brought there. The more powerful swimmers are able to reach these food-rich zones actively (Blackburn, 1965; pers.

obs.) and feed there.

The convergences play an important role in oceanic ecology in gathering organic matter around which faunal concentrations build up and a food web is established. This role may be of particular importance in areas of poor productivity. The ocean is not a homogeneous ecosystem, and food abundance, followed by faunal distribution, is patchy (Murphy, 1936; Wooster et al., 1963; pers. obs.) Murphy (1936) discovered this when he was studying the distribution of sea birds, which he found to be related to availability of food. A convergence such as a slick or front is a major sub-habitat of the pelagic life zone. It is a dynamic one, ever changing, forming, breaking apart, and reforming; and one which appears to be critical to the ecology of Pelamis.

Many examples of clumped distribution are known, since organisms tend to congregate in a limited number of available sites which provide the most favorable conditions, shelter, or food. One particular terrestrial sub-habitat which parallels the slick sub-habitat in the ocean is provided by tropical army ants. Army ants, especially Eciton burchelli and Labidus praedator, flush out arthropods from the forest litter during their migration phase. In doing so they create new niches for many forest species (Willis, 1968). Many of the species associated with army ants become highly dependent on them, or "professional" ant followers (about 50 species of birds are such "professionals"). Some bird species derive 90% or more of their food from following ants, and would die out if army ants ceased to march across the jungle floor (Willis, pers. comm.)

Such ecological situations, where many species share the same types of environmental resources in part of the habitat, were called by Root (1967) a "guild." He defined a guild as "a group of species that exploit the same class of environmental resources in a similar way. This term groups together species, without regard to taxonomic position, that overlap significantly in their niche requirements." Dunson and Ehlert (1971) called the assemblage of species about a slick a "biological community," a term which has a precise meaning in ecology. This term seems inappropriate, and not seeking to add new terms to a field overburdened with jargon, I propose that it be called a gulid. The slick guild includes all the nektonic species of high trophic levels in the slick food web. Members of this guild, in addition to sea snakes, are pelagic fish, sharks, rays, marine mammals, and marine birds. (Sea snakes, in spite of being carried passively by currents, are capable of active swimming, and therefore are considered to be nektonic, in agreement with Sverdrup _et_ _al_., (1942) and not with Dunson and Ehlert (1971) who called them "planktonic".)

Increasing evidence indicates that the slick guild is a significant aspect of oceanic ecology. Woodcock (1944) has pointed out the connection between the sailing characteristics of _Physalia_ _pelagica_, the Portuguese man-of-war, and Langmuir circulations. _Physalia_ has evolved a swimming position that minimizes the danger of having its tentacles entangled by flotsam. Gooding and Magnuson (1967) and Hunter and Mitchell (1967, 1968) studied fish which were associated with floating objects. Without getting into the debated problem of the adaptive value in attraction to flotsam, it will suffice to state that many fish species, from at least twelve families, are common drift line residents. Some even assume the appearance of drifting objects. The fact that fish are attracted to floating objects is of significance to the biology of Pelamis, as will be shown in the discussion of food habits. And as already mentioned, the economic value of slicks has not escaped the attention of commercial fisheries.

Slicks are important as oceanographic tools (Ewing, 1950a) and may be significant in studying mixing and chemical pollution. Their interest to the biologist, in addition to those aspects already mentioned, is in the role they may play in the dispersal of organisms. Among the flotsam on slicks are fruits and seeds which can be carried great distances (Beebe, 1926; pers. obs.) Large logs and whole trees may serve as rafts on which small animals or nests may be trapped and carried to islands. The pattern of distribution of the iguanid lizard Anolis in the West Indies is explained by dispersal among the islands (Williams, 1969), which was most likely accomplished by rafting on drifting logs swept by currents.

Finally, fronts do not only mark dense faunal concentrations, they also act as boundaries between distinct faunae (Deacon, 1963; Barkley, 1968; Backus et al., 1969). The zoogeographic importance of water movements, together with other factors, was recognized by Sverdrup et al. (1942), who stated: "The character of the fauna and flora is thus governed by the nature of the currents - namely, their origin, direction of flow, magnitude, coldness or warmth, degree of salinity or density, and their character as regards other attributes such as relative richness in nutrients."

V. Summary

Observations of sea snake aggregations along slicks have led to the discovery of a major sub-habitat, which is called here the slick guild (after Root, 1967). Slicks and other surface convergences were intensively studied by physical oceanographers, but their biological aspects have not been adequately evaluated. They play an important role in ocean ecology, man's economy, and the zoogeography of marine (and most likely some terrestrial) organisms.

The position of Pelamis in the oceanic food web is defined as being a member of the slick guild. There it assumes the role of a predator at a high trophic level. In comparison with terrestrial animals, members of the slick guild have a varied diet (see chapter 10 for Pelamis) and have greater freedom from restriction to features of the habitat.

MOVEMENT AND RANGE

Knowledge of the movement of any organism is significant to the understanding of its biology. Movement involves the animal's locomotory mechanisms, which determine its potential for dispersal and the range covered in its activities such as search for food, mate, or shelter. Locomotory mechanisms in the broad sense include both those possessed by the animal itself and the external agencies which play a role in movement (rising air currents, wind, ocean currents).

I. Locomotion in *Pelamis*

Pelamis swims by producing alternating lateral undulations. In forward swimming these lateral undulations progress caudad. This is basically identical with the movement of most land snakes, except that in the latter the movement is altered by irregularities in the substratum (Gans, 1962). *Pelamis* also exhibits a characteristic backward swimming in which the undulations progress cephlald.

This "serpentine" movement is the basic form of locomotion in limbless vertebrates (Gans, 1962) seen in fish and even some limbed vertebrates, such as salamanders, running monitor lizards, and crocodiles in their "belly run." It is based on lateral bendings of the trunk by waves of muscular contractions along the sides of the body. Each bend has a lateral and a posterior force component exerting pressure against the water. The overall effect is a forward movement (after Gans, 1962).

In *Pelamis* specialization for marine life brought about lateral compression of the trunk as well as loss of the ventral plates, which Smith (1926) attributed to "disuse." This explanation is not acceptable on a theoretical basis because of the ample evidence for evolution through natural selection. In swimming, the absence of ventral plates is a physical advantage whose evolution does not require the resurrection of Lamarckian theories. Due to the lateral compression, the snakes present a greater lateral surface area to the surrounding medium. To increase this effect, the lower part of the body is often compressed in the form of a keel. Whether this done voluntarily by the snake is not known. According to Johnson (1955) several vertebral modifications which aid in locomotion occur in sea snakes. The prezygapophyses are long, the condyle is reduced, and the neural spines are long in comparison with most other snakes. The neural and haemal spines are particularly long in the caudal vertebrae, as is easily shown by X-raying the animals. The condyles are reduced because in the water there is less need for shock resistance, and their reduction, Johnson says, helps in swimming; the prezygapophyses are larger to allow greater undulatory locomotion, and the long neural spines allow the deepening of the body (Johnson, 1955). Hofstetter and Gasc (1969) pointed out that in some hydrophiids and the Acrochordidae, also an aquatic group, the tuberculiform processes of the lateral heads are weak. The relation of this to swimming was not explained.

Contrary to some reports (Hopley, 1882; Wall, 1921) the tail of Pelamis is not prehensile, nor does it act as a fin or a paddle. Unlike fish, Pelamis lacks the skeletal support for the tail to act as a propulsion mechanism, and the most that Pelamis can do is use it as a rudder. The lateral tail movements observed in Pelamis, especially in their active underwater swimming, are a continuation of the bendings made by the body, and not an independent propulsion movement.

Pelamis was generally observed swimming slowly or lying motionless at the surface. Rapid swimming was observed occasionally at the surface, and usually during dives and feeding. The speed of rapid swimming was measured in the laboratory to be approximately 1 m/sec, but the snakes maintained such speed for short distances only. They were not able to swim against a current or to overcome near-shore waves.

When not actually diving, Pelamis stayed below the water surface, but very close to it, with the head usually bent downward, breaking the surface only for breathing. Sometimes the snakes swam with the head held above the water. This behavior was interpreted by Wall (1921) as "looking around," but since it occurred during rapid swimming, it may have hydrodynamic value, facilitating swimming. Natrix, graceful swimmers, are commonly observed with the head held above the water surface during rapid movement.

On land, Pelamis is completely helpless and cannot progress in spite of vigorous attempts to do so. This is another indication that this snake progresses in water by exerting force on the medium laterally. Lack of ventral plates does not allow the snake to move on land and use the irregularities of its surface as points where pressure can be applied. In fact, not having a true ventral surface causes Pelamis to roll laterally when on land.

Diving

An attempt to determine the diving activities of Pelamis was made both in the field and in the laboratory. Snakes were followed on dives in the field to a maximum depth of 60 ft, but Pelamis reaches greater depths - the snake which was followed to 60 ft. continued downward until it was out of sight. The snakes were seen to dive and emerge from dives rapidly and with great ease, indicating their ability to adjust to changes in pressure involved in these movements.

Dives observed in the field were short, and the snakes emerged every 5 to 10 minutes. In these dives a snake would stay 5 to 10 ft. below the surface. In the laboratory, the longest duration of a dive was 1 hour 58 minutes. Forced dives were not tried in this study, but Pelamis were reported to survive up to 24 hours when Dunson and Ehlert (1971) forced them to dive in cool water of 13°C. Nicol (1967) estimated the duration of hydrophiid submergence to be up to 8 hours.

Long and rapid dives by Pelamis are possible due to the increased functional area in the trachea and the posteriorly extended lung, which is believed to function as a swim bladder (Volsøe, 1939). Although Ditmars (1937) thought (but did not substantiate) that Pelamis was able to extract dissloved oxygen from water, the lung is the only respiratory organ. It is not known whether sea snakes possess any other special features to aid in diving, such as those possessed by cetaceans. These features, in mammals, are the possession of myohemoglobin which has high oxygen-storing properties, reduced sensitivity to accumulation of CO_2 and lactic acid, increased ability for muscle anaerobic metabolism, redistribution of the blood, and changes in metabolic rates during dives (Irving, 1939). In addition, structural modifications in the respiratory systems of mammals have been noted (Ridgway, 1972; Simpson _et al._, 1972). Ridgway also noted that in diving mammals oxygen storage in blood and muscle is increased. Transport capacity is also increased due to relatively large blood volume and high hematocrit and hemoglobin levels. Diving has been reported in mammals to be accompanied by bradycardia, peripheral vasoconstriction, and blood redistribution (Ridgway, 1972). Bradycardia was observed in free-living seals which were not constrained nor forced to dive (Harrison _et al._, 1972).

Many of these aspects have not been looked at in sea snakes, and it would be interesting to find out whether they possess adaptations similar to those found in diving mammals. Bradycardia was observed in _Pelamis_ as soon as diving started (Pickwell, pers. comm.) It should be remembered, however, that snakes have a lower metabolic rate than mammals and can probably adjust physiologically to the demands of diving more easily. M. Saint-Girons (1970), who studied 76 reptile species from 29 families, found that _Laticauda_, the only sea snake in the study, was among the six species with the largest erythrocytes, but the hemoglobin levels of these species were not given. Other reptiles with large erythrocytes were _Emys_ _orbicularis_, a fresh water turtle, _Sphenodon_, _Heteronota_, a gekkonid, _Lialis_ (Pygopodidae), and _Heloderma_. It is hard to make a case for the adaptive value of having large red blood cells, but, interestingly, cetaceans have been found to possess larger erythrocytes than terrestrial mammals (Ridgway, 1972). Ridgway, however, commented that "contrary to early beliefs, a small red cell size could improve the oxygen transport and storage capabilities of the blood."

To sum up, *Pelamis* are active but not powerful swimmers. They are capable of short bursts of high speed which are usually performed in dives or in escape from a disturbance. Sea snakes can remain submerged for long periods, but their diving physiology is little known. The lung of *Pelamis* is modified to provide a greater gas-exchange area and greater volume, and for hydrostatic function. Not persistent swimmers, *Pelamis* are easily carried by currents (see also below).

II. Range and population size

Three important questions regarding *Pelamis* in the Gulf of Panama are discussed in this section. The first is whether these snakes usually moved into and out of the Gulf of Panama, and if such a movement was seasonal. The second question, in case there was no such movement, concerned the size of the population enclosed in this area. A third question was how such movement took place within the Gulf, and what was the activity range of the snakes. A mark-recapture program was initiated to provide the answers to these questions.

The mark-recapture approach to this study was based on the following rationals:

a. A large number of marked snakes was expected to be released throughout the period of the study. Recapture would have indicated that the snakes remained in the study area. Survey of areas adjacent to the Gulf of Panama was planned for collecting and releasing *Pelamis* and for search for marked snakes which had been released within the Gulf. This was supposed to provide information on *Pelamis* movement into and out of the study area.

b. A mark-recapture program can be used to arrive at estimates of population size by application of the "Lincoln Index," a technique commonly used in ecological studies.

c. Recapture of Pelamis could have given some idea of their range of movement during their regular activities. This is the "activity range" as defined by Carpenter (1952) to be "the area covered by an animal in the course of its day to day existence," which is different from home range in the absence of a nest or perch as a center of activity.

Results

961 snakes were marked and released throughout this study (September 1969 - October 1970). Fig. 6 shows diagrams of the codes used in marking snakes, and Table 4 gives information on the released specimens. Plate 4 shows marked snakes after the marking wounds had healed. Although many snakes were regularly encountered in large aggregations, only one was recaptured. This individual was released on December 27, 1969, and recaptured on October 30, 1970 in a more northern part of the Gulf.

On March 19-21, 1971, Dr. George Pickwell of the Naval Undersea Research Center in San Diego, California, collected many Pelamis in Bahia Banderas, Jalisco, Mexico, during the Pelacan Expedition. Of these, 21 specimens had notched tails, but 18 of them carried notches of irregular shape of the type occasionally observed in Pelamis. The notches on three snakes appeared to be man-made, and were identical to codes used in marking snakes in the Gulf of Panama. One of them was notched as the group released on January 15, 1970; two bore notches identical to the code of the group released on February 13, 1970. The notches on these snakes were distinctly different from the naturally occurring notches. All three were gravid females. Dr. Pickwell's intensive inquiries and efforts to find other investigators who could have possibly marked Pelamis in the Eastern Pacific were to no avail. These snakes from Bahía Banderas are presumed to be individuals marked and released in Panama 13 and 14 months prior to recapture. Obviously, a marking technique by which individual snakes could be identified would have strengthened this case.

Discussion

When the release of large numbers of animals yields poor recovery or no recovery, there are several ways of interpreting the results:

a. The animals suffer increased mortality because of the technique used, either directly or as a result of the technique (i.e. infection of wounds) or because of increased predation due to the effects of the markings on the animals' locomotion.

b. The population is very large, and in order to obtain recoveries many more specimens must be marked and released.

c. Individuals continuously move out of the area, and new individuals move in. These possibilities are not mutually exclusive. Here, consideration is given to all of them.

The first possibility is ruled out because snakes marked in the laboratory recovered rapidly and never developed infections in the wounds. Furthermore, snakes which were injured naturally (see chapter 11, section I, on predation), sometimes severely, healed well. The problem of "increased predation" is irrelevant to this discussion since as far as is known, Pelamis does not rely on speed for escape from predators (see chapter ii). In comparison with the marking techniques commonly used on lizards (toe clipping), the method used in this study is considered to be relatively harmless to the organism studied.

The second possibility cannot be fully evaluated because no accurate estimate can be made of the number of sea snakes in the Gulf of Panama. Although some of the aggregations were estimated to include thousands of snakes, their total number in the Gulf can be merely guessed, and a guess of many thousands, perhaps even a million, appears not to be an exaggeration.

The third possibility, that of movement into and out of the Gulf of Panama, is a very real one. Fig. 7 shows the surface currents in the Gulf of Panama throughout the year. These currents enter from the Panama Bight in the southeast, move in a counterclockwise direction, and leave the Gulf around Pta. Mala in the southwest. Tidal currents influence the strength of these permanent currents, but not their direction (Hydrographic Office, Pub. 106). Considering the locomotory abilities of Pelamis, these animals must be swept by the steady surface flow into and out of the Gulf. This conclusion is contrary to what I had expected to find in this study.

Dr. Pickwell's finding of marked snakes in Bahía Banderas, 3000 km from their point of release, is remarkable. Examination of the longshore surface currents from Panama to the Gulf of California (Fig. 8) shows an increase in the prevailing northward currents from March on. These reach their peak in May and June, and continue throughout the summer. This fact alone does not constitute air-tight evidence that Pelamis uses these currents as a migrating route, but it indicates that they can do it, and that some individuals did do it. However, this hypothesis will be proven only when individually marked snakes (whose tail patterns were photographically recorded) are found to have traveled the route from Panama to Mexico. The conditions for such a marking method were not available to me in this study.

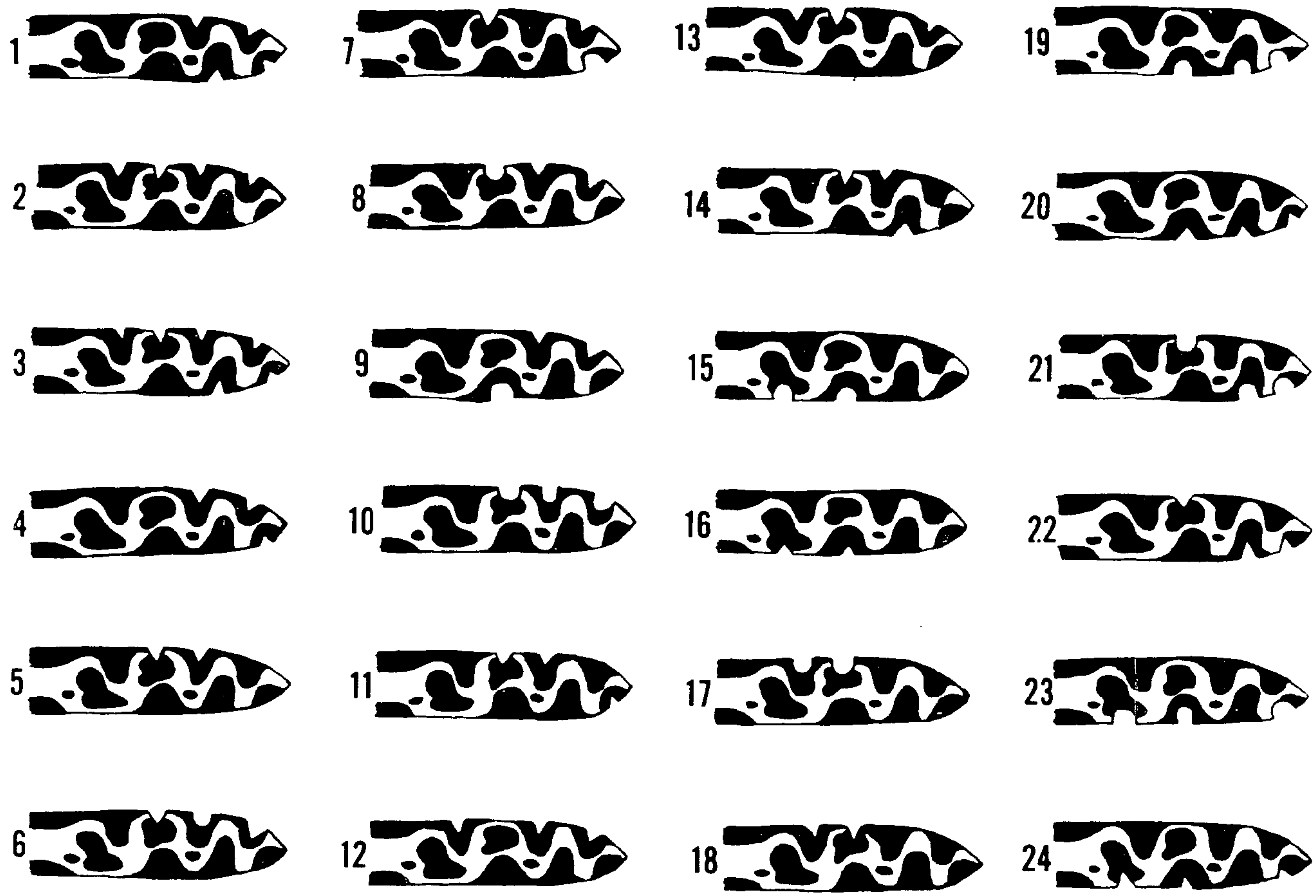
This finding adds much weight to the discussions in chapters 4 and 7 on the distribution of Pelamis and the relationships of this species to surface currents. Clearly, more data in this area should be collected. A study in which drift-bottles are used might yield additional information on the flow of surface currents in the Eastern Pacific.

The activity range of Pelamis could not be determined in this study. Such determination requires repeated recaptures within short intervals after release. One fact which emerges from this study, however, is that Carpenter's concept of activity range cannot be applied to pelagic animals in the same way as to terrestrial animals. Carpenter found in his study that terrestrial snakes move relatively little, mostly in search of food, mate, hibernation den, or shelter, and that barriers in the habitat limit the extent of movement in certain directions while habitat continuity allows movement (Carpenter, 1952). It is clear that pelagic animals are within a continuous, relatively homogeneous habitat which lacks "reference points" or restricting barriers, thus allowing, at least theoretically, for an unlimited activity range. While on a drift line a sea snake can be said to have temporarily a more limited activity range, but on the whole, the term cannot be applied to pelagic species in a useful way. Other sea-snake species which are reported to be restricted to the bottom (Herre, 1942; Shuntov, 1971) probably have a more limited range. This is also true for non-pelagic species such as coral-reef fish.

Summary

The mark-recapture program, together with data on surface currents in the Gulf of Panama and the Eastern Pacific, and capture of presumably marked snakes in Mexico suggest that there is movement of snakes into and out of the Gulf. The speed of such movement and turnover rates are not known. The number of snakes in the Gulf is not known, but it is guessed to be very large, perhaps reaching a million. The movement range of *Pelamis* is determined by surface currents and their speed, direction, and persistence.

FIG. 6



Codes used to mark Pelamis

Table 4. Numbers of snakes marked, and dates and localities of their release. * indicates snakes 40 cm or less, total length.

Code No. from Fig.	Numbers of snakes released	Date	Locality
1	27	Sept. 18, 1969	About 1 mile NE of Pacheca, Pearl Islands
2	* 4		
3	* 1		
4	14	Nov. 7, 1969	8° 48' N., 79° 12' W.
5	* 9		
6	27	Nov. 26, 1969	8° 51' N., 79° 15' W.
7	* 19		
8	13	Dec. 27, 1969	Vicinity of San Jose, Pearl Islands
9	* 9		
10	1		
11	* 11	Jan. 14, 1970	Between Saboga and Contadora, Pearl Islands
	1		
12	1	Jan. 16, 1970	8° 50' N., 79° 20' W.
13	158		
	23	Jan. 18, 1970	
14	* 133	Jan. 16, 1970	
	* 5	Jan. 18, 1970	
15	22	Feb. 13, 1970	Vicinity of San Jose, Pearl Islands
16	* 37		
17	10	Feb. 18, 1970	Near buoy marking the Canal anchorage area.
18	* 27		
19	11	March 13, 1970	8° 45' N., 79° 28' W.
	7	March 14, 1970	
20	* 17	March 13, 1970	
21	152	Aug. 16, 1970	8° 46' N., 79° 25' W.
22	* 25		
23	166	Oct. 27, 1970	8° 52' N., 79° 25' W.
24	* 31		
Total	961		

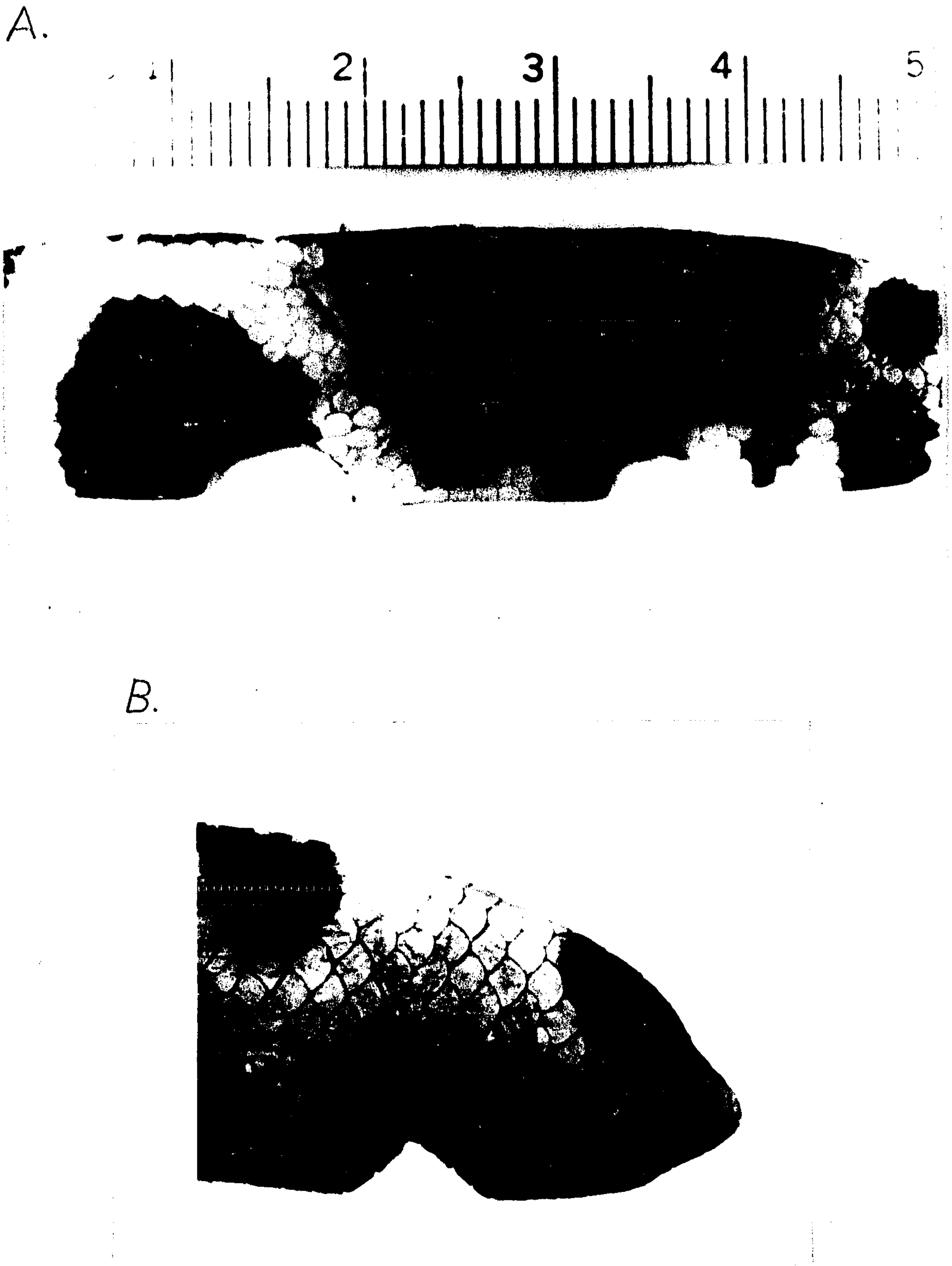


Plate 3. Healed notches on Pelamis tails:
A. U-shaped notches. B. V-shaped notch.

Fig. 7. (From Hydrographic Office Public. No. 106, current reprinting, 1963).

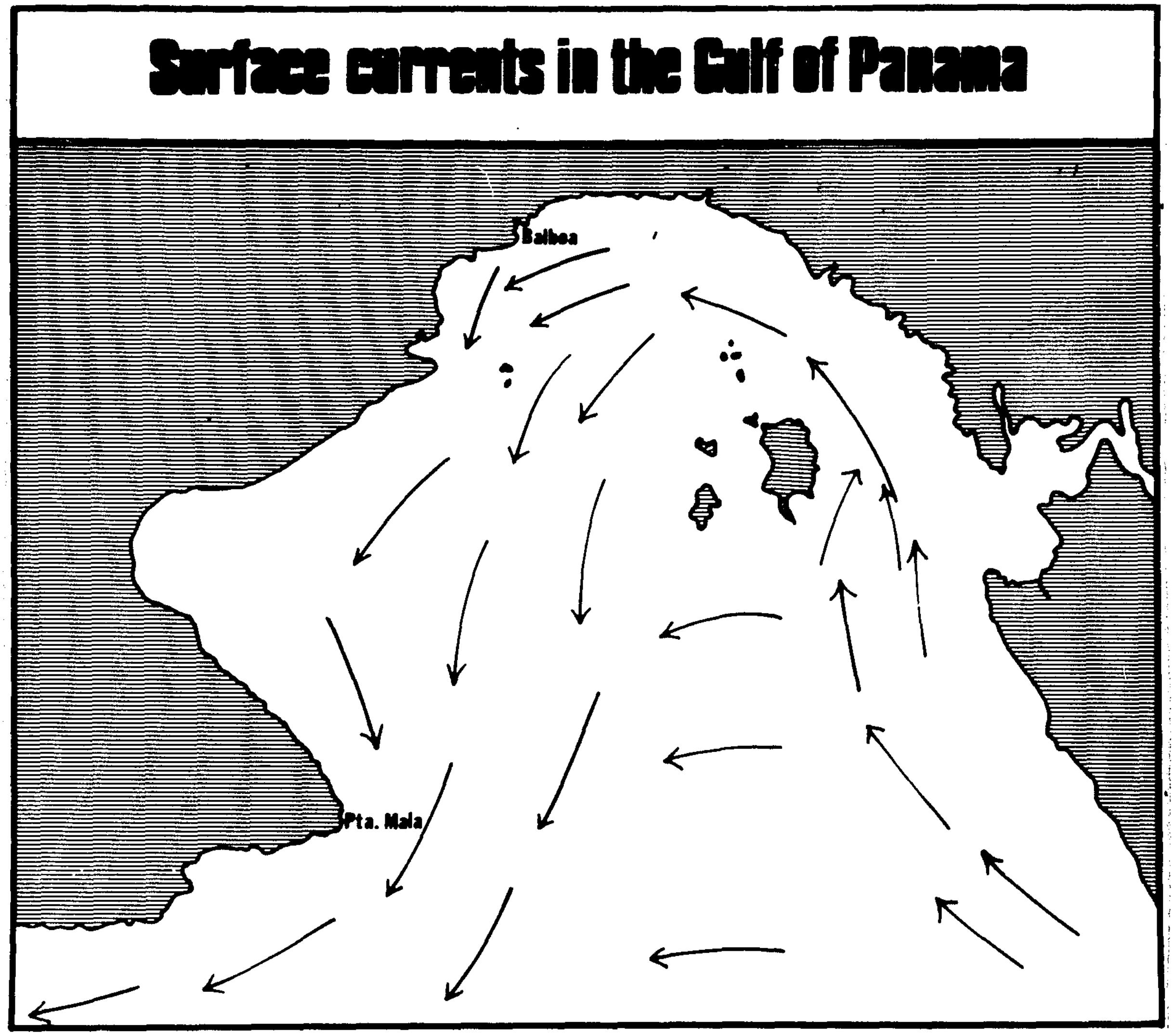
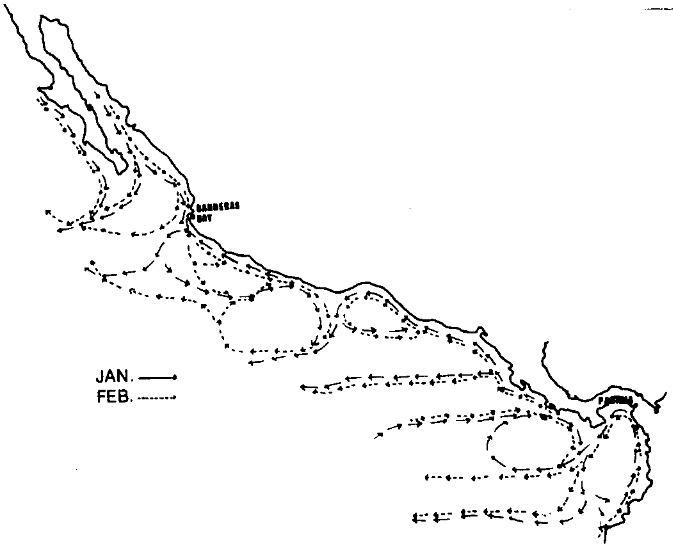
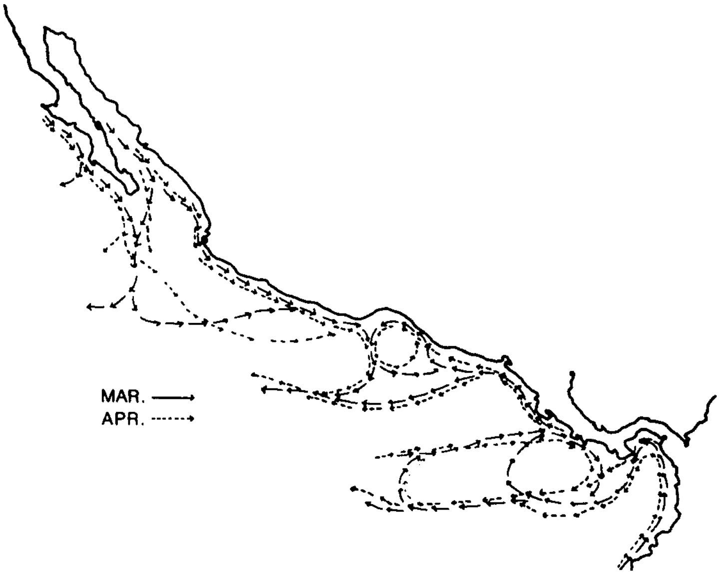
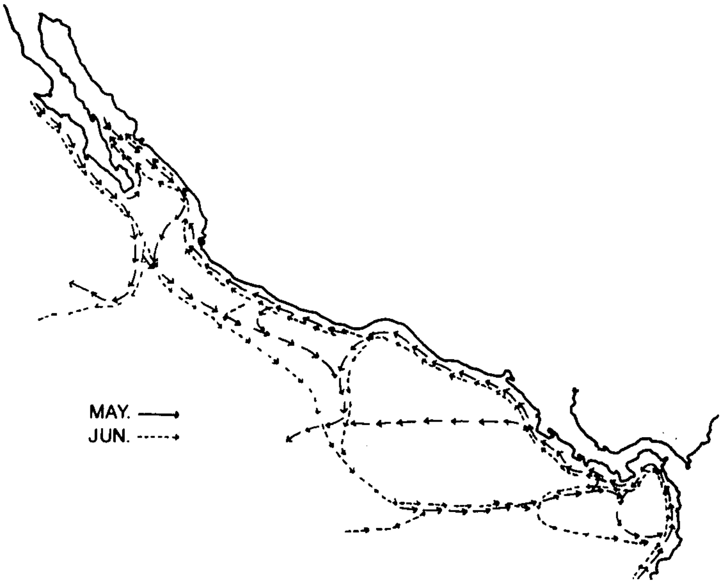
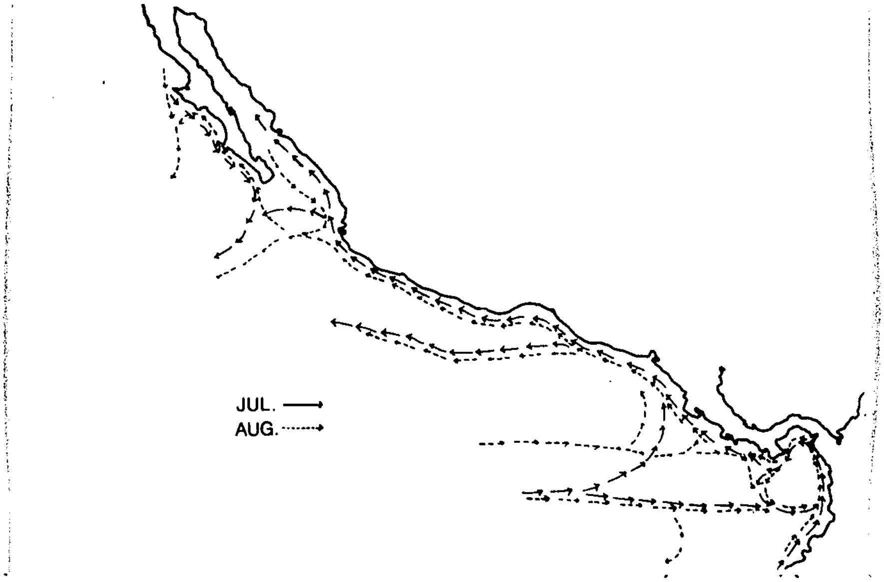


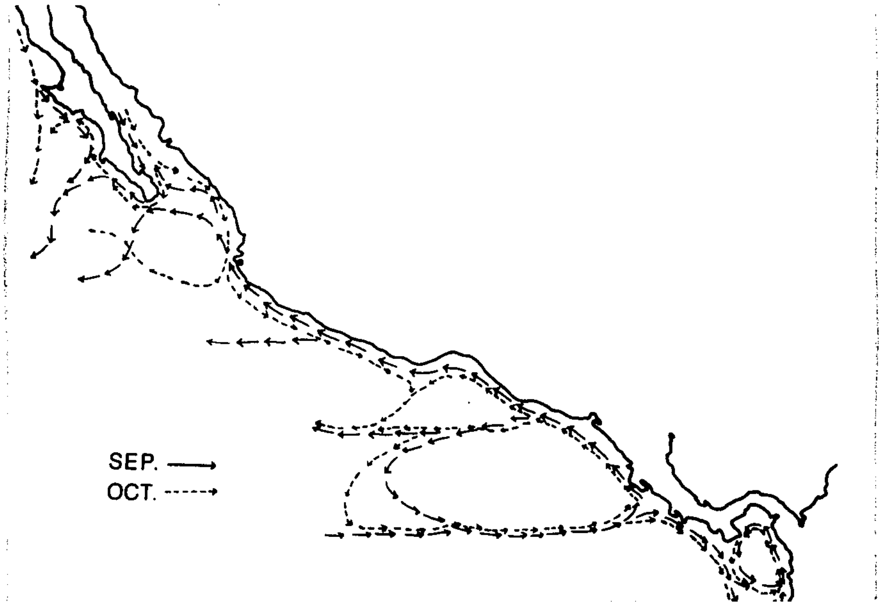
Fig. 8. Longshore currents in the Eastern Pacific throughout the year. (From Atlas of Surface Currents, Northeastern Pacific Ocean. Hydrographic Office Public. No. 570.)

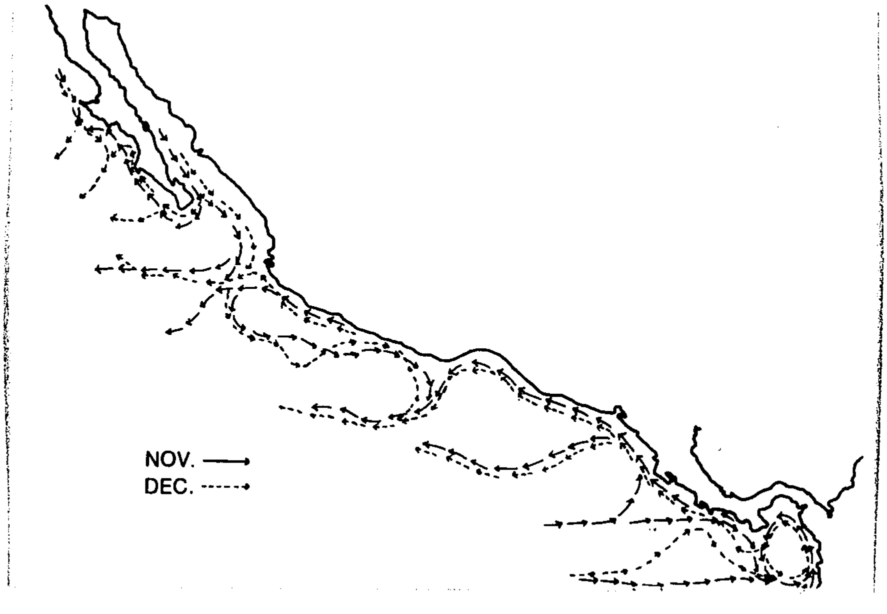

BANDERAS BAY
JAN.
FEB.


MAR.
APR.


MAY.
JUN.


JUL.
AUG.


SEP.
OCT.


NOV.
DEC.

BEHAVIOR OF PELAMIS IN THE LABORATORY

Specimens of Pelamis were placed in a large indoor tank for observations of those aspects of their behavior which could not be easily observed in the field, such as duration of diving, feeding behavior, shedding schedule, knotting, reaction to a light source and to a variety of structures presented to the animals, and social interactions among the snakes. The observations were made twice a day (with 6-hour intervals) and three times at night (3-hour intervals).

Results and discussion

A large group of snakes was present in the tank during most of the study, ranging in number from 50 to more than 100. They exhibited a relatively limited behavioral repertoire. The most noticeable behavior of the snakes in the tank was their tendency to move outward and thus spread along the tank walls, or to bump against them head-on. This is most likely due to the pelagic mode of life in an unrestrained habitat. As a result of this, a large number of the snakes was always present at the tank corners.

Another frequent habit of the snakes was to lie on the floor of the tank motionlessly or to move along it in what appeared to be "search movement." This term implies my early interpretation of this movement to be search for food. After observing the animals for a longer time, my conclusion is that this habit is, similarly to the one described above, a result of pelagic life. In the tank, the floor was probably not recognized as "bottom" analogous to the sea bottom but was another wall with which the snakes collided in their constant swimming outward. When food was spread on the tank floor the snakes moving there were not able to find it, and even when they passed close to it, it was ignored. The function of the snakes' habit of lying motionlessly on the bottom of the tank was not clear. This habit did not seem to be restricted to a particular part of the day (Table 5). Whether the snakes do this in nature in shallow water is not known, but Volsøe (1956) described sea snakes, without naming the species, as lying on the bottom in wait for prey.

To study the reaction of sea snakes to their structural environment, a simulated drift line (see Materials and Methods, p. 9) and a rock pile were prepared in the tank. None of the snakes was ever observed near or within the rock pile, regardless of the color given to it, and none showed any interest in the rocks as a hiding place. The drift line, too, was ignored by the snakes, although sometimes individuals were in its vicinity due to their random movements in the tank. Some snakes were trapped there, but when given a chance swam away from the line. Snakes were never observed to be actively interested in the floating wood. Table 5 shows a summary of the activities of 87 snakes during 10 days and nights of observation, and it represents behavior typical of the snakes throughout the year of study.

In several publications, *Pelamis* were reported to have been captured at night with the aid of a light (Klawe, 1964; Myers, 1945; Volsøe, 1956), and it has been suggested that the snakes are attracted to light (Ditmars, 1937; Smith, 1935), but my field work did not bear this out. The observations in the tank also showed indifference on the part of the snakes to a light source, but since the light was close to one of the tank walls several of the snakes could be seen passing under it occasionally (Table 5). It is quite possible that night collections had been made in areas where plenty of snakes were available all around, but the observer could be deceived into thinking that they were only under the light. Such was the situation described by Myers (1945), and the one I observed in Mexico during the Alpha Helix expedition. None of the authors who reported on the attraction of Pelamis to light gave consideration to the fact that the snakes may be attracted to the fish under the light. This is probably not the case, but the possibility should have been considered.

Although the snakes at the surface showed little activity and movement, a substantial portion of the group, between 1/4 and 1/3, was diving (Table 5). This term is used here in a general sense for all activities under the water surface. At least part of this diving activity was an artificial result of the laboratory situation, as the snakes would swim outward, be stopped by the walls, and then dive.

The keeping of reptiles in the laboractry for behavioral observations has been practiced in many studies, and its value as a source of supplementary data which cannot be obtained in the field is clear. In doing this, the emphasis is usually placed on the need to maintain in the laboratory simulated natural conditions. Even then, because of the abnormal situation of captivity, one cannot know how meaningful the observations in the laboratory are, and all interpretations must be made with caution (Fitch, 1949).

The conditions under which Pelamis were kept in the tank could be considered only a partial simulation of their natural habitat. It is, therefore, difficult to evaluate the significance of any of the observations made. An example is the typical "search pattern" over the floor, which is more likely to be an artifact of life in the tank than a real hunting habit. Another is the diving activities of <u>Pelamis</u>: it is tempting to suggest that about 1/4 to 1/3 of the snakes are underwater at any given time, and thus get estimates for sample sizes, or try to establish activity schedules for the snakes. But very likely a substantial portion of the diving activities is again an artifact of tank life, and the diving schedule of the snakes in the open waters of the Gulf of Panama may be different and yet unknown. So, in agreement with Fitch (1949), the observations in the tank are treated with caution, and the limitations of their value are taken into consideration.

Some questions, however, can be studied only in the laboratory. Data on shedding schedule, for example, cannot be gathered in the field, but can be accurately and easily collected in the laboratory. Duration of diving or diving frequency would be very difficult to study in the field, and even observations in the tank are not very satisfactory for the reasons given above. Social behavior in lizards was studied in the laboratory where, in spite of the artificial setting, some of its expressions such as territoriality and courtship could be released. Again, the value of the laboratory observations must be determined by the circumstances, the organism observed, the problems studied, and the laboratory settings.

If agonistic behavior had existed in <u>Pelamis</u> under natural conditions, very likely it would have expressed itself in the laboratory. In this study no social interaction of any kind was observed among the snakes. The only situation in which snakes bit each other was sometimes during feeding, and the bites were accidental. These bites sometimes developed into prolonged battles involving two or three snakes, but although some snakes were bitten for over 30 minutes, no casualty occurred. One snake was held by a bigger one for 30 minutes and then was taken in until its anterior 1/3 was ingested. At that point the attacker could not swallow any more and disgorged its victim. The latter swam away apparently unharmed, although its swimming appeared sluggish and "tired."

These mutual bitings provide another example which illustrates the limitation of laboratory observations. To a naive observer the sight of snakes biting at each other during feeding would mean that extreme agonistic behavior is the rule in this species. In reality Pelamis has never shown hostility toward conspecifics, and the frenzy of mutual bitings merely resulted from the abnormally overcrowded and restricted conditions in the tank. But from this abnormal behavior it was possible to learn that Pelamis is immune to its own venom, because no death resulted from the numerous bites, and my assumption is that at least in some of these bites venom would have been injected. Immunity of Pelamis to its own bites, also observed by Pickwell (1972), is not a surprise, since some venom may occasionally reach their circulatory systems during their regular activities, such as feeding. Old fangs are often swallowed by snakes after they have been shed, to be later found in the gut (pers. obs. on Bothrops atrox and Pelamis). These fangs may cause internal wounds, and immunity to their own venom may be required by the animals. Nonfatal bites are also known among cobras and rattlesnakes where individuals have been known to bite each other occasionally in captivity with no serious effects (Kauffeld, 1969).

Generally, no obvious rhythm was discerned in the activity of Pelamis in the laboratory. Wall (1921) claimed that this species was completely diurnal, and Smith (1935) that it was mainly nocturnal and during the day only basked at the surface. Myers (1945) thought that Pelamis fed during the day, and that at night it only surfaced to breathe. My observations do not support either view. Herre (1942) and Pickwell (1972) also thought that sea snakes were active both during the day and at night. Being active around the clock may be another adaptation for pelagic life.

Another observation of interest is the tolerance of Pelamis for water of low salinity. The Panama sea-level canal controversy led to the experiment of keeping some snakes in fresh water. Nine snakes were kept in fresh water for periods ranging from 31 days to 9 months and 7 days. Four died from a skin disease which plagued all captive Pelamis at that time, that is, from a cause unrelated to their life in fresh water. The other five were also apparently unharmed by their freshwater medium. This was done in the laboratory at Queens College, in conditions which rendered the keeping of Pelamis for over nine months a notable success, even in salt water.

Pelamis and other sea snakes are known to enter rivers and go upstream (Smith, 1926; Myers, 1972), sometimes for many miles. They get the salts required for their physiological balance from their food. When they swallow excess salts, their rate of salt excretion increases (Dunson et al., 1971a), and in fresh water it is probably at a minimum.

Summary

The data presented for a 10-day period (Table 5), typical of the behavior of <u>Pelamis</u> during the entire study, are evaluated with caution because of the unnatural conditions under which the observations were made. In general, I feel that observations on the physiology (i.e. shedding) of the animals in captivity yielded valuable information, but that the behavioral observations, in this case, were not of much value.

In the tank, <u>Pelamis</u> showed no attraction to light and no interest in floating objects or in a reef-type habitat. How the snakes react to light or flotsam in nature is not known. To me their activities suggested no diurnal rhythm. Whether this is indicative of their behavior in nature can only be guessed. No social interactions among <u>Pelamis</u> were observed, other than mutual bitings at feeding time. Most snakes tended to swim outward. Tolerance for a broad salinity range was demonstrated.

Table 5. Activities of 87 *Pelamis* in the laboratory in a period of 10 days.

	DAY				NIGHT			
Type of activity observed	No. of observations (out of total of 18)	No. of snakes involved	Average per observ.	% of total	No. of observations (out of total of 28)	No. of snakes involved	Average per observ.	% of total
interest in rock pile	0	0	-	-	0	0	-	-
near drift-line	9	24	2.6	2.98	16	32	2.0	2.29
motionless on bottom of tank	15	43	2.9	3.33	20	54	2.7	3.10
moving slowly on bottom	18	139	7.7	8.85	22	126	5.7	6.55
under light-source	10	44	4.4	5.05	18	74	4.1	4.71
swimming under-water	17	524	32.0	36.80	28	693	24.7	28.30
Knotting	10	20	2.0	2.29	12	19	1.6	1.83

FOOD HABITS

I. Feeding behavior

A. Laboratory observations

The observations on the feeding behavior of *Pelamis* started when I first met the practical problem of keeping four *Pelamis* alive in the salt-water tank at Queeens College. After experimenting with various methods I found that the best way to achieve successful feeding was to shake a freshly killed fish (*Fundulus* sp.) in front of the snake. The snake would then bite at the fish and manuever it into a position where it could be swallowed head first. Fish in the collected snakes were always oriented in the esophagus and stomach with their heads toward the posterior of the snake. In this manner the fish spines could not interfere with ingestion.

Another successful method which elicited feeding in *Pelamis* was a gentle rubbing of the fish on the mental or rostral surfaces or the sides of the jaw of the snake. I found later that this feeding method had been regularly used by the late Charles Shaw of the San Diego Zoological Society (Shaw, 1961, 1962). *Pelamis* was also fed in other ways, all of which had in common tactile or pressure stimulation of the head region: for example, placing them in a small dip net with several fish or placing them in a narrow compartment with fish. During the preliminary observations *Pelamis* showed no ability to capture fish which were freely swimming in the tank. When a snake accidentally dropped a fish it had in its mouth, the snake could not recover the dropped fish even though it passed near the fish in a frantic attempt at recovery. This was also observed by Shaw (1962).

The placing of many live Fundulus in the tank (about 50 in a 14-cubic foot tank) caused a "feeding frensy" among the snakes in which some fish would usually be caught. This "frensy" was characterized by unusually rapid movements of the snakes and indiscriminate biting of any object in their paths. This and the observations described above led me to believe that Pelamis in its natural environment feeds on fish schools and that the main sense organ(s) involved in food capture is tactile, pressure-sense, or olfactory, but not visual. In this kind of feeding, the ability to detect the entire school may have a greater importance than the ability to see a single fish, and one good way of detecting a school would be by sensing the vibrations it generates.

In Panama, the snakes in the tank were commonly fed live fish. When several hundred live fish were placed in the tank, they caused a feeding frensy as described above. The snakes caught the fish with a rapid sideways strike of the head, or with a rapid backwards movement if a fish were posterior to the snake's head. When a fish touched the snake in the trunk region it also elicited a backwards movement and a strike at the fish. This behavior could also be elicited by rubbing the snake gently with forceps on the trunk at a distance about 1/3 body length from the head. This shows that the response to tactile stimulation is not restricted to the head region. When the snakes were fed dead fish, shaking the fish 5 cm or less from the snake's head brought about the feeding reaction. This clearly indicates response not only to touch but also to pressure waves caused by the moving fish. This distance could obviously vary depending on the intensity of the vibrations. Backward swimming was often (but not always) a component of the feeding behavior. It was observed either as a separate and distinct action of "getting ready," followed by a pause and then feeding, or as a part of a continuous movement in which feeding followed without any pause.

Experiments were conducted to test whether the stimulus for feeding was olfactory or mechanical (tactile or pressure). In the first experiment, several objects (a twig, forceps, and a wire hanger) were vibrated in front of the snakes. All resulted in biting, indicating tactile stimulation. When the vibrating was too forceful, the snakes retreated. Occasionally during feeding the snakes bit the forceps, not the fish held at its end. Also during feeding excitement many mutual bitings occurred, showing that any source of vibrations would elicit indiscriminate attack after the release of a feeding reaction.

Other observations support the view that in feeding the snakes were stimulated by vibrations which the fish movements had generated. In repeated observations fish were shaken laterally to a snake's head. A typical response was a slight sideways bending of the head and a slow movement towards the source of vibrations, sometimes with an open mouth. If the fish continued to be shaken, the snake would eventually get hold of it, but if the fish were held still, the snake would be unable to catch it. There were other observations which suggested that Pelamis responds to vibrations around.

There is also good evidence for olfactory stimulation in feeding. First, snakes were commonly observed to extrude their tongues during swimming or diving (contrary to the statement by Cantor, 1841), and when the water in their immediate surroundings was agitated. The tongue can sense vibrations, but its main function is olfactory. An experiment in which chopped fish were thrown into the tank resulted in feeding excitement and mutual bitings. Normally there would be no such bitings, but during feeding they were very common. Although olfactory stimulation was exhibited by the snakes, they only rarely showed the ability to recover a dead fish which they had lost.

Swallowing a fish which is smaller than the snake's head is done in one quick gulp, clearly without envenomation of the prey. Larger fish which cannot be swallowed in the first gulp are held for a while (from several seconds to five minutes) by the snakes and are perhaps envenomated. Fish were observed, however, to escape from a snake's mouth and swim away seemingly unharmed. On other occasions the fish stopped wriggling in less than a minute and apparently were immobilized by venom. As stated above, all fish were swallowed head first.

The snakes often show the ability to discern between the two ends of the fish they are eating: when a fish is manuevered in the "wrong" direction which brings its tail to the snake's mouth the snake reverses the direction of its jaw movements until the fish is brought in head first. In an experiment a needle fish, Tylosurus sp., was offered to a snake which took it and started to manipulate it for swallowing. The fish was repeatedly manuevered by the snake to position the fish head first or tail first, but because of the fish's peculiar structure, neither position seemed "right" to the snake and the fish was eventually dropped. The same fish was offered to the snake again, but this time with its jaws (the "needle") removed. The snake took it and swallowed it head first on the first trial.

Several authors (Shaw, 1961; Tweedie, 1961; Wall, 1921) have repeated Dr. Annandale's account that fish spines can break through a snake's digestive tract and body wall without apparent harm to the snake. Such an observation was never made in this study, and it must be pointed out that the integument of Pelamis is strong and would probably resist most fish spines (especially those of the species and sizes found in this snake's digestive tract.

Accidents have been reported where catfish spines penetrated a predator's skin, and Annandale's observation must have been based on some such peculiar accident which was probably harmful to the snake involved. In any case such incidents are rare.

B. Field observations

A field observation of Pelamis feeding was reported by Klauber (1935). Because of its significance, it is given here in his words: "Wherever there was a stick, twig, or a branch of sea-weed floating on the water, there were usually several small fishes huddled alongside as if for protection... It is the habit of the sea-snakes Pelamis to lie motionless on the surface simulating such a floating object; shortly a few of the small fish gather about, when, by a sudden lunge, one will be captured by the snake. Seldom are they unsuccessful in securing prey by this method."

This description is significant because it explains the behavior observed in the laboratory. It is also one about which I was very skeptical until I had the occasion to observe it myself numerous times. Hunter and Mitchell (1967) and Paulson (1967) also observed Pelamis feeding on schools of fish aggregated beneath them. The snakes fed in the manner observed in the laboratory: by swimming backwards and thrusting the head sideways or downward. My observations were identical, except that snakes were also seen to feed under the surface, at depths ranging from 1 to 6 feet.

Stomach contents of *Pelamis* (see next section) also show that *Pelamis* feed on fish in schools: many of the snakes had in their stomachs numerous fish all of the same species, most likely taken from a school. Most of these fish were drift-line species which habitually are attracted to floating objects, and thus may also have gathered under *Pelamis*. These fish were usually small (many in the 4-20 mm range) and could have been swallowed quickly and without envenomation.

Discussion

Feeding in *Pelamis* appears to depend mainly on mechanical stimuli, but chemical stimuli apparently are also involved. Knowledge of the relative role played by each of the main sensory systems (visual, olfactory, tactile) could be derived from experiments involving the controlled blocking of input information through these systems (usually at the receptor level), and comparison of the behavioral responses. This was not done in this study.

Very little work has been done on hydrophiid sensory organs. Underwood (1970) discussed the capacity of sea snakes for accomodation in the air by contracting the pupil, but no report on underwater vision was given. Although little is known about hearing in the hydrophiidae, members of this group possess, like all other snakes, basilar papillae which allow some sound-pressure reception (Baird, 1970). These studies are based on only a few species and few observations. According to Klemmer (1962, 1967) *Laticauda laticaudata* fed in the laboratory exclusively on eels, which they actively pursued while flicking their tongues rapidly, and which they were able to catch quickly and efficiently. A similar account of Laticauda feeding is given by Pickwell (1971). The descriptions of the behavior of Laticauda suggest that these snakes rely mainly on their olfactory sense (and perhaps vision) for catching their food, and that, in comparison with Pelamis, they are much more active predators.

In connection with the discussion it is interesting to point out that oral papillae have been detected in Pelamis (Burns, 1969). These papillae resemble taste buds and are innervated by maxillary and mandibular branches of the trigeminal nerve. They most likely play some role in chemical reception. Such papillae, however, were discovered by Burns in some terrestrial snakes. Burns correctly points out that diffusion rates in water are slower than in air. It is very possible that tactile and pressure reception in Pelamis play a greater role than in other snakes as compensation for the slow diffusion rate in water and the resulting hindrance to olfaction. With it evolved a behavior which makes the snakes attractive to fish and thus facilitates the capturing of food. From Cott (1940) and others it is known that such behavior is not unique to sea snakes. Many fish (e.g. John Dory, Zeus faber, longnose garpike, Lepidosterus osseus, leaf fish, Monocirrhus polycanthus) use the deceptive, slow, stealthy approach to capture their prey.

II. Food species

About 160 snakes, collected throughout the year, were examined for their food contents. The diet of these snakes consisted entirely of fish, which included members of the following families:

Engraulidae: *Anchoviella* sp., *Engraulis* sp.

Atherinidae: *Melanorhinus cyanellus*

Fistularidae: *Fistularia corneta*

Serranidae (or Lobotidae): *Lobotes pacificus**

Carangidae: *Caranx caballus**, *C. marginatus**, *Chloroscombrus orqueta*, *Vomer declivifrons*

Coryphaenidae: *Coryphaena hippurus**

Lutjanidae: *Lutjanus* sp.

Kyphosidae: *Kyphosus* sp.

Mullidae: *Mulloidichthys rathbuni*

Chaetodontidae: *Chaetodon humeralis*

Pomacentridae: *Abudefduf troschelli**

Stromateidae: *Peprilus medius*

Mugilidae: *Mugil cephalus*, *M. curaemas**

Sphyraenidae: *Sphyraena barracuda*

Polynemidae: *Polydactylus approximans**

Blenniidae: *Blenniolus brevipinnis**, *Hypsoblennius* sp.

Acanthuridae: *Acanthurus xanthopterus*

Scombridae*: (not identified to genus)

Tetraodontidae: *Sphoerides* sp.

* indicates fishes which are known as common drift-line fish (Hunter and Mitchell, 1967).

In addition to these, I often observed (and collected) *Engraulis* sp., *Fistularia corneta*, *Abudefduf*, *Mugil*, and *Acanthurus* sp. on drift lines. Of the fish found in *Pelamis*, mullets (mugilids) were by far the majority. Also common were the jacks (carangids), anchovies (engraulids), Abudefduf, and dolphins (*Coryphaena*) (Table 6). In the snakes whose digestive contents could not be identified it was still possible to verify that they were fish remains: many fish bones usually remained in the rectal chambers as well as fish eyes, which, for some reason, had not been digested and were retained.

Discussion

From the study of stomach contents it is clear that *Pelamis* feeds along ocean slicks and that it eats whatever is available in a size which can be ingested. That there is no preference for food size is shown by the fact that small fish (5-10 mm long) are occasionally found in the stomachs of adult *Pelamis*, and that relatively large fish (40-50 mm) are often found in the stomachs of juveniles. It is apparent that there is no preference for prey shape: *Pelamis* diet includes elongate fish such as *Fistularia*, "typical" pisciform species such as *Mugil*, *Caranx*, and *Coryphaena*, and very compressed and deep fish such as *Chaetodon* and *Vomer*. Occasionally even twigs and small pieces of wood were found in the snakes' stomachs.

Although some authors have reported that sea snakes, especially *Laticauda* but also some *Hydrophis* species, feed on eels (Cantor, 1841; Klemmer, 1967), this was not seen in *Pelamis* in this study. Some sea snakes are said to feed, in addition to fish, on squid and crustaceans (Pickwell, 1972; species not given). This I did not find in *Pelamis*, which appears to feed exclusively on fish (although Kinghorn reported in 1956 that it also feeds on crustaceans).

Klawe (1964) found in Pelamis from Ecuador Polydactylus (Polynemus) approximans, mugilids, and Fistularia which were also found in my sample. Other species on his list were the mullid Pseudupeneus grandisquamis, two carangids, Selar crumenophthalmus and Caranx hippos, and Auxis, a scombrid, all known as drift-line fish. Hunter and Mitchell (1967) saw Pelamis feed on Polydactylus which gathered under the snakes much as they do under other floating objects. Visser (1967) found within Pelamis from South Africa the fishes Psenes whiteleggi (Nomeidae), Decapterus lajang (Carangidae), and a stromatid. Paulson (1967) concluded after his observations in the Gulf of Panama that Pelamis fed on surface-living fishes, including the young of scombrids and billfishes.

The absence of food specialization in the majority of sea snakes was also noted by Shuntov (1971), who wrote: "The chief food consists of numerous species of small fish, and to a lesser extent of cephalopods, molluscs, and crustaceans." (Species which feed on the latter invertebrates were not listed by Shuntov.) Pickwell (1972) similarly concluded that Pelamis feeds on a variety of fish "as long as the prey is of a suitable size and shape for swallowing." In fact, my data show that Pelamis even eats fish which appear to have the "wrong" shape (e.g. Chaetodon, Vomer). Klawe (1964) concluded that the "most abundant fish at a locality contribute most heavily to the diet of the snakes.

That Pelamis feeds on schools is clearly evident in that often many individuals of a single species are found in their stomachs.

Since the majority of the food species are unquestionably drift-line fish, that is, they are members of the "slick guild" (see chapter 7), this further strengthens my statements (chapter 7) that feeding is one of the major advantages (perhaps the most important) which Pelamis derives from coming to slicks. The occasional finding of twigs in sea snakes is also an indication that feeding in the area of slicks has taken place.

In sea snakes the species which are considered to be the less specialized ones (Laticauda spp.) are reported to have specific food requirements - they feed on eels. A specialized sea snake, Emydocephalus, is reported to feed exclusively on fish eggs (Voris, 1956). It is of interest to note that the most specialized sea snake is so remarkably generalized in its feeding. Being a surface feeder and having the ability to utilize a varied diet are two more adaptations of Pelamis to pelagic life. Both undoubtedly are of prime importance in allowing the species to expand its range. Broad food habits are also exhibited by pelagic predatory fish which I have examined.

Summary

Pelamis feeds on fish schools which it seems to detect by sensing vibrations caused by the fish movements. Their diet is variable and appears to include any fish which is available in its immediate environment and is of a size which can be ingested.

Table 6. Frequency of food species taken by _Pelamis_ in the Gulf of Panama.

stomach contents	number of snakes	percent
No food	31	19.50
Food cannot be identified, but definitely fish	33	20.75
Mugilidae	19	11.95
Carangidae	13	8.18
Coryphaenidae	11	6.92
Serranidae (_Lobotes_)	11	6.92
Pomacentridae	8	5.03
Engraulidae	8	5.03
Polynemidae	6	3.77
Atherinidae	4	2.52
Acanthuridae	4	2.52
Blenniidae	2	1.26
9 other families*, (1 fish each)	9	5.66
Total	159	

*Fistularidae, Lutjanidae, Kyphosidae, Stromateidae, Mullidae, Chaetodontidae, Sphyraenidae, Scombridae, Tetraodontidae

POPULATION-LIMITING FACTORS

An essential part of an ecological study is the determination of the factors which cause the loss of individuals from the population. These are commonly referred to as limiting factors and will be used here in this sense. My attention in this study was focused on three possible limiting factors: predation, parasitism and disease, and physical factors. Food availability is not considered a limiting factor of *Pelamis*.

I. Predation

A. Field studies

To investigate which animals, if any, prey on *Pelamis*, and the frequency of predation, two approaches were taken: direct observation in the field and in laboratory experiments (see next section) and the examination of stomach contents of potential predators on *Pelamis*.

During the observations in the field, attention was centered on the behavior of marine birds near *Pelamis* concentrations, and on the reaction of *Pelamis* to seemingly potential danger at or above the surface. It was also hoped that the activity of marine predators could be observed, as reported by Paulson (1967), but this would have been a difficult task.

The examination of stomach contents of potential predators of *Pelamis* involved large fishes and elasmobranchs, mostly pelagic but some more confined to rocky reef habitats (e. g. *Lutjanus* sp.) or to the bottom (*Ginglymostoma* cirratum). As "potential predators" I considered all marine animals large enough to ingest a sea snake (as determined by laboratory experiments) which are known to be active predators. I excluded plankton feeders and turtles from this investigation because the killing of these animals, as well as birds, did not seem justifiable for the purpose of this study. Preference was given to typical pelagic predators such as the scombrids and coryphaenids and most shark species, but all other available material was also examined.

Results

Although field time for this study was limited, there were ample opportunities to observe marine birds near Pelamis concentrations, as birds would normally congregate along ocean slicks. The species observed were brown boobies, Sula leucogaster, brown pelicans, Pelecanus occidentalis, man-of-war, Fregata magnificens, and occasionally gulls.

Never, in the entire study, was a bird seen to pick up Pelamis or to show the slightest interest in the snakes. The snakes normally did not show any reaction to disturbances at or above the surface. They did not seem concerned about the presence of birds, men, or a noisy outboard engine. Sometimes snakes which were disturbed one or more times remained at the surface and were picked up on the next round with the boat. Only twice was a different behavior observed, where the snakes showed apparent tendency to escape by diving. This behavior was very unusual for Pelamis, and it could not be explained.

A total of 457 potential predators belonging to 25 species was examined. All of these specimens were collected in the study area, where Pelamis was known to occur. Many (28.0%) were caught in the same place and at the same time that Pelamis were seen in large numbers and there was no question of availability of Pelamis as potential food. All those examined are without a doubt faster swimmers than the sluggish Pelamis, and as a whole, efficient predators (pers. obs.). A large number (58.4%) had food in their stomachs (Table 7), usually showing a rich and varied diet which never included the remains of sea snakes. On five occasions dead boobies were found floating on the water. These too were examined, but had empty stomachs.

The Katsuwonus (Euthynnus) examined were probably mostly K. pelamis, but other bonitos occur in the Gulf of Panama. Most, but not all, of the typical tunas were the yellowfin, Thunnus albacares. The category "others" in Table 7 includes four Centropomus sp. (snook), four Tylosurus crocodilus (needlefish), two "corbina" (probably Cynocion sp.), one Nematistius pectoralis (papagallo), two Tetrapterus sp. (marlin), and four Epinephelus sp. (grouper).

Discussion

The field data suggest that Pelamis does not suffer from predation in the Gulf of Panama. Admittedly, some of the predators listed in Table 7 do not live where Pelamis is available as food (these are Ginglymostoma, Mustelus, Lutjanus, Centropomus, Cynoscion, and Epinephelus). But even when these are deleted from the table, there remain 58 sharks and 361 fishes which showed no indication of feeding on Pelamis. Dr. William F. Perrin, a researcher at the U. S. National Marine Fisheries Service (NMFS) in La Jolla, California, examined the stomach contents of 169 spotted dolphin (Stenella graffmani) and 45 spinner dolphin (S. longirostris). Although they were caught in areas where Pelamis were plentiful, none had sea-snake remains in its stomach (Perrin, pers. comm.) Dr. Susumu Kato of NMFS, Tiburon Fisheries

Laboratory, Tiburon, California, examined about 1000 Eastern Pacific sharks, most of which were within the range of Pelamis. Almost 2/3 of them had food in their stomachs, but never a sea snake (Kato, pers. comm.) Even so, I feel that the data are only suggestive, and that thousands of predators should be examined before it is concluded that they avoid Pelamis all the time.

The questions which deserve special consideration in this context are:

a) Is there any animal species which is predator-free? If there is, and the phenomenon must be rather rare, what are the limiting factors operating on the species? How is the reproductive potential adjusted to a predator-free situation? At present too little is known about the reproduction of Pelamis to allow its evaluation in terms of adjustment to the presence or absence of a given limiting factor.

b) What is the source of the injuries of the tails of Pelamis? These injuries have, after healing, the appearance of bites. 48 snakes collected in this study had tail wounds, of which 39 appeared as bite marks. Snakes with healed wounds were also found by Pickwell in Mexico (p. 83). The answer to this question is of great interest and may prove to be important in the understanding of Pelamis ecology. (The question of anti-predator strategy in Pelamis will be discussed later).

c) Is it possible that predation on sea snakes takes place in some parts of their range, but does not occur in the Gulf of Panama? If they have a specialized predator, is it possible that this predator was not able to migrate across the ocean and colonize the Eastern Pacific? These questions are raised because of the numerous reports on predation which presumably takes place on sea snakes in the Old World. Cantor (1841) reported that sharks and sea eagles, *Haliaetus*, eat sea snakes. Wall (1921) thought that in addition sea snakes fall victim to the kite *Haliastur indus*. Ditmars (1933) mentions predation by large fish and large birds, and Barret (1950) described *Haliaetus leucogaster* as a specialized predator in tropical Australia, under whose nests sea snake skeletons were abundant. Smith (1926) also reported a case of predation on a sea snake by *Haliaetus*. Unfortunately, in none of these reports (and many others which appear to have repeated them) is there a mention of the species of sea snake involved, and the evidence of predation was mostly indirect - like the finding of sea snake remains on a buoy (Smith, 1929).

A report of predation on sea snakes by sharks comes from McCormick *et al*. (1963) who described the diet of tiger sharks in the Philippines. It included turtles, squid, crabs, sea birds, sea snakes, and "an unlucky black cat." Due to the untimely death of McCormick I was not able to ascertain the identity of the hydrophiids in his report, but Dr. Stewart Springer (of the U. S. Bureau of Commercial Fisheries) assured me of its accuracy. An even more interesting report is that of Wetmore (1965), which is therefore given here in full: "In June 1953 scores of frigates [*Fregata magnificens*], most of them immature, ranged over the open water at the head of Montijo Bay... Twice I saw one pick up a sea snake swimming at the surface and carry it, as it twisted and coiled, for a short distance with other frigates in close pursuit, and then finally let it drop."

This observation is interesting because it took place in Panama, and because there can be no question regarding the identity of the bird or the snake. It is also interesting because frigates are not known to be efficient at picking up food from the sea surface, and they have earned a reputation as thieves that rob other birds. It should be interesting to observe the behavior of cormorants who are related to frigates, when sea snakes are available to them, because cormorants feed occasionally on eels and the shape of the snake may attract them. I had no opportunity to test the reaction of cormorants to Pelamis. Another interesting aspect of Wetmore's observation is that although Pelamis was picked up twice by frigate birds, it was not ingested. This implies that the bird received some signal (visual, olfactory, pain?) which made it change its mind about its potential meal (see next section).

Another incident perhaps indicates that birds occasionally pick up Pelamis: one snake which was found trapped in a tidal pool in Panama had a deep wound in its side about midbody. The wound, which healed completely and remarkably fast, looked as if it had been made by a bird's beak.

An interesting observation was reported by Paulson (1967), who saw in the Gulf of Panama billfishes "striking sea snakes, knocking them completely out of the water and presumably swallowing them as they sank." The evidence, though, is incomplete because predation was not actually observed (Paulson, pers. comm.), and it is not known whether the snakes were merely knocked out accidentally while a billfish was pursuing smaller fish. Billfishes are known to eat normally active pelagic fish such as the scombrids. Verrill (1937) also reported predation on sea snakes in Panama Bay by sea birds and porpoises. But from his description (p. 26) I gather that he saw a drift line and erroneously interpreted its faunal concentration.

Van Bruggen (1961) reported that in a laboratory tank a juvenile Pelamis (300 mm long) was preyed upon by Octopus. Unfortunately there were no witnesses to this unusual case, and therefore another possibility must be considered - that of scavenging. In the big tanks at STRI I occasionally saw that kind of scavenging when a snake which had died during the night would be badly mutilated by lobsters and crabs I had placed in the tank to clean the bottom of dead fish. The impressive part of Van Bruggen's report is that the octopus, 90 mm in mantle length, was able to swallow the entire snake. My experience was that snakes had been mutilated but not completely ingested. Similarly, Duellman (1961) saw many partially ingested Pelamis protruding from crab holes on a Mexican beach. These are certainly snakes which had been washed onto the beach and were taken by the crabs sometime when they were dying or thereafter. Van Bruggen's report may be a good example of the risk involved in misinterpreting laboratory observations, as discussed in chapter 9.

Summary

No direct evidence was found for predation on Pelamis in the Gulf of Panama, but occasionally snakes may be picked up by birds (Wetmore, 1965). This is probably very unusual, and does not constitute a limiting factor. It is hard to imagine that sharks do not eat sea snakes occasionally, as pointed out by McCormick et al. (1963), but no evidence for this was found in this study. I found remains of eels in sharks (Sphyrna) and dolphin (Coryphaena), a proof that they take prey of a general serpentine form (see also next section). Most predation on sea snakes is scavenging on the dying or dead animals, which may be dragged into crab holes or onto buoys. In the Gulf of Panama there is no known predator which specializes in utilizing *Pelamis* as a source of food. In the Western Pacific, however, an apparently specialized predator (*Haliaetus*) operates at least on some sea snake species.

B. Laboratory experiments

These experiments, conceived by Dr. Ira Rubinoff of STRI, have been published (Rubinoff *et al*., 1970), and are therefore summarized here briefly. While we were searching for a possible *Pelamis* predator, we placed several carnivorous Pacific fishes (*Ginglymostoma*, *Epinephelus*, *Lutjanus*, *Centropomus*, and *Scianus*) in a large tank and tested their reactions to *Pelamis*. Snakes were offered to the fish under a variety of circumstances, but were rejected even though the fish were starved. Only once did a snapper grab a snake immediately when offered, presumably before the fish could examine it, but it spat out the snake at once.

When *Pelamis* were offered to Atlantic snappers which were unfamiliar with them, the fish showed a marked interest in the snakes, and soon started to attack them. In the course of these observations 3 fish were bitten by *Pelamis* and died. Altogether 316 trials with Pacific fish resulted in one attack on *Pelamis*, a regurgitation, and no snake bites; 383 trials with Atlantic fish resulted in 35 successful attacks and 3 deaths from *Pelamis* bite. Pacific fish did not attack

Pelamis, even when, mixed with Atlantic fish, their interest in Pelamis was increased due to social facilitation: upon inspection of the snakes they avoided them.

In these experiments Pacific snappers rejected Pelamis on the basis of what appeared to be visual recognition. Ginglymostoma, which are known to be essentially olfactory feeders, also rejected Pelamis, even after they had been deceived into swallowing pieces of sea snakes hidden within squid. This suggests that some predators recognize Pelamis by olfaction. This view is supported by the fact that snakes painted all black or red-and-black and skinned snakes were also rejected by Pacific fish.

The experiments have shown that avoidance was exhibited only by species which in their natural habitat may come in contact with Pelamis, and that Pacific fishes can recognize Pelamis by visual or chemical clues. Species vary in their responses to these clues. The coloration of Pelamis is believed to be aposematic (see next section), but avoidance is also elicited by chemical signals.

Since ophichtid (Myrichthys tigris) and muraenid (Priodonophis equatorialis) eels were immediately attacked and eaten by Pacific fish, serpentine shape and bright colors alone may not be sufficient to produce the avoidance reaction.

One experiment may suggest a mechanism for increased venom potency in sea snakes. In this experiment an Atlantic snapper had eaten two Pelamis and died an hour later, probably from an internal bite. The snakes were regurgitated but survived the ordeal. The evolutionary implication is clear.

Additional experiments were done on Pacific snappers (Lutjanus) and groupers (Epinephelus). In these experiments the fish were given pieces of Pelamis, cut into different lengths and offered with the skin removed or left intact. They were also given Pelamis skin, sometimes everted to conceal the colors, and fish coated with Pelamis skin. The purpose of these experiments was to determine whether the reaction of the fish to Pelamis would change when the shapes and sizes were altered and when the colors were concealed, and also whether different Pacific species vary in their reaction to Pelamis. Table 8 shows the results of these experiments.

The results show that by offering small Pelamis pieces to fish they can sometimes be deceived into taking them, that as the pieces increase in size the frequency of regurgitation or outright refusal to eat intensifies, and that the groupers were willing to taste Pelamis more readily than the snappers were. In all trials the fish were able to inspect the items offered to them, sometimes not only visually but also by touching them (particularly the groupers, because of their feeding habits which are more cautious than those of the snappers). Live young Pelamis were also offered to the fish when they were in a "feeding frenzy," but even in such a situation they never took a sea snake.

Other observations were made in connection with this subject. A large Pacific nurse shark was observed to pick up a snake which was lying on the bottom. The snake was held for about 30 seconds, then dropped unharmed. The same shark ate fish which were offered to it afterwards. A marine turtle (Chelone imbricata) which had become used to feeding at close range on fish and squid also refused pieces of Pelamis.

Discussion

The observations in these experiments indicate that the avoidance reaction is evoked by Pelamis not only visually but chemically, by operating on the receiver's sense of taste or smell. Pelamis do emit a strong musky odor, which is particularly noticeable when many snakes are kept in a small enclosure. The difference between various Pacific fish may be a matter of taste - some species may have a greater tolerance for foul odor and taste than others.

The experiments might be criticized because the species used as predators were not those which usually encounter Pelamis in nature. Because of this, the experiments cannot answer our quest for a "Pelamis predator." This should be looked for among the truly pelagic species such as scombrids, coryphaenids, and billfishes. These fish, however, are extremely difficult to keep under laboratory conditions. The comparison of Atlantic and Pacific fish was valid, though, because closely related species were compared under identical experimental conditions, and the great attention given to these experiments seems justified. Similarly, the comparison of different Pacific fish was done under identical conditions, and the different reactions to Pelamis are probably real. Repeating these experiments with more species and more individuals of each species will provide more information on the subject, but, in addition, new experiments can be designed to obtain more information in the field.

Table 7. Marine fishes examined in search of Pelamis predators.

Predator	No. examined	No. with food	No. sighted with Pelamis
Carcharhinus sp.	1	1	
C. limbatus	23	8	2
C. leucas	12	5	2
C. porosus	2		
C. velox	1		
Triaenodon obesus	1	1	
Negaprion fronto	4	2	1
Galeocerdo cuvieri	2		1
Sphyrna sp.	3	1	
S. lewini	2	2	
S. media	4	4	
Prionace glauca	1		1
Ginglymostoma cirratum	2	2	
Mustelus lunulatus	1		
Katsuwonus sp.	112	49	9
Coryphaena hippurus	139	115	92
Acanthocybium solanderi	13	6	3
Scomber sp.	19	9	5
Thunnus spp.	45	34	14
Caranx spp.	28	10	1
Lutjanus spp.	25	11	
Others*	17	6	
Total	457	267 =58.4 %	131 =28.0 %

* See text for spp. included in this category.

Table 8. Reaction of Pacific fishes to Pelamis offered as food.

	SNAPPERS			GROUPERS		
Pelamis offered	refused after inspection	taken and dropped or regurgit.	swallowed	refused after inspection	taken and dropped or regurgit.	swallowed
3 cm, skinned	8	4	10	-	-	15
3 cm, skin on	-	11	5	3	-	7
6 cm, skinned	5	4	3	-	-	-
6 cm, skin on	10	2	2	10	-	4
12 cm, skinned	2	6	-	-	-	1
12-15 cm, skin on	12	4	-	14	-	3
10-15 cm, with tail pattern	6	11	-	-	-	5
6 cm skin, everted	4	4	8	-	-	6
6 cm skin, not everted	9	-	-	4	2	6
12 cm skin, everted	2	7	-	-	3	8
12 cm skin, not everted	6	-	-	-	-	5
fish in Pelamis skin	-	4	4	-	-	6
young snake 30-35 cm	5	-	-	5	-	-

C. Function of coloration in Pelamis

The coloration of animals has been of great interest among biologists, especially since Cott (1940) reviewed the subject and demonstrated its importance in animal adaptations. Clearly a study of the natural history of an organism is not complete without some attention to the coloration and its role in the organism's life.

The coloration of Pelamis platurus is conspicuous. Although many variations are known in this species (see next chapter), all possess bright yellow color ventro-laterally which, except in a rare color variety, comes in contact with black dorsal marking (Plate 1). This coloration is unique among sea snakes - none of the other hydrophiids resembles it even remotely. (An exception may be Hydrus caerulescens, which is shown in Halstead (1970) to have Pelamis pattern; no color is given, however.)

One of the most common methods of deceiving a predator is by countershading whereby surfaces normally directed toward the source of light are countershaded (darker), and those normally in the shade are counterlighted (brighter), with a gradual transition between the dark and light surfaces forming a continuum. This is common in swimming vertebrates, and perhaps for that reason the coloration of Pelamis has been interpreted as another case of countershading (Curran et al., 1937; others). This may be true about some other sea-snake species whose color approaches the blue-gray of many fishes, but it does not hold for Pelamis. One author writes: "Pelamis is an excellent example of 'obliterative' shading. The sea snake's dark brown back is almost invisible when seen from above, and its bright yellow belly - when viewed from beneath - blends perfectly with the sunlit sky. But the tail, which is in constant motion stirring up wavelets, has a mottled brown and yellow pattern - a good compromise since any one part of the tail may be either skyward or downward directed" (Schall, 1969). This description is contrary to my field observations, in which *Pelamis* proved to be highly conspicuous both above and below the surface, and this does not strengthen the case for the countershading hypothesis.

Another method of concealment is that of disruptive coloration. It is characterized by the surfaces of highest contrast, the brightest and the darkest, being adjacent to each other without color gradation. This creates in the eye of the viewer new lines which are not there, while the true outline of the organism is broken. A classical example is the Gaboon viper, *Bitis gabonica*, but many snakes and other vertebrates illustate this principle. The coloration of *Pelamis*, in spite of the dark and light surfaces touching each other with sharp transitions, is not disruptive, although some authors (Wall, 1921; Paulson, 1967) thought it to be so.

The function of a certain pattern in an organism must be evaluated against a given ecological background, and not by the animal's appearance in a tank or a collection jar. In disruptively colored animals the patterns exist on backgrounds which help conceal them, such as the litter of a forest floor, spotted by light and shade. A *Bitis* or a copperhead would have little use for their patterns on a sandy dune or in blue water. Also, in the cases known to me, disruptive coloration is associated with a certain attitude that the animal assumes, which tends to intensify the disruptiveness. This is well illustrated in frogs. *Pelamis* is found in a relatively uniform surrounding and its coloration renders it highly conspicuous.

An alternative to the hypotheses of countershading and disruptiveness is that of advertising coloration. Cott (1940), in his discussion of "methods by which conspicuousness is attained," pointed out that the colors used in advertising are bright, usually black in combination with red, orange, white, or yellow. These colors are found in the animal and plant worlds, where advertising is clearly demonstrated (Wickler, 1968). The same colors, which cut across unrelated groups, are also used widely for advertising or warning in the human world. Cott used Pelamis as an example of advertising, and Shuntov (1963) assumed their black-and-yellow combination to be warning coloration.

To prove that the coloration of Pelamis is aposematic it is necessary to show that:

a. The snakes are conspicuous in their natural habitat.

b. Potential predators (fishes and birds) can discriminate the patterns presented by the snakes.

c. Predators avoid Pelamis.

My experience with Pelamis in the field shows that they are highly conspicuous, both at the surface when looked at from above, and from any direction underwater, particularly when viewed from below against the sunlit sky. Often, when viewed from below the surface, a snake appears "double" because of the image reflected from the surface. This makes the snakes even more conspicuous, but at the same time may also confuse predators. When the snakes move, their tail movements advertise their presence in a way reminiscent of a boy scout signalling with a flag. Only under two situations was it difficult to see Pelamis in the field: first, at a certain angle glare prevents seeing any object at the surface. This, however, would not affect birds which fly above and are not at a fixed position where glare can permanently prevent them from seeing. Secondly, when a snake is among vegetation on a drift line it may be camouflaged among the floating yellow stems, especially when seen from below. But this kind of camouflage is based on the snakes' conspicuousness, and is due neither to countershading nor disruptiveness (sometimes the snakes are completely concealed by the white or yellowish foam, or they can hardly be seen through it, but this does not apply to this discussion).

Many fish which have been studied can discriminate colors (Cott, 1940). In fact, many fishes depend in their intra- and interspecific communication on color signals. Classical examples are the cleaning wrasses, some of which (i.e. *Labroides dimidiatus*) have black and yellow color (Wickler, 1968). It is also known that birds can discriminate colors and are particularly sensitive to the red-yellow end of the spectrum. The experiments with predators show that at least some avoid *Pelamis*, and visual recognition was strongly suggested in some cases. Wetmore's observation (1965) of a *Fregata* dropping its sea-snake catch also suggests a recognition of some sort.

Barlow (1972) stated that elongate fish have one long horizontal stripe which makes it harder for predators to focus on them while the fish move rapidly. This, however, does not seem to apply to *Pelamis* which spends most of its time floating, and which moves slowly in comparison with fish.

The analysis above leads to the conclusion that the coloration of *Pelamis* is aposematic. Clearly, in some situations it may be acting to camouflage the snakes, but aposematic coloration and camouflage need not be mutually exclusive. On the contrary, the selective value of this color combination may increase because of its adaptiveness for a variety of environmental situations. Predation experiments, in which black-and-yellow eels (i.e. *Rhinomuraena* and *Moringua*) will be offered to Pacific predators, should help to analyze further the function of coloration of the type exhibited by *Pelamis* in the oceanic environment.

Additional comments:

1) The tail pattern - the consideration of the mottled tail pattern to be a "compromise" between the yellow venter and the black dorsum (Schall, 1969) is unacceptable to me. In its place it may be suggested that the tail pattern acts to deceive predators and attract them to bite at the spotted posterior end. This "eye-spot" trick is suggested to me by our laboratory observations in which several Atlantic fish attacked *Pelamis* by seizing the tail first, after which they were bitten and died. In the field *Pelamis* were occasionally found with sections of their tails missing and with healed wounds. Interestingly, *Pelamis* habitually lie on the surface with the tail hanging somewhat below the surface. Volsøe (1939) thought that this was for hydrostatic reasons, but the possibility that it serves, in part, to distract potential predators from the head region merits consideration.

Even if only 10% of the predators on *Pelamis* start by approaching the tail, and only 1% of these end with an effective bite by the snake, the probability of eliminating a predator is .001 - still a strong selection against predation. Actually, if this hypothesis (that predators may be attracted to the spotted pattern) is correct, more than 50% of the predators should attack the tail first, and the selection for retaining a spotted tail and against predation would be intense.

2) Color variations in Pelamis - these are discussed in the next chapter.

3) Other species - An interesting question is how the other hydrophiids, all venomous, compare with Pelamis with respect to their coloration. Examination of museum specimens and of published plates (Halstead, 1970) shows that other hydrophiids are highly variable species (as is Pelamis). Patterns do not only vary from individual to individual, but also on the same snake. Thus, a snake may have saddles anteriorly which develop into horseshoe-shaped bands more posteriorly and eventually change to complete rings. In some Disteira lapemoides the change is seen as the dorsal part of each ring is wider than its ventral and lateral parts. This is not surprising - a change from a pattern of saddles to irregular rings and then to regular rings is known in the American genus Lampropeltis, and perhaps is potentially present in every "saddled" snake (but in Lampropeltis such changes occur among populations).

More than half of the hydrophiids exhibit annular patterns: 3 species of Laticauda, 2 Emidocephalus, and 12 or more Hydrophis (or Disteira) species. Rings are known to be associated with warning coloration, as in Micrurus and many tropical caterpillars (and their mimics). In most hydrophiids, however, the rings are on a dark background, only slightly lighter than the rings themselves, or are incomplete (Lapemis curtus), and it is hard to make a case for warning patterns. In some, countershading can apply because the rings are connected by dark areas dorsally. This multitude of patterns may have several explanations: it could indicate relaxed slection, since there is an advantage in both the darker countershading and the ringed patterns, especially if bright coloration is attained. It could indicate genetic plasticity, but it could also mean that sea snakes are still undergoing evolution which may result in complete annulation.

Only a few hydrophiids exhibit what is regarded as warning pigmentation: *Hydrophis mamillaris* is yellow with dark rings; *H. obscuris*, *H. melanocephalus*, *Hydrelaps darwiniensis*, *Laticauda colubrina*, and *L. schistorhynchus* have yellow pigmentation (Halstead, 1970; pers. obs.) at least sometimes. Others, mainly in the genera *Disteira* and *Hydrophis*, have alternating dark and white rings (pers. obs.) The annular pattern is also highly pronounced in *Laticauda laticaudata* and *Hydrophis stricticollis*. In some snakes the rings unite dorsally into a dark line, which may suggest the ancestral pattern, still retained in *Pelamis.* From this it can be suggested that conspicuousness in sea snakes was attained in two ways: by retaining the black dorsum and evolving bright surfaces adjacent to it, or by breaking the pigmented surfaces into bands and rings. Some snakes exhibit both tendencies, having rings which are accentuated by the yellow pigment.

Summary

The coloration of *Pelamis* is unique among the sea snakes, and it is interpreted to be aposematic. The "strategy" of *Pelamis* is explained in the following way: warning coloration is the first line of defense against predators which use visual cues. If it fails, a second line of defense is to deceive predators into biting the tail. If this fails, foul odor and taste should discourage the predator. The latter is, obviously, the main defense against predators which depend upon olfaction in their search for prey. When floating among debris and vegetation, *Pelamis* may be camouflaged due to its coloration.

Many of the hydrophiids are probably in a transitional stage in their evolution of complete annulation. It "would be wise" for them to evolve similar patterns in order to make pattern-recognition easier for potential predators, and perhaps this is what is really occurring in this group. With the exception of *Hydrophis caerulescens*, however, for which only a plate was available, no hydrophiid is known which has a pattern like *Pelamis* and might be said to be its mullerian mimic.

II. Parasitism and disease

A. Disease

In the laboratory, Pelamis was afflicted with infections in the cephalic region, especially in the mouth and around the eyes. In an epidemic of skin disease, the snakes developed sores all over the body. In some of these sores polychaetes could be observed microscopically, but these might have settled there after the sores had developed and were not necessarily the cause of them. None of these pathological conditions was seen on Pelamis in the natural habitat, and it is doubtful that this is a significant cause of mortality in the population. One snake was found with an extensive cancerous growth in the esophagus. The growth completely blocked the passage of food, and undoubtedly would eventually have caused the death of the snake.

B. Internal parasites

Search for internal parasites yielded only a few: out of 60 snakes examined one had three proglottids of a platyhelminth, each measuring 1 x 0.1 mm, in the large intestine; two other snakes had nematodes, one on the wall of the small intestine and one on the stomach wall. The exact taxonomic identity of these parasites is not known. Only 15 snakes were examined for lung and liver parasites, and none was found. Other sea snakes, however, were reported to occasionally be host to lung flukes (Vercammen-Grandjean et al., 1964).

Organisms which are at high trophic levels in the marine environment are usually heavily burdened with parasites (pers. obs.) In comparison with these Pelamis is relatively parasite-free, and my conclusion is that internal parasites are not one of the population-limiting factors.

C. Epizoic organisms and external parasites

Several species of invertebrates were found on Pelamis. These were two barnacles, Conchoderma virgatum (Spengler) and Lepas sp. (Plate 5), the ectoproct (bryozoan) Membranipora tuberculata (Bosc), and a turbellarian (Platyhelminthes).

The barnacles were rare on Pelamis and occurred on only 5 of the 2000 snakes observed in this study. Ectoprocts, somewhat more frequent, were found on 10 snakes, of which 6 were in a sample of 283 Pelamis which I collected in Costa Rica (i.e. 2.1%). The ectoproct colonies were of various sizes. The platyhelminths were seen on only 4 Pelamis in the entire study, but on each of these they were numerous and covered almost the entire body surface. These snakes were in a bad state of health, and one of them was also ridden with barnacles. The flatworms were elliptical in shape and small, 1.5 x 2 mm or smaller.

The barnacles were usually attached to Pelamis at the tail tip, or less frequently, tail side. One exception was an adult female Pelamis from Mexico, now at the Kansas University Museum of Natural History (KU 63421, courtesy of W.E. Duellman). This snake was covered with C. virgatum from its neck to the tail tip, and surprisingly seemed to have been in good health at the time of capture. Ectoprocts were found on the trunk and tail, but one extensive colony covered more than half of a snake's head, including an eye and a nostril.

Occasional reports on the fouling of sea snakes have listed barnacles as the primary offenders (Beebe, 1926; Dean, 1938; Minton, 1966). Barnacles reported on Pelamis were, in addition to Lepas and Conchoderma, the following: L. anserifera, L. tenuivalvata, and Bichelaspis *warwicki* (Wall, 1921; Deraniyagala, 1955). Barnacles on other sea snakes were *Octolasmis* sp. and *Chelonibia patula* (William Newman, Scripps Inst. of Oceanography, pers. comm.), *Anatifa* spp., on *Hydrophis schistosa* and *H. nigrocinctus* (Cantor, 1841), and *Platylepas* spp. (Wall, 1921). The commonest barnacles reported on *Pelamis* were *Lepas* spp. and *C. virgatum* which are cosmopolitan and opportunistic with respect to substrate (Balakrishnan, 1969; Roskell, 1969).

The ectoproct *Membranipora tuberculata* is a warm-water species, often associated with algae. Most commonly it is found on the blades and floats of *Laminaria* and *Sargassum*. For this species *Pelamis* provides a most unusual substrate (Kropach and Soule, 1973). Reports on associations between ectoprocts and sea snakes are rare. Cantor (1841) found *Cellepora* on *Hydrophis gracilis*, and Wall (1921) reported the occurrence of *Alcynidium mytiti*, *Triticella pedicellata*, and *Membranipora hippopus* on *Enhydrina*. Harmer (1931) discussed the role sea snakes may play in the distribution of ectoprocts, but he did not give additional reports on associations between the two groups. In a recent communication Cuffey (1971) stated that a bryozoan "tentatively identified as *Electra angulata*" was found on the "Pacific sea snake *Pelaonis* [Sic] *platurus*." The colony he reported on came from the sample I had collected in Costa Rica during the *Alpha Helix* Expedition, 1970, and which I have not been able to examine since then.

Wall (1921) also reported that the hydroids *Bimera fluminalis* and *Campanularia serrulata* had been found on *Hydrophis*. Hydroids were also found on *Pelamis* from Mexico by Pickwell (pers. comm.), but none was observed on these snakes in my study.

Several observations indicate that the species attached to sea snakes are harmful. The ectoproct colony which covered the snake's eye and nostril interfered with functions basic to the animal's physiology. In another case the shed skin of Pelamis remained attached at the tail tip where a cluster of barnacles was firmly anchored, and the snake took 15 hours to complete shedding.

Discussion

The main advantage which fouling organisms would seem to derive from their association with Pelamis and other sea snakes is transportation, and thus a continuous food supply. Another may be protection from predation, to which colonies on stationary objects may be subjected more easily. One ecological situation which allows invertebrates to settle on sea snakes is the ocean slick (chapter 7), where organic matter, plankton, diverse oceanic fauna, and flotsam are accumulated. There Pelamis are exposed to the floating larvae of their parasites. But it is possible that C. virgatum settle on Pelamis in deeper waters, which they seem to prefer (Roskell, 1969).

Although they are not generally considered to be parasites, fouling organisms are harmful to Pelamis (e.g. ectoprocts on eye and naris). The attached clusters of barnacles cause a threefold disturbance to sea snakes: they are a hindrance to the snakes' locomotion by changing their hydrodynamic properties and by causing a drag and perhaps affecting buoyancy; they injure the skin and expose open wounds to bacterial infection, and they may impede shedding. During such periods of disturbance the snakes are not free to pursue their regular activities such as locomotion and feeding, and they may be more susceptible to whatever unfavorable pressures their environment may present. The fouled snakes (with the exception cited above) were in a bad state of health and at the point of starvation.

The view that barnacle clusters attached to Pelamis may be beneficial to their hosts in camouflaging them (Curran et al., 1937; Dean, 1938) seems unacceptable to me. If this were true one would expect fouling to be more common (perhaps even evolve into a tighter mutual relationship?) than it is.

Theoretically, the selective value of a symbiotic relationship is determined by the balance between all the advantages the relationship confers upon each of the species involved and the disadvantages suffered by them. Even if one accepts the argument that Pelamis benefits from the camouflaging effect of barnacles on its skin, it is hard to see how this questionable advantage balances the obvious damages the host must endure in such a relationship. My conclusion is that, much to the contrary, Pelamis have no use for the epizoic organisms, and that these snakes have evolved special adaptations against fouling.

Plate 5. Fouling organisms on Pelamis

A. Conchoderma virgatum on sloughed skin.

B. Lepas sp. attached to a snake's tail.

D. Adaptations for skin hygiene

Fouling appears to be a problem for marine organisms (as it is for man, in his experience with the ocean). Most marine vertebrates are protected to some degree by a mucous layer, and in coral communities many fish pay regular visits to cleaning stations.

Pelamis exhibits two anti-fouling adaptations. One, physiological, is the high frequency of shedding (Table 9). The other, behavioral, is the habit of knotting. The average interval between sheddings was 19.5-25.4 days, with a minimum of 5 days and a maximum of 65 days. Shaw (1962) reported average intervals for two *Pelamis*, of 13.7 and 23.8 days, ranging 7-27 and 12-37 days, respectively. Zeiller (1969), also reporting on two *Pelamis*, found the average shedding interval to be 22 days, ranging 9-43 days. The significance of the information in Table 9 is that, for the first time, data have been gathered from a large number of snakes over a long period.

In comparison with *Pelamis*, *Laticauda* spp. shed less frequently. Klemmer (1967) reported that *L. laticaudata* shed 19 times in 5 years and 2 months, that is, an average interval of 99 days (range 55-150 days). Mays *et al*. (1968), reporting on their observations on *L. semifasciata*, gave an interval of 90 days.

Pelamis sheds its skin, as other snakes do, in one piece, and everted. This was also noted by Volsøe (1939) and Pickwell (1971). *Laticauda* spp. also shed in one piece (Klemmer, 1967; Mays *et al*., 1968). The claim that *Pelamis* sheds piecemeal (Wall, 1921; Rose, 1962; and others) was not confirmed by this study.

The habit of knotting is characteristic of *Pelamis*. It involves swimming with a circular motion to form a loop, swimming through the loop, and thus forming a tight knot (Plates 6, 7). This can be done very rapidly and vigorously, and at times persistently for hours.

Evidence that knot-tying serves to clean the snakes is provided by three observations: 1) The snake which struggled for 15 hours in order to complete shedding did so mostly by tying itself in knots, and eventually it removed both barnacles and skin (Plate 5a). 2) A snake removed a beetle which accidentally landed on it in an indoor tank. It did so by going into a series of knots, and successfully removed the beetle with the first knot. 3) In an experiment I placed small pieces of tape on three *Pelamis*, 1-3 pieces on each snake. In all cases this elicited knotting as soon as the snakes were placed back in the tank, which resulted in removal of the tape within seconds.

Discussion

1) Shedding

Such high frequency of shedding as exhibited by *Pelamis* requires a continuous output of energy. It must have evolved in response to stringent pressures in the pelagic habitat, whereby individuals with higher sloughing frequency were able to spend more time on feeding, had greater freedom of movement, reproduced more, and lived longer than those with a low sloughing frequency. This selection pattern would have continued until a point was reached where the demand for energy output needed for sloughing became too great a burden for the metabolic machinery of the animals. The trend for increased rate of shedding was stabilized, then, to give optimal interval between successive sloughs which was sufficient for maintenance of health.

My data and others' indicate that this optimal interval is in the order of 19-23 days, with variations among individual snakes and the intervals of each snake (one snake shed three times in 14-day intervals, then changed to two 7-day intervals, then to 19, 14, 30-day intervals, and so on). It is interesting to note, in this connection, that in one field study 14 days were required for *C. virgatum* and *Lepas* spp. to attach to floating logs (Hunter *et al.*, 1967).

2) Knotting

The knotting behavior of *Pelamis* was shown by Pickwell (1971) to be associated with shedding, but he also recognized its importance in cleaning, escaping potential predators, and "stretching" during growth. Generally, Pickwell considered knotting to be a method of obtaining leverage in the absence of a solid substrate. Knotting was also associated with shedding in *L. semifasciata* (Mays *et al.*, 1968). Shaw (1962) thought that it served for cleaning, while Dean (1938) strangely stated that most sea snakes, except *Pelamis,* clean themsleves by knotting. Dean's statement is not supported by what is known about ophidian biology.

It is true that *Pelamis* exhibits knotting behavior in situations other than cleaning, as when picked up with forceps, or without apparent reason. This does not contradict or disqualify the statement that knotting serves for cleaning. Several advantages may be derived from this behavior, and the importance attributed to each may depend on the context in which it was observed and the situation most frequently encountered. All the different advantages contribute to the selectiveness of this habit. The fact that barnacles are commonly found on the tail tip may provide indirect evidence that knotting is important in cleaning, because it is at the tail tip where knotting would be least effective as a cleaning method. The examples of the damage caused by epizoic organisms illustrate the pressure which led to the evolution of frequent shedding and cleaning behavior.

The knotting behavior of Pelamis platurus is very similar to that exhibited by the hagfish Eptatretus stoutii (Jensen, 1966). The hagfish also forms knots in order to clean itself of slime, escape predators, and apply leverage while feeding, thus suggesting the possibility of convergence in behavior. The difference in knot formation between the two is that Pelamis moves in an anterior direction, the head entering the loop and tying the knot (Plate 7) while the hagfish moves in the posterior direction, the tail entering the loop first. Some eels also exhibit knotting while attempting to escape capture; presumably they do this to gain leverage (Pickwell, pers. comm.) Perhaps knotting is a widespread habit among elongate marine species when a solid substrate is not available to them.

Summary

Fouling organisms disturb Pelamis in its normal activities. They cannot be considered, however, a limiting factor because they are maintained at a low level by a high shedding frequency and cleaning behavior.

Table 9. Average intervals between successive sheddings in *Pelamis platurus*. Left side: average taken from large groups; right side: averages from data on individual snakes.

Group No.	Period	No. of snakes	Average interval, days	No. of snakes observed	Period, days	Average interval, days	Minimum-maximum
1	55 days, Oct.-Dec.	84-100	19.5	1	546	21.0	7-30
2	63 days, Jan.-March	80-95	22.0	2	329	27.4	19-65
3	42 days, May-June	44-54	21.5	26	120	22.1	5-35
3a	"	7-11, juveniles	21.1				
3b	"	35-43, adults	19.9				

Plate 6. Pelamis in a knot.

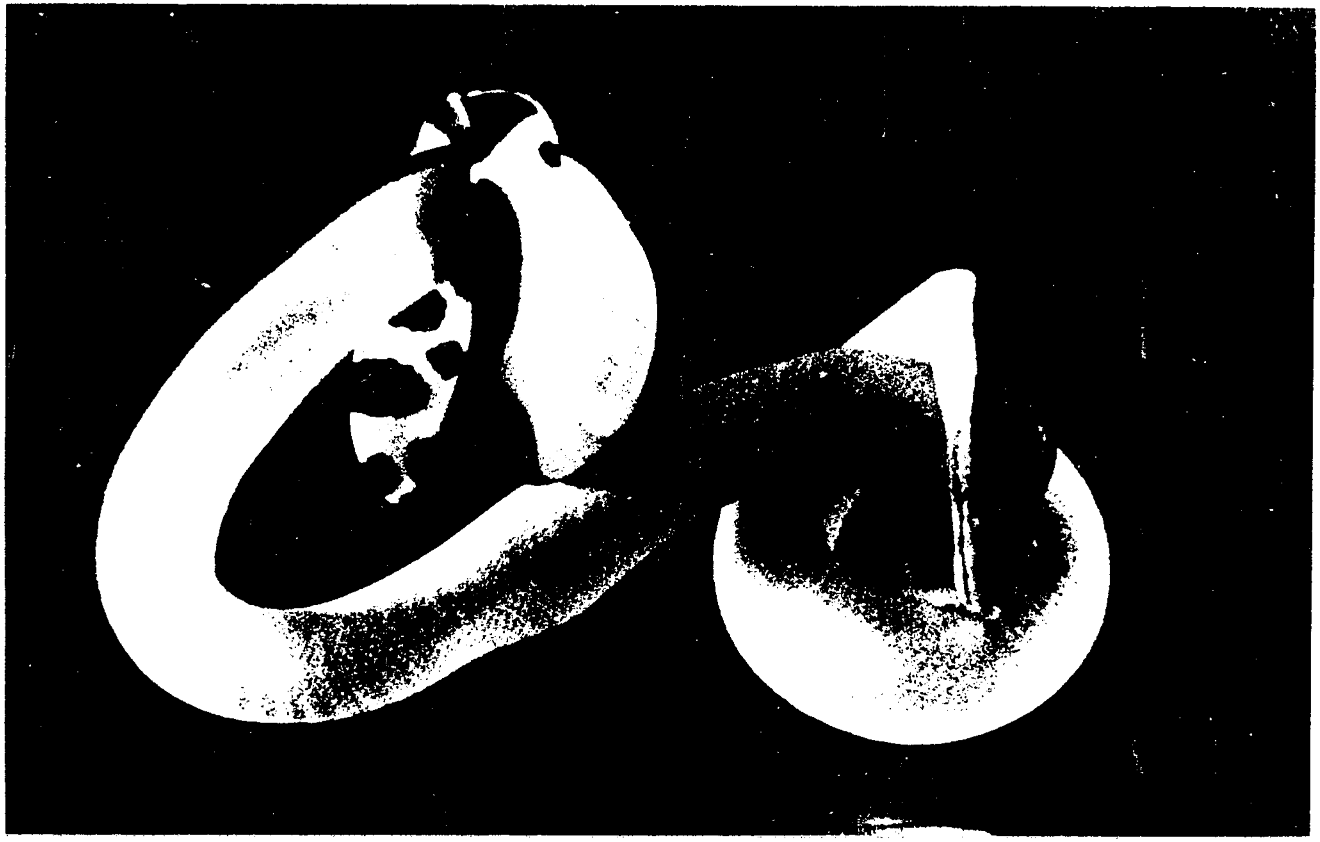


Plate 7. Pelamis swimming out of one knot and starting another.

III. Physical limiting factors

The term physical factors refers to non-biological, mostly geophysical aspects of the environment. Oceans, especially tropical and subtropical, are relatively stable environments where phenomena such as sudden freezing, flooding, fire or other catastrophes, short of volcanic eruption do not take place. The changes which the Gulf of Panama undergoes seasonally cannot be considered catastrophic (although they are sometimes associated with red tide and fish kills). It would seem, then, that the population of Pelamis should not be limited by physical factors.

Observations in the study area revealed, however, the strong influence of one physical factor, currents, in limiting the population. Specimens of Pelamis were washed onto local beaches 5 times in the period September-March. Information from local residents indicated that sea snakes had been washed ashore rather regularly, at all times of the year. Since they were seen, at times, very close to shore, it is not hard to imagine how they could be deposited on beaches in large numbers.

Early naturalists were familiar with this phenomenon (Cantor, 1841; Fayrer, 1872). It was noticed particularly after storms (Ditmars, 1933; Glauert, 1950; Sachet, 1962). The high incidence of this phenomenon is attested to by the numerous records of snakes being cast ashore in different parts of the species range. This was reported from Australia (Glauert, 1950; Kinghorn, 1956; Cogger, 1959), Pakistan (Minton, 1966), South Africa (Rose, 1962; others), and the Eastern Pacific shores (Zweifel, 1960; Duellman, 1961; Shaw, 1961; Hardy and McDiarmid, 1969; Pickwell, 1972).

Discussion

The observations in this study and those recorded in the literature point to currents as a major source of mortality of Pelamis. Once cast onto a beach, the snakes are helpless. They cannot move or struggle back into the ocean, and they are subject to dehydration, predation, or scavenging by beach animals such as crabs (Duellman, 1961). Even when trapped in a tidal pool their death is almost certain, even if somewhat delayed.

It is worth considering why Pelamis has not evolved some behavior which would prevent it from being swept by currents. It should be remembered that the strategy of the species appears to be based on utilization of currents (chapters 4 and 7) for reaching food and mates and for expanding the species range. The loss of individuals stranded on beaches may be the price the species is paying for maintaining this strategy.

IV. Summary

The only severe mortality factor of Pelamis for which there is evidence is a density-independent physical factor - that of being swept by currents onto the shore. This phenomenon is known throughout the entire species range and is one of the most widely observed facts of the life and death of Pelamis. It is also possible that many individuals are lost by being carried by currents into areas of cold water but the evidence for this is circumstancial (i.e. Pelamis found in deep oceanic waters in areas marginal to its distribution.)

THE POPULATION

I. Sex recognition and sex ratio

To the human eye the two sexes of Pelamis appear indistinct; they cannot be separated on the basis of external morphology. The claim that the males can be recognized by a bilateral swelling at the base of the tail (Kinghorn, 1956) was not upheld in my study. Although statistical differences are discernible between the sexes with respect to several characters, there is a wide range of overlap between males and females, so none of these characters can be used to distinguish the sex in the live animals.

Initial sexing of my samples was done by injecting the tail base and everting the hemipenis in the males. Subsequently the sexes were determined by dissection. It should be pointed out, however, that X-rays can be used to sex live adult Pelamis since the calcified spines of the hemipenis in adult males appear on the X-ray plates. This method is not useful for juveniles, and its limitation in a field study is apparent.

The characters which are sexually dimorphic in Pelamis are the following:

1) The tubercules on the male's scales (p. 19) are more prominent than on the female's. In both sexes they are larger on adults than on young snakes. This character cannot be objectively measured and for this reason alone may be regarded as a poor one. The function of the tubercules is not known but they may help the male to hold on to the female during copulation.

2) Caudal vertebrae, 32-45 in the males, are more numerous than in the females, where the range is 30-40 (p. 19). This difference is reflected in the tail length, which in the male is proportionally longer, on the average, than in the female (Table 10).

3) The females, on the average, are larger than the males (Table 10). This difference in body length can be seen when the ten largest specimens of each sample are arranged in descending order of size (Table 11). It is seen that the females are consistently the largest individuals (with one exception), and that the males, in spite of their usual 1:1 ratio in the population, are usually poorly represented in the "upper ten" class. The biological reason for having a greater snout-vent length seems obvious in that the females bear the fetuses in their body cavities until development is completed.

4) Comparisons of head-scale counts of 126 female and 114 male Pelamis were made. Within each sex group comparisons were made between small and large snakes. The five characters compared were the numbers of upper and lower labials, preoculars, postoculars, and anterior temporals. Within each sex group the differences in scale numbers are not significant, but the differences between small males and small females, as well as those between large males and large females, are highly significant for four of the traits (Table 10). The only exception is the number of anterior temporals, where no significant difference was detected.

The degree of overlap in the dimorphic characters is so great that only when large samples are available does the dimorphism become apparent. Although a difference of only a fraction of a scale between males and females seems meaningless, it is a real difference whose value in terms of the biology of the animals is not clear. Head scutellation may affect the kinetics of this region, but this does not explain why females should have more labials and preorbitals, and fewer postorbitals than males, whose skulls are slightly larger. I doubt that to the individual snake such small differences are of any significance.

How sex recognition in Pelamis is accomplished is not known, but it may involve olfaction. Snakes of this species secrete a strong musky odor, but it was not determined whether this secretion is restricted to a given sex.

Sex ratio in all collected samples was close to 1:1 (Table 12), but in 9 out of 14 samples the number of females exceeded that of males. When sex ratios within the different size classes were compared, approximate 1:1 ratio was retained (with one exception). The deviations from the 1:1 ratio are probably due to the females' slightly larger size. This difference in size between the sexes becomes apparent when the animals reach the size of 50 cm. It is in this size class (50-60 cm) that there are more males than females, and in one case the male:female ratio is significantly different from 1:1 (Table 13). Apparently when the males reach the size of 50 cm they mature and their growth rate slows down, while the females maintain their growth rate. The available data, however, indicate that the sex ratio does not change with age (Table 13), and that there is no differential survival of either sex.

Table 10. Sexual dimorphism in some *Pelamis* characters. N = sample size; $\bar{X}$ = mean; S = standard deviation; $S_{\bar{X}}$ = standard error. Scale characters refer to adult *Pelamis*.

Character	Males				Females				t	P
	N	$\bar{X}$	S	$S_{\bar{X}}$	N	$\bar{X}$	S	$S_{\bar{X}}$		
total length (TL)	359	51.43 cm	10.92	.58	391	54.22 cm	13.56	.69	3.080	<.01
snout-vent length	359	45.20	9.74	.51	391	48.11	12.13	.61	3.426	<.001
tail length as % of TL	242	12.10 %	2.08	.134	259	11.42 %	.711	.044	4.966	<.001
number of upper labials	77	8.12	.74	.060	74	8.36	.84	.069	2.630	<.01
number of lower labials	77	11.22	.83	.067	74	11.43	.92	.076	2.080	<.05
number of preorbitals	77	1.05	.24	.019	74	1.16	.37	.030	3.034	<.01
number of postorbitals	77	2.06	.37	.029	72	1.97	.41	.034	2.021	<.05
caudal vertebrae	74	38.86	5.04	.586	53	35.51	4.96	.682	3.718	<.001

Table 11. The ten largest snakes of each of ten samples, all collected in the Gulf of Panama in 1970, arranged in descending order. Size refers to total length in mm; N= sample size.

May		June 11		June 12		June 13		June 14		Aug. 15		Sept. 10		Sept. 19		Sept. 20		Oct. 26	
sex	size	sex	size	sex	size	sex	size	sex	size	sex	size	sex	size	sex	size	sex	size	sex	size
♀	765	♀	754	♀	789	♀	833	♀	697	♀	811	♀	728	♂	684	♀	735	♀	786
♀	761	♀	731	♀	746	♀	773	♀	696	♀	755	♂	651	♀	684	♀	705	♀	782
♀	737	♀	684	♀	710	♀	766	♀	678	♀	738	♂	649	♂	683	♀	633	♀	764
♀	737	♀	670	♂	698	♀	727	♀	669	♀	725	♂	647	♀	673	♀	633	♀	760
♀	716	♀	647	♀	690	♀	710	♀	659	♀	718	♀	645	♀	667	♂	619	♀	750
♀	673	♂	617	♂	689	♀	708	♂	643	♀	717	♂	627	♀	664	♀	617	♀	731
♂	670	♂	617	♀	683	♂	707	♀	641	♀	697	♂	611	♂	657	♀	614	♀	731
♀	668	♀	615	♀	661	♀	703	♂	635	♀	693	♂	609	♀	656	♀	614	♀	717
♀	667	♂	591	♀	646	♀	690	♂	632	♀	693	♂	608	♂	630	♂	613	♀	696
♀	666	♂	590	♂	641	♂	670	♂	621	♀	689	♀	606	♂	629	♂	600	♀	677
N =	25		14		55		141		19		101		96		57		48		67

Table 12. Sex ratio in samples of *Pelamis platurus* collected in the Gulf of Panama, 1970. N = sample size; P values are approximate.

sample	N	♂	♀	ratio ♂/♀	X^2	P
March 13	10	5	5	1.0		
April 15	14	6	8	.75	.286	>.70
May 30	25	10	15	.67	1.000	>.50
June 11	14	6	8	.75	.286	>.70
June 12	55	30	25	1.20	.254	>.70
June 13	141	64	77	.83	1.198	>.30
June 14	32	15	17	.88	1.125	>.30
Aug. 15	101	43	58	.74	2.228	>.20
Sept. 10	96	51	45	1.13	.374	>.70
Sept. 19	57	26	31	.84	.438	>.70
Sept. 20	48	29	19	1.53	2.082	>.20
Oct. 26	73	37	36	1.03	.007	>.95
Oct. 30	25	9	16	.56	1.96	>.20
Jan. 26, 1971	21	9	12	.75	.428	>.70
total	715	340	372	.914	1.438	>.30

Table 13. Sex ratio in different size classes of three samples of <u>Pelamis platurus</u> from the Gulf of Panama, 1970. N and P as in Table 10.

June:						
class size, mm	N	♂	♀	♂/♀	X^2	P
300 - 399	52	21	31	.68	1.922	>.20
400 - 499	34	15	19	.79	.470	>.50
500 - 599	80	51	29	1.76	6.05	>.02
600 - 699	59	23	36	.64	2.864	>.10
700 - 799	16	5	11	.45	2.250	>.20
800 -	1		1			
August:						
300 - 399	7	2	5	.40	1.286	>.30
400 - 499	20	8	12	.67	.800	>.50
500 - 599	18	11	7	1.57	.889	>.50
600 - 699	45	20	25	.80	.556	>.50
700 - 799	10	2	8	.25	3.6	>.10
800 -	1		1			
September:						
200 - 299	3	3				
300 - 399	90	45	45	1.0		
400 - 499	39	19	20	.95	.025	>.90
500 - 599	33	20	13	1.54	1.485	>.30
600 - 699	33	18	15	1.20	.273	>.70
700 -	3		3			

II. Size classes

The mean total length for each of the samples collected during the year of the study was determined, separately for males and females (Table 14). The mean, standard error, size range and sample size for each sample are shown in Fig. 9.

Analysis of variance of these samples indicates that they are significantly different, and therefore that the population structure changed during the year. In fact, examination of samples which were collected during the same month (i.e., June and September) shows them also to be significantly different.

The frequencies of individuals in various size classes are given in Table 15. The divisions to size classes are arbitrary, as they must be when dealing with a continuous character. I believe, however, that individuals below 300 mm in total length are juveniles in their first year; those above 500 mm are adults, and the range 300-500 mm probably includes both juveniles and adults as well as the subadults.

Discussion

The size classes of a sample are supposed to reflect the age structure of the population from which the sample was taken. Theoretically, the appearance of juveniles in a population, if it is seasonal, should be detected as a large group of individuals in the smallest size class known for the species. In time, the proportion of the size class in the population diminishes as members of the cohort grow up and enter higher classes. Also, the cohort size is reduced as it ages, due to mortality. In a population whose breeding is nonseasonal, young of the smallest size will not appear as a distinct class in a pronounced proportion; rather, they will make their appearance during the entire year, and their proportion in the population at any given time will be small.

There are several weaknesses in the hypothesis that size-class distribution yields the population age structure. The first is that it assumes that the age of the animals is known, and that their size indeed reflects their age. Secondly, it assumes knowledge of the growth rate of the animals and of changes in growth rate as the animals age. While it is fair to assume that there is a correlation between age and size, this correlation should be held true only up to a certain age which is not known. Finally, the hypothesis implies that individuals of a given sex at a given size are of the same age. This is not necessarily so, and probably is often not true and, in the case of sea snakes, is not known.

The information which can be derived from size-class data is limited, then, to situations in which the "power of resolution" is sufficient for interpretation of population events. An example could be a situation in which a large group of juveniles (about whose age there should be no doubt) first appears in the population, or one where a whole class of adults is missing (if females go to give birth in some sheltered area where sampling is not done), or the reverse - where only one class is found (i.e. gravid females). In general, the more is known about the species, the more can be learned from the population structure and changes therein.

At present, there is no reliable method for determining the age of snakes. Bryuzgin (1939) thought that calcium in snakes' bones is deposited seasonally, and suggested that thus a permanent record of an animal's growth and age might be formed. This hypothesis, even if correct, would not seem to hold for tropical animals. Griffiths (1961) has shown that there were many reasons for rejecting Bryuzgin's hypothesis, so at present the problem of correctly estimating a snake's age remains open.

In *Pelamis*, newborn snakes can be recognized, since their size at birth is known from the laboratory. Because growth rate is not known, the observer cannot rely on size alone. Juvenile *Pelamis* retain for some time (perhaps several weeks) the umbilical opening, which I call the umbilical slit because of its shape. As long as the slit is open, the juvenile can be recognized as newborn, not older than several weeks, depending on the degree of closure of the slit. After it closes, an umbilical scar remains and is apparent for a long time, sometimes for many months. The scar could be seen even on one subadult, 410 mm TL. Therefore the presence of a scar cannot be used for estimating age. (The umbilical slit can be found at a distance of 10-15 snout-vent units anterior to the vent.)

The data in Table 14 show significant shifts in the means of the population samples. Even samples which were expected to be homogenous, as the June 11-14 samples, collected on four consecutive days in the same general area, are significantly different. It appears, then, that the *Pelamis* population in the Gulf of Panama is extremely large, and that at times only part of the population is picked up.

Another phenomenon seems to be the reduction of sample mean with increase in sample size (Table 14, June 13 and September 10 samples). If this is really so, it may mean that only when a large concentration of snakes is present (from which the large samples are taken) is the population truly represented. That could be the case if large snakes reach ocean slicks earlier or faster than small snakes. Two groups of snakes which were marked and released in January (344 snakes) and February (108 snakes) 1970 had mean sizes of 44.40 and 41.14 cm respectively. Several factors complicate the evaluation of this observation: in the two samples above (January and February) live snakes were measured, and it is not known how much of the smaller mean size is a result of this fact. Live snakes are difficult to measure accurately, as they tend to contract their muscles during handling. It is also impossible to separate the effects of the different factors which may influence mean size: in the June 13 sample it can be assumed that the low mean is the effect of a large sample size, since snakes from the same area were collected on the days before and after, and showed larger mean sizes in the smaller samples. The September 10 sample (Table 14) was collected at a different place (Pinas Bay, at the outer margin of the Gulf of Panama) than other September samples, and 9-10 days separated the collections. The small size of most samples, and the gaps between collections further complicate the analysis of this data.

In conclusion, more data are required on population structure and its changes. The available data suggest that the population is not homogeneously distributed in the habitat, but this may be a result of poor sampling. Perhaps the pattern of distribution of pelagic reptiles in their habitat is such that different sampling methods are required. More on the subject of population structure will be discussed in the next section, in connection with reproduction.

III. Reproduction

Pelamis are ovoviviparous as are most sea snakes. Becoming live bearers was one of the most significant adaptations for pelagic life, because it allowed the snakes to break the link with the terrestrial habitat, and become completely independent marine animals. *Laticauda*, the more primitive sea snakes, are oviparous (Smedley, 1930), but even they were reported to be ovoviviparous occasionally (Smith, 1930). It is quite possible that the genus is in a transitional state (as it is with respect to other hydrophiid features), and it therefore exhibits both the egg-laying and live-bearing modes of reproduction (Smedley, 1931), the former being the more common.

The largest brood size known in *Pelamis* is 6 embryos (Visser, 1967; pers. obs.), and the brood is divided between the two oviducts. The smallest brood observed in this study was two, but Visser (1967) found a gravid female with one fetus. *Pelamis* are small snakes and 6 embryos may be the largest brood size. A larger brood, if it occurs at all, would be a rare exception. Other sea snakes may have 10 embryos, as in *Hydrophis obscuris*, 16 as in *H. cyanocinctus* (Wall, 1921), 14 in *Astrotia stokesii* (Volsøe, 1939), 18 in *H. ornatus*, and 24 embryos in *H. elegans* (Shuntov, 1971). These are all larger snakes than *Pelamis*. Cochran (1943) stated that "all sea snakes bear their young alive, 2 to 18 at a time."

The gestation period of *Pelamis* is not known exactly. One gravid female was observed in the laboratory for 4½ months before giving birth to 4 young. So this period has to be regarded as a minimal estimate of the gestation period. Cantor (1841) thought that gestation in hydrophiids was about seven months, and Pickwell (1972) estimated it to be on the order of eight months. Bergman (1943) estimated gestation to last about six months and the entire ovarian cycle about eight months. He suggested that there is only one cycle per year. The length of the embryonic stage will vary, undoubtedly, among populations of different geographic locations, or within a given population as environmental conditions, mainly temperature, change throughout the year.

The young are approximately 22-26 cm long at birth. The four born in the laboratory measured 25.4 cm each, but embryos in one gravid female measured 26.2 cm. Smaller young are occasionally observed in the field: Minton (1966) found a 23.0 cm Pelamis in Pakistan; Wall (1921) reported young Pelamis which measured 23.7 and 25.6 cm, and Myers (1945) found a 22.0 cm Pelamis in Panama. When a brood of 6 advanced embryos, ranging 18.6-19.7 cm, was examined, they all appeared slightly premature for birth, and yolk was still present in the embryonic sacs. Another brood measured 21.5 cm each. It can be concluded, then, that the minimum size of Pelamis at birth is about 22.0 cm. The young are born with a rich fat storage and they are capable of feeding during their first day of life.

Rate of growth of the young is not known, but Kinghorn (1956) thought that they double their size in their first year of life. Exactly when sexual maturity is reached by Pelamis is not known, but the males probably become sexually mature when they reach 500 mm total lenght. Table 13 shows that at the 500-600 mm size class the male:female ratio increases abruptly. This could be due to a slower growth rate in the males after they reach maturity, while the females still maintain their growth rate. The strong correlation (.894) between the length of testes and body length in snakes below 500 mm (Fig. 10) drops (to .424) above this size class. The regression of testes length on body length drops from .196 to .095. This also shows that at about 500 mm body length the males become mature. The onset of reproductive activity in females probably occurs when they are larger. The gravid females in my sample ranged 645-765 mm total length (579-672 S-V). But a greater sample of breeding females is required for a more accurate estimate of their size at maturation. The gravid females reported by Visser (1967) ranged 623-758 mm snout-vent length (average 677 mm). Bergman (1943) who reported on several sea snakes from Java (not Pelamis) assumed that at the beginning of maturity males and females were of equal size, but that this size was different from species to species (ranging 425-700 mm).

One of the important aspects of reproduction is the breeding season. Seasonal breeding is expected to take place in areas marked by distinct, regular climatological change, such as in the temperate zone. In reality the tropics are also influenced by seasons, which are distinguished mainly by a change in humidity, not temperature.

Because of seasonality in the Gulf of Panama, marked by a lower water temperature and greater food abundance in the dry season (chapter 6), Pelamis was expected to have a seasonal mode of reproduction. Size-class data do not show a definite season in which young appear in the population. This alone does not mean that Pelamis reproduces all throughout the year. Absence of a large class of newborn may be due to gaps in sampling, or to the fact that sampling did not cover the entire study area. Several observations suggest, however, that *Pelamis* does not reproduce seasonally: young snakes were observed throughout the year; the occurrence of gravid females and the sizes of the fetuses (Fig. 11) also suggest that young are not born in one short period, or perhaps a bimodality in the appearance of the young. If young indeed appear twice a year, one time around April-May and the other around August-September, this may be viewed as nonseasonal mode of reproduction, because each of these periods of parturition probably covers several months, and young may appear, then, during most months of the year. Whether newborn snakes appear during the dry season in the Gulf of Panama is not known. The only two gravid females from this period carried embryos in an early stage of development.

Virtually nothing is known about the mating habits of *Pelamis*, but presumably pairing should not be a problem since the opportunity for finding a mate exists when the animals are congregated along slicks, which is a common event. Cantor (1841) reported that in the Ganges delta pairing of *Enhydrina* and *Hydrophis* spp. occurs in February and March.In the Iranian Gulf mating of sea snakes (not *Pelamis*) was observed during April-May (Volsøe, 1939). The tubercles on the male's skin, which in some species are enlarged to spines, may help the males to hold on to the females.

The time of birth of *Pelamis* seems to be different in different localities, as might be expected. In Sidney, Australia, completely developed embryos were found in June and July (Cogger, 1959). In northern Australia hydrophiids (not including *Pelamis*) gave birth throughout the period September-May (Shuntov, 1971). In Ceylon (Wall, 1921) and in the Gulf of Siam (Smith, 1926) sea snakes are born in

March-April. The most extensive data on the subject were published by Visser (1967) on 8 gravid females, of which 5 were of known dates. He found in South Africa fully developed Pelamis embryos in February, May, and October. Visser's data suggest (although he does not state so) that Pelamis are born throughout the year. In Banderas Bay, Mexico, Pickwell found newborn Pelamis and females with full-term fetuses in November 1968. A large number of full-term fetuses was also found in March 1971 in the same locality, while gravid females brought to the laboratory gave birth in May, June, December, and January (Pickwell, pers. comm.)

From the available data, mainly Visser's, Pickwell's and my own, it appears that Pelamis does not breed in one particular season. Even if most of the females give birth at one part of the year, still a large number bear young at other times. This reproductive pattern will become clearer when sampling methods are improved and data are gathered for more than one year. Shuntov, working in northern Australia, also noted birth of young hydrophiids (not Pelamis) throughout an extensive period, although he still concluded that they breed seasonally. He stated that birth took place in the summer "and to a lesser extent in the autumn... but also in other times" (Shuntov, 1971). Similarly, Pickwell (1972) noted that "young are born throughout the year but in Mexican waters the peak period appears to be in the late fall and early winter (this period is extended since Pelamis were born in Pickwell's laboratory in May and June 1971; by pers. comm.)

Evidence for seasonal breeding in Pelamis was found in Golfo Dulce, Costa Rica. In the mouth of this narrow gulf (8° 20.5' N, 83° 09.3' - 83° 11.3' W) 278 Pelamis were collected on September 8, 1970, during the Alpha Helix Expedition. 43% of the specimens were newborn snakes. This is reminiscent of Ditmars, account that "previous to the young being born they [the females] seek tide pools and shallow flats of deserted shores" (Ditmars, 1931). Myers (1938) also thought that the females came to Bahía Honda, Panama, for parturition. Pickwell's observations in Bahía Banderas, Mexico, also suggest that females came there to give birth. But among them were gravid females with embryos in early development which were 2-3 months prior to birth (pers. comm.) Clearly, more data are required in order to understand the reproductive strategy of Pelamis.

The possibility may exist, then, that all gravid females caught in the Gulf of Panama during my study were marginal members of the breeding population, while the main class of breeding females was not discovered due to insufficient sampling. Table 12 does not show the disappearance of a whole class of females, but when the size of the population is considered, it is realized that such an event might have gone unnoticed. This may explain why only seven gravid females were collected in the course of the study. Another possibility is that the snakes give birth outside of the Gulf, thus indicating that the population in the Gulf is a transient one. The important aspect of Pelamis reproduction is, however, the capacity for reproduction over a broad period. It is not important whether a 6-8 month reproductive period is termed seasonal or nonseasonal. The significance of such plasticity in reproduction lies with its potential for expansion of the species range and adaptations for life in a variety of ecological conditions in newly colonized areas.

Although seasonality of the Gulf of Panama was expected to influence the mode of reproduction of Pelamis it should not be too surprising if its influence remained minimal. Reptiles are known to be ectothermic and regulate their body temperature behaviorally. When the water temperature in the Gulf of Panama drops, the air temperature usually remains unchanged or even rises, and all that *Pelamis* has to do in order to keep warm is to spend a greater amount of time at the surface. In short, *Pelamis* in the Gulf of Panama is not in the same situation as are reptiles in the temperate zone, which have to endure winter, and they may continue their normal activities, including reproduction, right through the dry season.

Table 14. Samples of <u>Pelamis</u>, collected in the Gulf of Panama in 1970. N = sample size; $\bar{X}$ = mean total length in cm; S = standard deviation; $S_{\bar{X}}$ = standard error.

	Males				Females			
sample	N	$\bar{X}$	S	$S_{\bar{X}}$	N	$\bar{X}$	S	$S_{\bar{X}}$
March 13	5	43.78	12.34	5.520	5	44.71	11.87	5.309
April 15	6	40.60	4.72	1.926	8	60.90	8.87	3.138
May 30	10	56.18	8.75	2.742	15	63.42	12.26	3.167
June 11	6	57.78	4.27	1.742	8	65.70	6.58	2.326
June 12	30	55.32	8.69	1.586	25	57.19	11.42	2.284
June 13	64	50.01	10.41	1.291	77	49.89	13.35	1.532
June 14	15	55.22	10.23	2.643	17	55.72	11.93	2.892
Aug. 15	43	57.09	9.04	1.379	58	58.65	12.62	1.657
Sept. 10	51	42.74	9.35	1.309	45	41.73	8.330	1.242
Sept. 19	26	53.70	11.16	2.190	31	50.61	12.07	2.167
Sept. 20	29	42.00	10.09	1.875	19	49.40	13.19	3.026
Oct. 26	37	55.67	7.99	1.390	36	61.80	11.34	1.944
Oct. 30	9	61.80	4.278	1.426	16	61.85	7.950	1.988
Jan. 26, 1970	9	54.9	5.014	1.671	12	61.70	5.73	1.654
F value:	10.090				10.044			

Fig. 9. Pelamis samples: solid line - males; broken line - females; line length - size range; horizontal bar - mean; rectangle - standard error; figures - sample size.

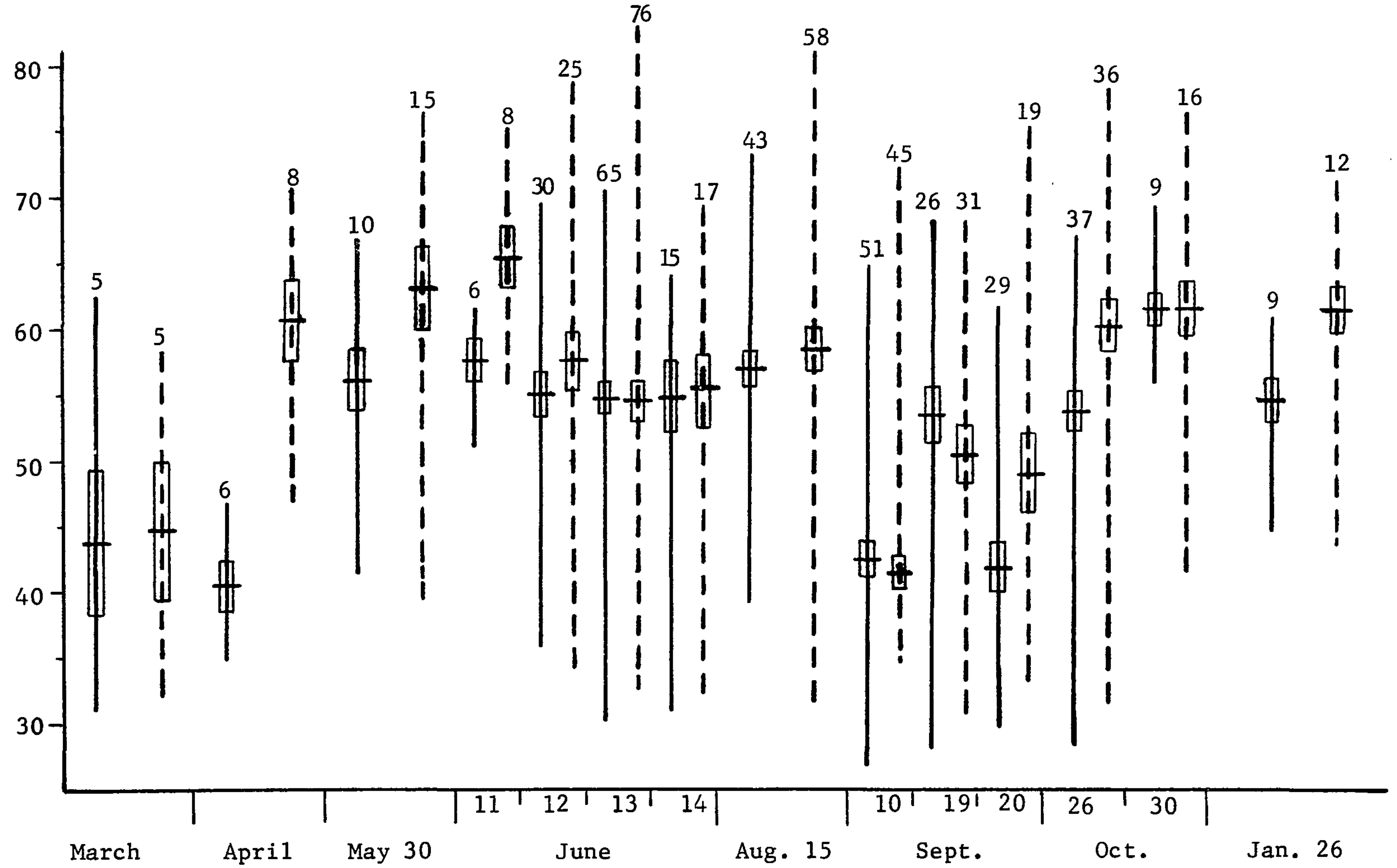


Table 15. Size-class distribution in *Pelamis* samples. Frequencies are in %.

sample size in mm.	April		May 30		June 11		June 12		June 13		June 14	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
N	6	8	10	15	6	8	30	25	65	76	15	17
200-299												
300-399	33.33			6.7			10.0	8.0	26.15	32.89	13.33	17.65
400-499	66.67	25.0	30.0	13.3			10.0	16.0	16.92	18.42	6.67	5.88
500-599			20.0	6.7	66.67	25.0	56.67	24.0	38.46	21.05	33.33	29.41
600-699		62.5	50.0	40.0	33.33	50.0	23.33	40.0	16.92	18.42	46.67	47.06
700-799		12.5		33.3		25.0		12.0	1.54	7.89		
800-										1.32		

Table 15. Cont.

	Aug. 15		Sept. 10		Sept. 19		Sept. 20		Oct. 26		Jan. 26	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
N	43	58	51	45	26	31	29	19	45	52	9	12
200-299			2.0		3.84		3.4		2.2			
300-399	4.6	8.6	52.0	58.6	11.53	32.25	55.2	42.1	8.9	5.8		
400-499	18.6	20.7	26.0	30.4	7.69	9.67	13.79	15.8	4.4	9.6	22.2	8.3
500-599	25.6	12.1	6.0	4.3	46.15	32.25	17.24	5.26	48.9	28.8	66.7	16.7
600-699	46.5	43.1	14.0	4.3	30.76	25.8	10.34	26.3	35.6	36.5	11.1	66.7
700-799	4.7	13.7		2.2				10.52		19.2		8.3
800-		1.7										

Fig. 10. Testes lengths versus snout-vent lengths in 105 snakes collected June, 1970, in the Gulf of Panama. Line represents the regression for snakes up to 450 mm snout-vent.

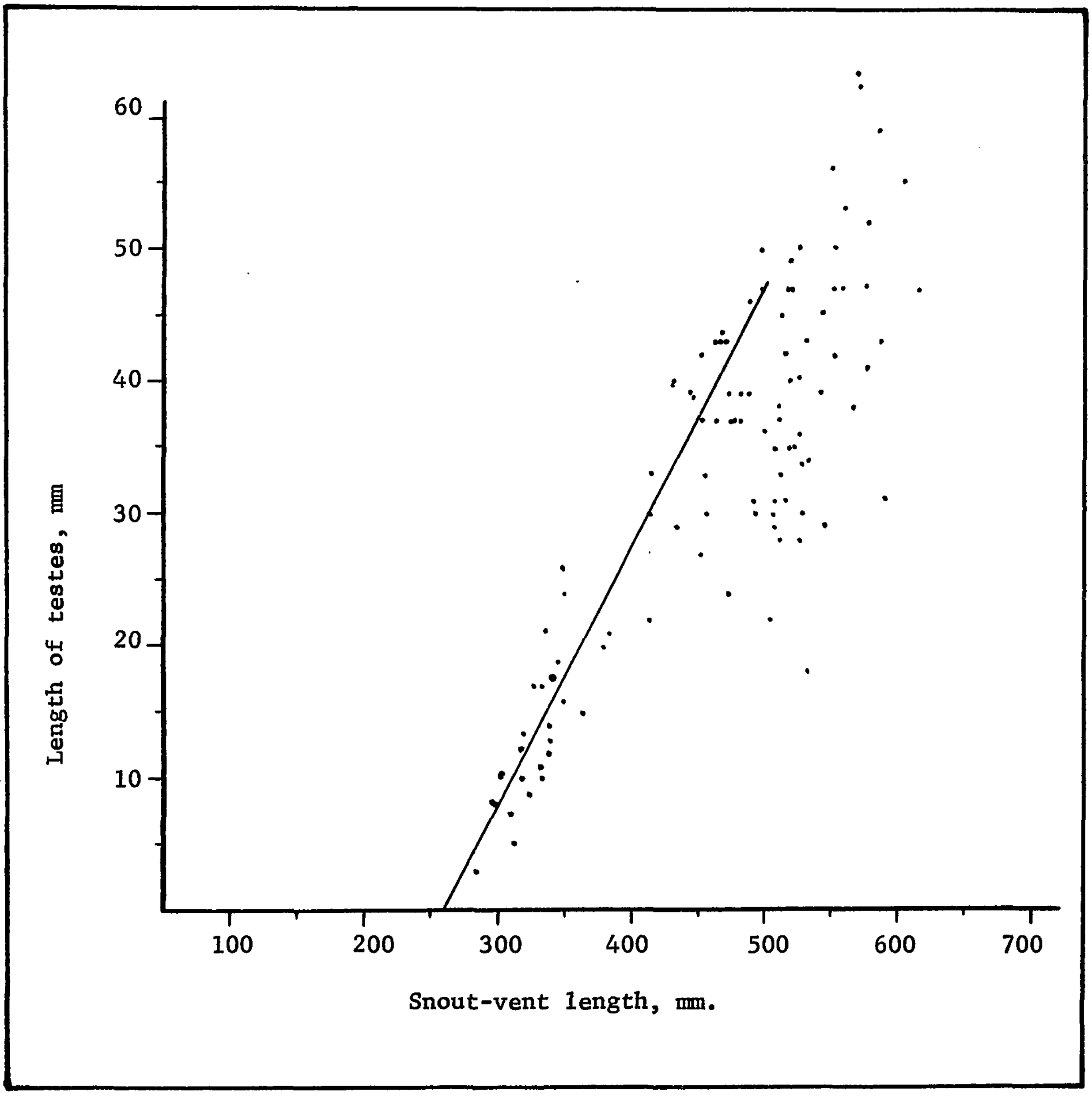
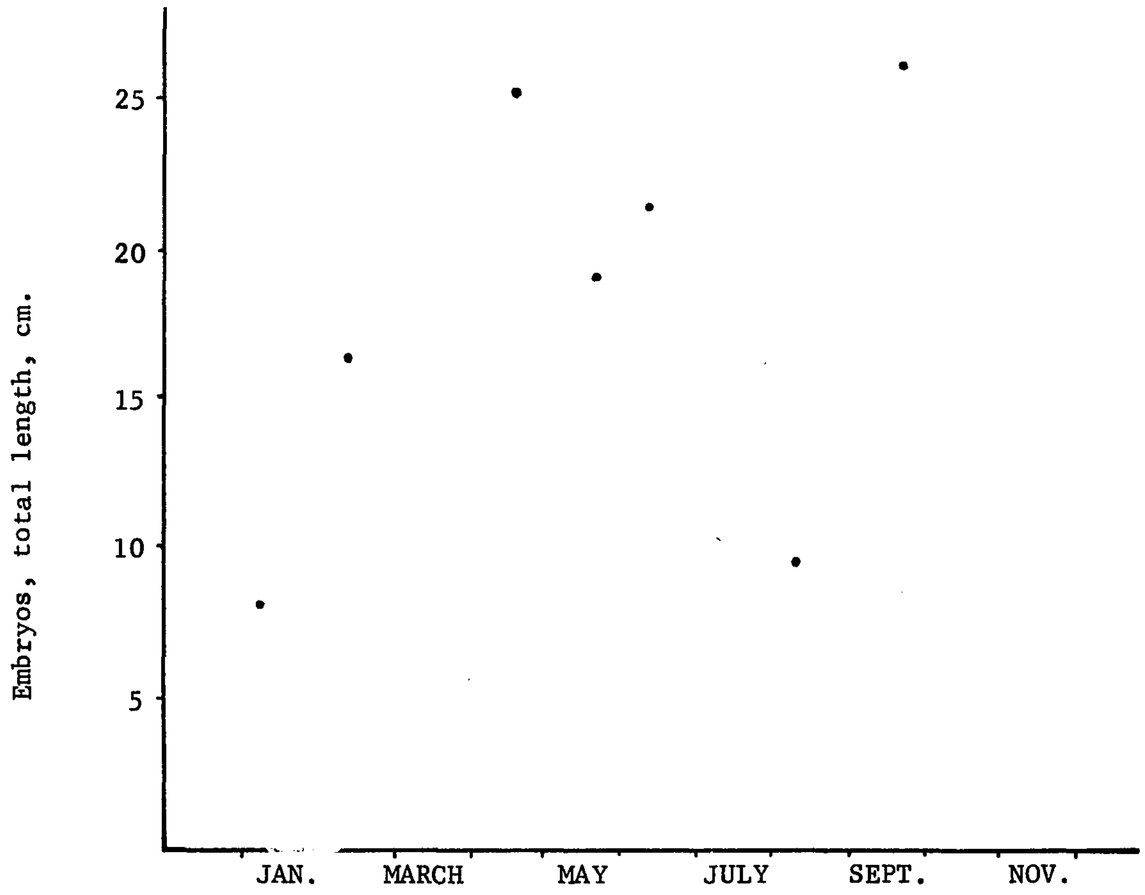


Fig. 11. Size distribution of Pelamis embryos during the year.



IV. Variations in the population

A. Color variations

Pelamis is known to occur in highly variable patterns. FitzSimons (1912) listed seven color types, Wall (1921) described four varieties, Smith (1926) described seven, each with its respective geographical range, and Deraniyagala (1960) recognized "at least ten color varieties." Taylor (1950) described three color forms from Ceylon and suggested that *Pelamis platurus* represented more than one species.

The known specimens show variations on the basic *Pelamis* pattern of black dorsal and yellow-brown ventrolateral coloration, with black bars and spots on a yellow tail (Plate 1). Variants differ in the relative abundance and specific configuration of their black, brown, and yellow surfaces (Plate 8; for color plates see Pickwell, 1972). Many intermediate forms exist among the recognized color groups. Specimens with reduced melanin are reported (Minton, 1966), and a rare all-yellow variety was discovered during this study (Kropach, 1971b). This variety is not recorded in the literature on *Pelamis*, but Rafinesque (1817) referred to a sea snake named *Ophinectes luteus*, which was presumably an all-yellow snake.

The variations in *Pelamis*' color are not regarded as polymorphism because they are continuous. For this reason division of a given sample to color types is difficult and often not practical. For example, the most frequent types, the black-yellow and the black-brown-yellow are often the same type, because as the skin ages it darkens, and after shedding the previously brown surface may be bright yellow. Superimposed on this pattern may be black ventrolateral spots, a black ventrolateral line, or line segment, which may extend throughout the entire body length or only along part of the body.

Other variants exhibit black lateral stripe, resulting in a black-yellow-black-yellow pattern; checkered ventral surface; standard pattern with a wavy boundary between the black and yellow surfaces; standard pattern with bars descending from the black surface which form horseshoe patterns; as above with black spots in the centers of the black horseshoes - resulting in a wavy yellow line laterally; and others. Fayrer (1872) describes some interesting color patterns in Pelamis. As stated, variations may occur within each color type, and combinations of or intergradations between "types" are numerous.

The mode of inheritance of color patterns in Pelamis has not been studied, but is probably by multigenic action. Embryos often do not have the patterns of their mothers, or when they do the pattern may not be as extensive as in the mother. The tail pattern seems to be unique to each individual, but some shapes of the black spots are repeated with high frequency. Often the tail pattern is not bilaterally symmetrical.

The great variability in color patterns is difficult to understand in view of the hypothesis (chapter 11, section I, C) that the coloration of Pelamis is aposematic. Theoretically, it would seem beneficial for the species to have a uniform pattern in order to facilitate recognition by potential predators. It should be interesting, then, to see whether selection against pattern variability is evident in Pelamis. To study this, the variability of juveniles should be compared with that of adults.

The nature of the pattern variants is such that it was not possible to measure pattern variability. But when the frequencies of uniform (black-yellow and black-brown-yellow) snakes versus those with broken patterns (Plate 8) are compared between juveniles and adults, they do not appear different. Different results were obtained by Camin and Ehrlich (1958), who found strong selection against banded water snakes (Natrix sipedon L.) The nature of the pattern in this species permitted the use of a rigorous quantitative analysis. The selection against banded patterns operated in a given ecological background, and the authors were able to point out the poor adaptiveness of the banded snakes in their habitat.

The fact that there is no apparent selection against color variability in Pelamis has also to be reviewed against the ecological background of the species. To a visual predator Pelamis may appear first as an array of contrasting black and yellow surfaces. It is possible that any black and yellow combination acts aposematically and that there is no selection for one particular pattern.

B. Other variations

Studies of several reptile populations have shown that as juveniles the degree of variability in a given population is reduced due to selection. Inger (1943), Hecht (1952), and Camin and Ehrlich (1958) were able to point out the importance of the characters which were selected for to the survival of the animals studied. Dunn (1942) found almost a universal tendency in snake populations for decrease in scale variability with age.

Pelamis also exhibits variations in head scales and for that reason I decided to compare the variability of six head scale characters in young and adults. In the category of "young" were included snakes up to 350 mm total length. As shown in Table 10 significant differences were found between males and females, both among adults and young Pelamis. But no significant differences were found within each sex group between young and adults (Table 16). Similarly, no significant difference was found between vertebral numbers of young and adult Pelamis.

The scale characters, as pointed out by Dunn (1942), may not be the ones selected but merely serve as external, visible "markers" that there was or was not selective elimination of individuals from the population. These characters may be accompanied by more important, invisible ones.

The question to be asked is why is Pelamis not differentially selected for reduction of variability as many terrestrial snakes are? The answer to this question must deal with the different environmental pressures in the terrestrial and oceanic habitats. Both Inger (1943) and Hecht (1952) showed that decrease in variability was involved in selection for some functional character (body size or vertebral number) important for survival. For example, selection favored those individuals whose vertebral numbers were optimal for locomotion (Inger, 1943). Perhaps locomotion in the ocean puts less of a demand on Pelamis for a narrow vertebral range, and thus the variability at birth is retained. Similarly, the pressures involved in reducing scale variability on land are not known; they may be related to feeding or other functions involving the kinetics of the cephalic region, or they may be operating on other characters altogether. At any rate, these pressures probably do not operate on Pelamis in their marine habitat.

In summary, it appears that Pelamis, at least in the Gulf of

Panama, maintains the variability which does not change in the population as the animals age. This variability may be one more reason for the success of the species as a colonizer of new areas (see conclusions, next chapter). It would be interesting, however, to compare the variability of Pelamis in the Eastern Pacific with that of populations in the Western Pacific and the Indian Ocean, where other sea-snake species exist. The absence of competition (if it indeed exists in the oceanic habitat in the same sense as on land) and predation may also be responsible for the maintenance of high variability in the species.

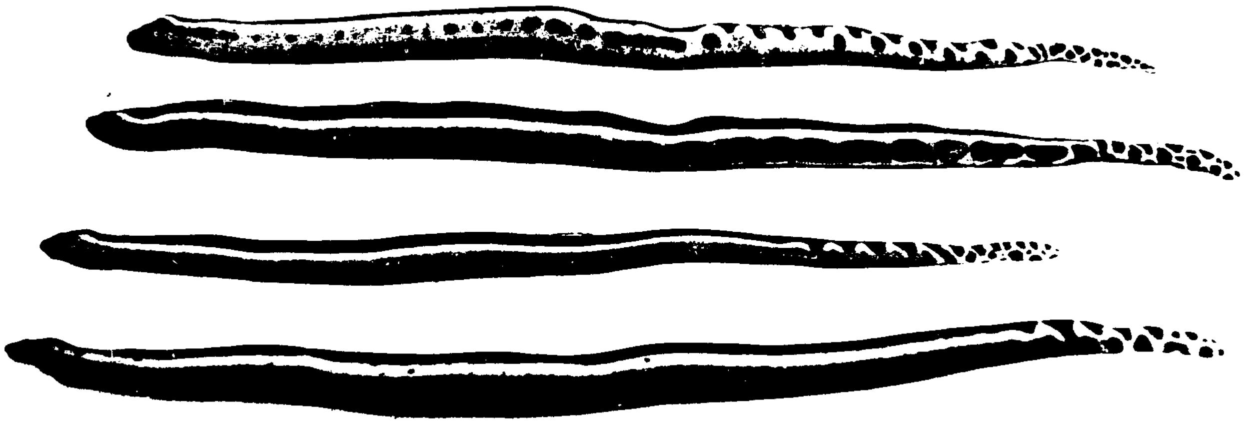


Plate 8. Some of the color varieties of Pelamis platurus from the Gulf of Panama.

Table 16. Comparison of variability in head scales between young and adult *Pelamis*. N = sample size; $\bar{X}$ = mean; S = standard deviation; CV = coefficient of variation; $S_{\bar{X}}$ = standard error; Y = young; A = adults; M = males; F = females.

character	N	$\bar{X}$	S	CV	$S_{\bar{X}}$
upper labials	53 YM	8.20	.72	.088	.084
	77 AM	8.12	.74	.090	.060
	52 YF	8.40	.73	.087	.072
	74 AF	8.36	.84	.101	.069
lower labials	53 YM	11.09	.86	.078	.100
	77 AM	11.22	.83	.074	.067
	52 YF	11.26	1.01	.089	.099
	74 AF	11.43	.92	.080	.076
preorbitals	53 YM	1.05	.23	.216	.026
	77 AM	1.05	.24	.228	.019
	52 YF	1.18	.41	.349	.040
	74 AF	1.16	.37	.318	.030
postorbitals	53 YM	2.07	.25	.122	.029
	77 AM	2.06	.37	.178	.029
	52 YF	1.90	.41	.214	.040
	74 AF	1.97	.41	.209	.034
anterior temporals	53 YM	2.57	.58	.225	.068
	77 AM	2.62	.59	.224	.047
	54 YF	2.60	.57	.219	.057
	74 AF	2.71	.60	.221	.049

CONCLUSIONS

A field study which is conducted on a species for the first time is burdened by many problems which can be avoided in subsequent studies. But this more than balanced by the opportuntiy of being among the first observers and of revealing new facts about the organism studied. Not all these facts are of equal interest. The finding of a parasite or a peculiar disease, observation of a new color variety, additional knowledge of food habits, reproduction, or other aspects of the species' biology are all of interest, but each has only a minor value when it is viewed separately from the others. The information which I consider of much greater importance is that which helps in the understanding of the species strategy. It is based, much like a mosaic pattern, on putting together the knowledge derived from all observations and from the reports found in the literature.

Three important facts emerge from my study.

1) Pelamis platurus, a pelagic and presumably the most specialized sea-snake species, possesses several features which allow it to be a successful colonizing species. These features are:

a. Complete independence from land by becoming ovoviviparous, and by being surface feeders. If deep water has indeed been a geographic barrier for sea snakes, it does not constitue a barrier for Pelamis.

b. The fact that Pelamis is a general feeder allows it to utilize any type of fish species of the right size. Specializing on certain food species has its advantages in the ability to compete with other species, but it also restricts the predator to the range of its prey.

c. *Pelamis* is apparently relatively predator-free. If a specialized predator occurs in the center of sea-snake distribution (Indo-Malayan Region), *Pelamis* seems to have extended its geographic range beyond that of its predators. Experiments show that when *Pelamis* reaches new areas it may initially be preyed upon heavily, but that selection against predation is intense. This selection may lead to evolution of predators which avoid *Pelamis* and allow the undisturbed growth of a population.

d. *Pelamis* is capable of utilizing surface currents. This allows them to arrive at food-rich areas with relatively little energy expenditure, to find mates, and ultimately to expand the species range. In fact, locality records of *Pelamis* suggest waif distribution in which snakes often arrive at areas not suitable for colonization. The disadvantage involved in this adaptation is the loss of individuals stranded on beaches, and perhaps occasionally in cold waters.

e. The variability found in a given cohort at birth is maintained as the cohort ages. The apparent lack of stabilizing selection helps maintain a rich gene pool and increase the chance of a successful colonization when a new area is reached.

f. *Pelamis* breeds over a wide period of the year, perhaps during the entire year. The species seems able to modify its reproductive pattern, again a trait with obvious advantages for potential colonization.

The properties possessed by *Pelamis*, mainly its versatility, as seen in its specialized adaptiveness for oceanic life yet generalized food requirements as far as food species are concerned, are reminiscent of the properties of effective colonizers given by Williams in his classical paper on the genus <u>Anolis</u> (Williams, 1969).

2) The poor recovery of marked individuals, the finding of only seven gravid females during the entire study, the possibility of snakes moving by currents to Mexico, and the direction of currents in the Gulf of Panama all indicate that the population of <u>Pelamis</u> in the Gulf of Panama may be a transient population. Snakes may be washed into the Gulf, reach its northern part, and then be carried outward by the currents.

3) The work on <u>Pelamis</u> <u>platurus</u> revealed some of the biological aspects of ocean slicks. The slick guild is a unique faunal association to which little or no attention has been paid by biologists. It plays an important role in the oceanic food web and species interactions. Another fact which I found interesting is that because of the vast differences between terrestrial habitats and the ocean, some biological concepts, such as competition and activity range, all first formed on and applied to terrestrial organisms, will have to be modified. For example, food along a slick appears to be plentiful, and although many species feed on similar food types it is questionable whether they really compete with each other. Another complex relationship is illustrated by the possibility that juvenile predators may be preyed upon by the species on which they feed as adults.

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