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Diet, Gastric evacuation, and daily ration of the gray smoothhound shark

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DIET, GASTRIC EVACUATION, AND DAILY RATION OF THE GRAY
SMOOTHFOUND SHARK.

A Thesis

Presented to

The Faculty of Moss Landing Marine Laboratories
San Jose State University

In Partial Fulfillment

of the

Requirements for the Degree

Master of Science

By

Richard A. San Filippo

May, 1996

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ABSTRACT

DIET, GASTRIC EVACUATION, AND DAILY RATION OF THE GRAY SMOOTHHOUND SHARK.

by Richard A. San Filippo

Stomach contents of 68 live gray smoothhound sharks were collected from the Elkhorn Slough National Estuarine Research Reserve using a stomach eversion technique.

Crabs were the dominant prey group with the yellow shore crab, *Hemigrapsus oregonensis*, being the dominant species.

Gastric evacuation was found to proceed in a slow but exponential manner and the gut emptied in about 95 hours at an experimental temperature of 15°C. The instantaneous rate of gastric evacuation was -0.04.

The change in caloric value of the meal with time suggests that higher energy components (i.e. muscle) are digested first, and lower energy components (i.e. exoskeleton) last. Fecal material contained no measurable caloric value.

No pattern in the diel feeding activity was found. Feeding in the population was asynchronous and intermittent.

Estimates of daily ration ranged from approximately 1.3 to 1.6% of the shark's wet body weight using four methods.

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INTRODUCTION

Gray smoothhound sharks (*Mustelus californicus*) are common coastal, temperate, bottom-dwelling sharks abundant seasonally in Elkhorn Slough and have frequently been observed in the marsh restoration area throughout the year. Their occurrence may be tied to seasonal events such as reproduction, increased availability of prey, water temperature and salinity, or day length.

Sharks are generally considered as apex predators in marine ecosystems, and thus, may regulate their prey assemblages and may also impact other species competing for the same prey. To understand the influence of this animal as a predator, its feeding habits and food consumption potential, should be evaluated.

Knowledge of the energetic requirements of a particular consumer, enables evaluation of the importance of its primary prey species in terms of energy transfer between consumer and prey. Bioenergetics models that estimate energy transfer among trophic levels can be used to infer ecological relationships. Few data on shark bioenergetics are available. The scarcity of studies on shark consumption rates is related to the difficulty maintaining these animals in captivity (Gruber, 1980), and need for standardized measurements of growth, metabolism, digestion, and excretion (Mann, 1978). The only integrated budget was reported by Gruber (1984) for the lemon shark, *Negaprion brevirostris*.

Direct estimation of daily consumption (C_t) by sharks in the field is often derived from the quantity of food found in stomachs of fish sampled at regular intervals over a 24 h. period. Indirect methods employ bioenergetic models that estimate the amount of food required to meet energetic demands of growth and metabolism.

The major objective of this study was to use field and laboratory techniques to identify diet, daily food intake, rates of food passage, and energy content of prey of the gray smoothhound. The goal was to understand the influence of the gray smoothhound as a top carnivore in Elkhorn Slough National Estuarine Research Reserve.

MATERIALS AND METHODS

STUDY SITE

The Elkhorn Slough National Estuarine Research Reserve (ESNERR) is part of 1,510 acres of uplands and wetlands acquired by the Wildlife Conservation Board (WCB) and managed by the California Department of Fish and Game. The objectives of the WCB were to provide a "living laboratory" for research and education of habitats and biotic communities within the slough system. The sanctuary is made up of marine marshes and tidal creeks for invertebrates, fishes and birds.

The ESNERR is connected to Elkhorn Slough, which opens to the sea some five miles away (Figure 1). Access to the ESNERR is restricted to tidal creeks and channels except

during extreme high tides that cover the salt marsh. The ESNERR consists primarily of restored salt marsh wetlands formerly used as pasture land.

FIELD STUDIES

Areas of high gray smoothhound abundance and easy accessibility for sampling were identified by visual surveys on foot and by boat. Six weekly observations of 2 to 3.5 hours duration were conducted between April and May 1990 on high and low tides during daylight hours. Four areas, including shallow coves (0.6-1.2 m deep) with gently sloping shores and deeper main channels (0.9-1.8 m) with steeply sloped banks, were chosen as primary sampling sites (Figure 2).

Gray smoothhounds were sampled in these 4 areas within the ESNERR several days a month throughout a 24-hour period from July 1990 to August 1992. Sharks were captured using a 30 m, 1.25 cm stretch mesh beach seine deployed from boat or land. Each shark was weighed (± 0.25 kg), measured (TL to nearest mm), sex determined, and marked or tagged. Location of capture (cove or channel) for all species of elasmobranchs, and catch per unit effort for gray smoothhounds, were recorded throughout the study. Sharks were marked with color-coded disk tags secured into the first dorsal fin (n=42), floy tags (n=12), or a hole punched through the first dorsal fin (n=136).

A subsample of all sharks captured were anesthetized in a rectangular container filled with approximately 40 L of water and 10 ml of quinaldine or 2 grams of MS 222. Once anesthetized, the shark's stomach was everted using large forceps by positioning the shark vertically (snout down over a collecting tray) and everting the stomach. After collecting prey items, the stomach was returned to its normal position and the shark released. The technique was evaluated from repeated (biweekly) use on captive sharks, which showed no loss of appetite, and no behavioral changes indicating few or no ill effects by this technique. Date, time of day, location, and state of digestion of stomach contents at the time of collection were recorded.

LABORATORY ANALYSIS

Stomach contents were identified to the lowest possible taxon. Because crab parts were difficult to separate into different species, all species were lumped as "crabs" for calculations of volumetric dietary importance. For numerical importance, crabs were easily delineated by the presence of identifiable carapaces and were separated by species. It was not possible to identify bivalve taxa because only the tips of siphons were found in stomachs, and were labeled "clam siphons."

All food items were weighed to the nearest 0.1 g, after removing excess water by blotting with a paper towel. Volume of each prey type was determined to the nearest ml by water

displacement in a graduated cylinder. Widths of crab carapaces were measured to the nearest millimeter when possible.

The contribution of various prey items was assessed by:

- 1) numerical importance (%N), number of each prey item found in the stomach expressed as a percentage of the total number of prey items;
- 2) frequency of occurrence (%FO), ratio of stomachs containing a particular prey to total number of stomachs containing prey, expressed as a percentage;
- 3) volume and wet weight (%V, %W) of a prey category compared to the total volume or weight of all stomach contents, expressed as a percentage; and
- 4) index of relative importance (IRI) (Pinkas et al., 1971), calculated as:

$$IRI = (\%N + \%V) * (\%F) .$$

For each stomach examined, a fullness and recency index was assigned. An arbitrary state-of-digestion value (recency index) ranging from 1 to 4 was assigned to each gut with 1 being the most recent and 4 least recent. A value of 1 was given when an estimated 100 to 75% of the contents by volume were fresh, 2 when 75 to 50% was fresh, 3 when 50 to 25% was fresh, and 4 when 25% or less was fresh. Items were considered fresh if the entire body of the crab was intact and little if any discoloration of the carapace was noticeable.

Assuming sharks of different sizes have different stomach capacities, a relative fullness value was determined

for sharks in 100 mm length classes. Recency of feeding, however, was assumed to be independent of size; therefore, absolute recency values were assigned. Maximum fullness was the largest volume of prey found within each length class, and were assigned a numerical value of 4. Stomachs containing ≤ 75 , ≤ 50 , and $\leq 25\%$ of the highest values were assigned 3, 2, and 1, respectively. Empty stomachs received a value of 0. In cases where the maximum prey volume found in the stomach in a certain size class of fishes did not meet or exceed the maximum volume found in the next smaller size class, the larger of the two volumes was used to assign the relative fullness index. An index combining stage-of-digestion values and fullness (recency/fullness index) was assigned to each stomach and evaluated with time of collection to determine periodicity of feeding. These values ranged from 1 to 4, and were arranged as a matrix (Cailliet and Ebeling, 1990).

Feeding periodicity was estimated using condition of prey items and fullness of stomachs at time intervals throughout the day and by comparing the amount of food in guts (mean percent body weight) with collection times. Periods of greatest feeding were those with the highest percentage of recency indices (index 2 and 3) (Kruskall-Wallis test, Sokal and Rohlf, 1981) or periods in which significant differences in mean amounts of food were found (Kruskall-Wallis test).

DAILY RATION

Four models, the Elliott and Persson (1978), Thorpe (1977), Winberg (1956) and an empirical model based solely on field stomach contents, were used to estimate daily ration in the gray smoothhound (Table 1). For the Thorpe (1977), and Elliott and Persson (1978) models, mean wet weight of stomach contents (expressed as percentage of wet shark weight) for each 3 hr. time interval, were used as values of S_t . S_o values were back-calculated by applying the exponential gastric evacuation equation to the S_t values. These values were then substituted in each model to calculate consumption rate (C_t) for each three hour interval and summed to estimate the amount consumed over all intervals (Table 1). Estimates of metabolism were unavailable for gray smoothhounds and was substituted using leopard sharks (*Triakis semifasciata*, Scharold et al., 1989). Estimates of growth were from Yudin and Cailliet (1990).

All estimates of daily ration , except those from the bioenergetics model, are based on an eighteen hour period between 0600 and 2400 h. No sharks were found in the study areas between 2400-0600 h and it is assumed that they were not feeding in these areas. Daily ration estimates were therefore site-specific and only for the hours in which stomach samples were taken.

GASTRIC EVACUATION

Gastric evacuation of 4 gray smoothhounds, 915 to 953 mm TL (mean = 935.8 mm) and 2160 g to 3100 g (mean = 2565 g) was studied in a 6700 L, flow-through, circular tank (3 m diameter x 1 m depth) maintained outdoors (natural photoperiod). Temperature fluctuated between 14° and 17° C (mean = 15.5° C) during the eight month period. The tank measured approximately 3 m in diameter and 1 m in depth. Before being released into the experimental tank, sharks captured in the ESNERR were measured (mm TL), weighed (± 0.1 Kg), sex determined, and were marked by punching small holes in the dorsal fin for visual identification. Sharks were acclimated and allowed to evacuate all gut contents for a minimum of two weeks prior to experimental trials.

Once sharks accepted food voluntarily, each animal was fed a pre-weighed meal of shore crab (*Pachygrapsus crassipes*.) Crabs were collected the day before each experiment and held in small aquaria. On the day of an experiment, crabs were immobilized by poking one to three small holes along the carapace, weighed, and placed in a box divided into numbered compartments.

Crabs were placed in the tank one or two at a time, and the shark which consumed them noted. This continued until each shark fed to satiation. Ration levels ranged from 1.0-4.8% BW (mean $2.2 \pm 0.8\%$ SE). All experiments began between 1200 and 1300 hr.

At prescribed times after feeding (between 6 and 95 hr.), sharks were removed from the tank, lightly anesthetized with quinaldine or MS-222, and the remaining food removed by everting the stomach with a pair of forceps. Individual sharks were used repeatedly in this study, and allowed a two week recovery period between experiments. Between experiments sharks were fed *ad libitum* for one week, then starved for one week to allow all food present in the gut to be evacuated.

Wet and dry weights of recovered contents were measured to the nearest 0.1 g. Samples were dried at 60° C until a constant weight was achieved. Percentage of food remaining in each stomach was determined by dividing the dry weight of food remaining by the initial dry weight and multiplying by 100. Dry weights were estimated using the following equation:

$$Y = -0.06791 + 0.40086X \quad (r^2 = 0.91)$$

where X is the wet weight of the meal. This equation was obtained by least squares regression of wet weight against dry weight for a sample of 40 crabs (*Pachygrapsus crassipes*).

Fecal samples were collected by carefully siphoning the bottom of the tank, dried, and stored in a desiccator for caloric evaluation.

Linear, exponential, and logistic functions were used to describe the relationship between percentage of food remaining in the stomach and time after feeding (Table 2).

The curve which produced the best fit was used to estimate the rate of gastric evacuation (R). The program FISHPARM was used to obtain estimates of the parameters of the non-linear models. Exponential and logistic functions were transformed to linear form and then a least squares regression performed. The coefficient of variation (CV) of residuals was chosen as the measure of goodness-of-fit, with CV expressed as:

$$CV = \frac{\sqrt{\frac{RSS}{N-K}}}{\bar{Y}}$$

where RSS is the residual sum of squares, N is the number of data values, K is the number of parameters in the model, and Y is the mean of the dependent variable (percentage of food remaining). A smaller value of CV indicates a better fit. Predicted values of Y at X = 0, (initial meal size), given by the three mathematical expressions, and an examination of the ANOVA table for each regression were used as additional measures of goodness-of-fit.

CALORIMETRY

Samples of stomach contents from randomly-selected sharks were evaluated for caloric value as evacuation proceeded. Caloric content (calories per gram) of the recovered meal, using 3 to 5, 0.2-0.3 g pellets (dry weight, weighed to the nearest 0.1 mg), from each time period was measured using a Parr Semimicro oxygen bomb calorimeter Model

1411, following standard methods (Parr Instrument Company). Caloric content in calories of an experimental meal was calculated for each time period by multiplying calories per gram of the meal by mean meal size (gm.) for that time period. Fecal samples collected in the tank after a meal were also evaluated for caloric value. To determine if meal absorption was different in the laboratory and field, four fresh fecal samples were collected one afternoon from different exposed mud flats in the study area by carefully lifting the entire fecal pellet from the substrate and evaluating caloric content.

RESULTS

VISUAL OBSERVATIONS, CATCH COMPOSITION, TAGGING

Sharks were observed more frequently on low tides, and in the north part of the marsh (Figure 3). From July 1990 to September 1992, 337 sharks out of 415 elasmobranchs were captured in the ESNERR. Of six elasmobranch species found, the gray smoothhound, *Mustelus californicus*, was the dominant species (312 ind.) The bat ray, *Myliobatis californica*, was the second most numerous elasmobranch captured (63) followed by the leopard shark, *Triakis semifasciata* (25), the shovelnose guitarfish, *Rhinobatos productus* (20), the thornback, *Platyrrhinoidis triseriata* (11), and the round stingray, *Urolophus halleri* (2).

No statistically significant seasonal periodicity was found in beach seine catch rates of gray smoothhounds

(Single-Factor ANOVA, $p > 0.75$; Sokal and Rohlf, 1981) . Catch rates were lowest in late fall and winter months (Figure 4). No sampling occurred during December and January because of low catch rates during late Fall 1991 (e.g. only 6 sharks were captured in the last 22 sets spanning from late August, 1991 to mid-October, 1991 and no sharks were captured in the last 18 sets in September-October 1991), and because the study was ended prior to those months in 1992. The months February through May were sampled only in 1991.

Catch rates for gray smoothhounds were not significantly different among times of day (Kruskall-Wallis test, $P > 0.25$). They were however greatest between 0600-1200 h (Figure 5). The fewest number of sharks were captured between 1800-2400 h.

Sharks were captured more frequently in coves than in main channel areas but there was no statistically significant difference in mean catch rates between these areas. (Kruskall-Wallis test, $P > 0.25$,). While catch rates for shovelnose guitarfish and bat rays were divided equally among the two habitats, all of the round stingrays were captured in main channel areas (Table 3).

A polymodal size frequency distribution was found for gray smoothhounds collected over the duration of the study (Figure 6). Thirty-two gray smoothhounds were thought to be Young-of-the-Year (YOYs) based on their length (299-454 mm

Compagno, 1984; Yudin and Cailliet, 1990) and presence of an umbilical scar and were captured from June to September.

Mean size of YOYs per month captured appeared to increase from June to September (Figure 7). Mean length increased approximately 17 mm between months. Excluding YOYs, females outnumbered males 2.7 to 1 and were larger (females: 932 ± 16.9 mm (SE); males: 686 ± 26.8 mm).

Of 190 tagged sharks, five were recaptured or resighted, three in 1990 and two in 1991. Two sharks tagged on July 24, 1990 at the deadfall were recaptured on August 3 and 5 of the same year near the boat dock (Figure 2). A third shark tagged on July 28, 1990 at the deadfall was resighted just outside the entrance to the ESNERR in Elkhorn Slough 100 days later. Two additional sharks were recaptured at CIMC, but no longer retained tags. They were identified as tagged sharks by a characteristic scar on the first dorsal fin. No sharks tagged in 1991 or 1992 were recaptured or resighted.

DIET

Stomachs of the 75 gray smoothhounds collected in all seasons, 70 contained identifiable material and 4 were empty (Figure 8). Gray smoothhounds fed almost entirely on crabs in the ESNERR (IRI of 19,659). Several crab species were eaten but the yellow shore crab, *Hemigrapsus oregonensis*, was the most abundant prey. *Cancer* sp. was the second most common prey, followed by market squid, *Loligo* sp., clam siphons, mole crabs, *Emerita analoga*, and inkeeper worms,

Urechis caupo (Table 4). Of three genera of crabs eaten, 89.9% were *Hemigrapsus oregonensis*, 9.3% *Cancer* sp., and 0.9% *Pachygrapsus crassipes*.

Forty sharks contained measurable crab carapaces (56% of total stomachs). Thirty contained measurable carapaces of *Hemigrapsus oregonensis*. Size of consumed *Hemigrapsus oregonensis* varied little and had a mean size (14.8 ± 0.19 mm SE). From 1 to 57 *Hemigrapsus oregonensis* carapaces were measured from each stomach. Two stomachs (5%) contained measurable carapaces of *Pachygrapsus*. Ten stomachs (25%) contained measurable carapaces of *Cancer* sp. The mean length of *Cancer* sp. crabs was 40.4 mm (± 4.7 SE). In 10% of the cases, only claws or pieces of carapace were found in the stomachs. There was no relationship between length of shark and size of *Hemigrapsus oregonensis* eaten. However, there was a weak, positive relationship between the size of sharks and *Cancer* spp. eaten ($r^2 = 0.367$; Figure 9).

FOOD CONSUMPTION

Stomachs of field caught sharks contained an average of $1.1 \pm 0.1\%$ (SE) of each shark's body weight for sharks less than 1000 mm TL and $1.3 \pm 0.2\%$ (SE) for sharks greater than 1000 mm (Table 5). Mean amount of ingested food varied with length of shark due to increasing stomach capacities with length of shark. Mean percent body weight (%bw) eaten, however, remained relatively constant (Figure 10).

Fullness and recency values of the stomach contents varied with time of day but no significant diel periodicity was found (Kruskall-Wallis test, adj. H = 4.47, $P > 0.25$, $n = 70$). However a significant difference was found when comparing %bw of food eaten (Kruskall-Wallis test, adj.H = 14.35, $P < 0.025$, $n = 70$; Figure 11).

DAILY RATION

Mean amount of food consumed per day was estimated to be $1.57 \pm 0.57\%$ BW (Elliott and Persson), $1.53 \pm 0.55\%$ BW (Thorpe), 1.53% (Winberg) and $1.32 \pm 0.18\%$ BW (non-model technique; Table 1). The Elliott and Persson and Thorpe models use mean amount of food consumed during the sampling interval minus whatever was lost through digestion to estimate amount consumed throughout the entire period (daily consumption). The Winberg model estimates daily consumption by calculating the amount of energy required (obtained from prey) by the shark for growth and metabolism. The non-model technique sums the mean amount of food in guts over the sampling periods and has no factor accounting for digestion.

GASTRIC EVACUATION

The exponential function: $Y = 100.56e^{-0.04t}$, best described the gastric evacuation for gray smoothhounds in this study (Figure 12; $R^2 = 0.95$;))

The linear model produced the worst fit to the gastric evacuation data as shown by the high CV value of 0.2087 and lowest proportion of the sum of squares explained by

regression ($SS_{\text{reg}} = 85.1\%$) (Table 2). The estimated Y-intercept (93.74 %) was somewhat lower than the initial meal size indicating that the linear model underestimates the amount of food remaining in the stomach in the early hours after feeding. The CV for the logistic function was considerably lower than that of the linear function (0.000346, $SS_{\text{reg}} = 94.6\%$) and had a closer estimate of the Y-intercept (100.89) making it a better fit of the gastric evacuation data. The exponential function has the lowest CV value (0.000012), the highest proportion of the sum of squares explained by regression ($SS_{\text{reg}} = 100\%$) and a Y-intercept estimate very close to the experimental value (100.56).

Qualitative descriptions of experimental meals as evacuation proceeded indicated that digestive indices were meaningful (Table 6). Digestive index 1 represents 24 hours of digestion with little change in the experimental meal. Digestive index 2 represents 32 hours of digestion: the limbs become separated from the main body, color loss occurs, the eyes are digested, there is a softening of the exoskeleton, and some of the flesh is being removed from within the exoskeleton. After 64 hours of digestion (Digestive index 3), the main body of the crabs were broken and reduced to mush, most of the legs were reduced to individual segments, and most of the flesh was removed from within the exoskeleton. Remaining pieces of exoskeleton were

nearly without color and appeared translucent, and were soft and pliable. Digestive index 4 represents 95 hours of digestion. By this time nearly the entire exoskeleton was reduced to mush including the main body, all flesh was removed and any exoskeleton remaining consisted of thin, small pieces that were transparent and pliable.

BOMB CALORIMETRY

The mean caloric value of the starting meal (whole specimens of shore crab) was 2908 cal/g dry weight. Changes in the caloric value of ingested meals (cal/g) increased as evacuation proceeded, peaking at 4378 cal/g after 80 h. The final value of 4218 cal/g after 95 h, approached the caloric value of pure carbohydrate of 4100 cal/g. (Figure 13). At this point 90% of the initial meal by weight had been evacuated.

The mean total caloric content of experimental meals (total calories) decreased as evacuation proceeded (Figure 14). Mean total caloric content in initial meals was about 52 Kcal. The caloric content decreased in an exponential manner (as did prey biomass) and after 80 hours had decreased to around 4 Kcal. Most of the changes in caloric value had taken place within the first 30 hours of evacuation. Fecal material contained no measurable caloric value, indicating all nutritional value had been adsorbed.

DISCUSSION

SPECIES CATCH COMPOSITION, TAGGING AND MOVEMENTS

Gray smoothhound sharks were the most abundant and commonly found elasmobranchs in this study. It is not apparent whether this is indicative of their relative abundance's or biases in sampling methods. Beach seines were often set in areas where sharks were seen swimming in shallow water therefore biasing estimates of density.

Most smoothhounds captured were of adult size and reproductively mature with a number of females containing active embryos *in utero*. This, coupled with the appearance of YOY sharks in net samples starting in June, supports the idea the ESNERR serves as a nursery ground for a variety of fishes in general (Antrim, 1981; Barry, 1983; Talent, 1985).

This area may also serve as a food resource for all age classes of gray smoothhounds. Nursery areas typically provide an adequate food supply to support its inhabitants (Antrim, 1981; Odum and Heald, 1975; Dando, 1984). Recruitment of *Hemigrapsus* crabs occurs in estuaries in spring and summer months (Hsueh, 1988, Sliger, 1982; Willason, 1981) the shark's primary prey item. Ten additional YOY sharks captured in Elkhorn Slough, outside the study area, also had eaten *Hemigrapsus* crabs (San Filippo, pers. data).

Tagging produced little helpful information. One objective was to determine if the population in the ESNERR was closed. In the first year only three sharks were recaptured or resighted and it appeared that the population was quite large, or that immigration and emigration was occurring.

The only evidence of a shark returning in another year occurred in 1991 when two tagged sharks were recaptured in the ESNERR bearing scars from tagging in 1990. Tag return data revealed that the sharks were present during the pupping season, then leave the reserve. Sighting tagged sharks with groups of untagged sharks suggests they associate with different groups of sharks while in the reserve. Presently, estimation of population size is not possible.

While seasonal periodicity in catch rates was not found for the gray smoothhound in the ESNERR, seasonal changes in abundance were reported for this and other species of elasmobranchs in Elkhorn Slough (Talent, 1985). Detecting seasonal abundances was not an objective in this study as it was in Talent's (1985) study, therefore sampling was not designed to test for it. In addition, Talent admits that information he obtained in the summer months was limited because green algae fouled his nets preventing capture of elasmobranchs.

DIET AND FOOD HABITS

While the total number of prey taxa of the gray smoothhound was near ten, all but crabs were of minor importance. *Hemigrapsus oregonensis* was the most common prey species consumed. *Hemigrapsus* sp. may dominate the smoothhound diet owing to high relative abundances, greater ease of capture, or smaller size.

Pachygrapsus crassipes was also abundant in the study area, yet were poorly represented in the diet. *P. crassipes* while overlapping the distribution of *H. oregonensis* along intertidal mud banks, generally occurs higher in the intertidal zone (Willason, 1981; Sliger, 1982) and is less available to smoothhounds. Although *H. oregonensis* take refuge in small, shallow burrows excavated throughout the intertidal, and in alga mats of *Ulva* and *Enteromorpha* in the lower intertidal (Sliger, 1982; pers observation), they are vulnerable to predation throughout the tidal cycle. Gray smoothhounds investigate mats of alga in the low intertidal and open areas along the water line in the proximity of *H. oregonensis* burrows (pers. observation). Therefore tidal level would only affect the availability of *Pachygrapsus*, and may explain the low occurrence of *Pachygrapsus* in the diet.

The size distribution of *H. oregonensis* taken by smoothhounds may represent the range of *H. oregonensis*

in the ESNERR or the preferred or vulnerable size classes. However, those eaten were similar in size to *Hemigrapsus* found in Goleta Slough, CA (Willason, 1981) and Yaquina Bay estuary, OR (Batie, 1982). Because *Hemigrapsus* do not reach a large size, sharks of all lengths are able to eat them.

Clam siphons were the most abundant non-crab prey, in terms of numerical importance and frequency of occurrence, but were found in only four stomachs that contained food items. Talent (1982) did not find clam siphons in the gray smoothhound's diet in Elkhorn Slough. Although clams with exposed siphons (*Tresus* sp. and *Zirfaea* sp.) occur in both Elkhorn Slough and the ESNERR (Rikk Kvitek, pers. comm.) they were not found in the stomachs sampled. Clam siphons, along with other soft-bodied benthic infauna and epifauna, were also uncommon in smoothhound's diet in San Francisco Bay estuarine habitats (Compagno, 1984). Additionally, smoothhound dentition is molariform and asymmetrical and not suited for siphon snipping, but is better adapted to crush rather than grasp prey (Compagno, 1984). Clam siphons may also be digested quickly and thus underrepresented in stomach samples.

There is evidence to suggest that some gray smoothhounds probably fed before their arrival and capture in the ESNERR. One prey taxon, *Emerita analoga*,

does not occur in Elkhorn Slough but is found on nearby wave swept sandy beaches. Another prey, *Urechis caupo*, is not known to occur in the ESNEER but are abundant on muddy sand beaches (Morris et al, 1980) at the mouth of Elkhorn Slough. The shallow, inshore, muddy sandy areas in Monterey Bay favor the presence of *Loligo* sp. in May and June (Morris et al., 1980) which coincides with their occurrence in the smoothhounds diet.

FOOD CONSUMPTION AND MEAL FREQUENCY

Feeding periodicity was not evident from analysis of gut fullness and recency indices. It was expected that peak fullness should follow peak recency if periodicity of feeding exists, which was not seen. Combining recency and fullness indices gave a single index to investigate periodicity of feeding. A recency/fullness index of 2-3 (recent but not full becoming recent and full) should have indicated peak feeding. No such distribution of indices was found.

Statistical tests show a significant increase in the weights of the stomach contents in the early evening however. But because of the relative indigestibility of crabs I do not believe a single measure of weight is adequate to detect periodicity accurately.

Continuous, or intermittent probably better describes gray smoothhound feeding. A continuously feeding shark's gut should contain numerous food items

at several stages of digestion and rarely be empty. In this study all stomachs with identifiable material contained three or more prey items representing two or more stages of digestion. The proportion of empty stomachs was also very low. The proportion of empty stomachs found in other shark species was generally greater (Strasburg, 1958; Stevens, 1976; Medved and Marshall, 1981; Stillwell and Kohler, 1982; Medved et al., 1985; Medved et al., 1988; Cortes and Gruber, 1990). Therefore it seems reasonable to assume feeding may be continuous. However, if sharks feed on small prey items (e.g. *Hemigrapsus* spp.) and have a long gastric evacuation time (95+ h is among the longest for any shark), then even an intermittent feeder would contain multiple food items at various stages of digestion.

Holden (1966) and Jones and Geen (1977) reported that the spiny dogfish, *Squalus acanthias*, ceases feeding until the previous meal has been completely digested. Similar behaviors were suggested for young sandbar (Medved et al., 1988) and lemon sharks (Cortes and Gruber, 1990). Although I was unable to determine meal frequency, the few empty stomachs, and few cases of all items being at a late stage of digestion (3%), suggests that gray smoothhounds do not cease feeding before taking a new meal.

There are no studies documenting the diurnal activity patterns of the gray smoothhound. The available literature states that their primary prey are more active at night, leaving their burrows more frequently to forage. However, I have witnessed *Hemigrapsus* sp. out of their burrows at midday, and a number of midday stomach samples from gray smoothhounds were relatively full, indicating recent feeding and thus available prey. The high variability of food present in the stomachs at all sampling times suggests a lack of diel feeding patterns. However, the small sample size for late night and early morning periods prevent strong conclusions about nighttime feeding activity.

DAILY RATION

Estimates of daily ration ranged from 1.32% BW to 1.57% BW. The lower value associated with the non-model estimate (Table 1) is expected since there is no factor accounting for the digestion of the food present between sampling periods. Therefore the amount in the stomach is underestimated and consequently so is the daily ration.

The bioenergetics approach (Winberg, 1956) yielded a similar estimate of daily ration to the other two models. Knowledge of growth and metabolism of the shark is required for use of the Winberg equation. Reliable growth estimates of the gray smoothhound were provided

from Yudin and Cailliet (1990), but no value for its metabolic rate was available. Therefore the metabolic rate of a closely related species, the leopard shark, *Triakis semifasciata*, was substituted (Scharold et al., 1989). Both species have similar life histories, and occupy bays and estuaries for a portion of their life, but differ in growth rate (Yudin and Cailliet, 1990; Kusher et al., 1992).

For the purpose of determining daily ration a value of routine metabolic expenditure was needed that simulated routine activity exhibited by the sharks in search of food. The daily ration estimate is directly proportional to the metabolic expenditure value chosen. A value of 37.2 Kcal/day was chosen and corresponds to a swimming speed of about 0.7 body lengths/sec. This value taken from Scharold et al. (1989) seems reasonable based on field observations of gray smoothhound activity (pers. obs.).

The bioenergetics approach has also been used for the lemon shark (Cortes and Gruber, 1990; Cortes and Gruber, 1992) and the sandbar shark (Medved et al., 1984) with varying success. In the latter case the metabolic rate was based on that of two similar species, the spiny dogfish and the lemon shark, resulting in the highest of three estimates using three different

methods. The estimate for the lemon shark agreed well with other independent measurements of daily ration.

The Elliott and Persson (1978) and Thorpe (1977) models used in this study assume constant feeding and an exponential rate of gastric evacuation. It is difficult to evaluate if the assumption of constant feeding is violated. If long periods of feeding do occur, the assumption is satisfied, however long intervals between meals may violate the assumption. Elliott and Persson (1978) indicate that when feeding is not continuous their model will produce a biased estimate of daily ration. However, studies comparing estimates based on this model with data on the actual food intake of fishes in the laboratory indicate that the error is generally small ($< 10\%$) if the interval between samples is kept short (< 3 h; Elliott and Persson, 1978; Persson, 1982). The evacuation of large, nutrient-rich prey items tends to follow a linear function and that of small more easily digested prey follow a Gompertz, logistic, or exponential one (Jobling, 1981). Almost all prey found in stomachs of smoothhounds were small, with relatively low caloric values, supporting an exponential rate of evacuation.

When considering all assumptions of the model and uncertainties in parameter estimates, it is apparent that none of the methods are perfectly suited for

estimating daily ration of gray smoothhound sharks. However, since most of the assumptions are somewhat satisfied and the fact that the estimates fall in a narrow range using all of the different models, suggests that the true value is not much different.

The estimated daily ration values found in this study fall within the range of values found for other sharks. Jones and Geen (1977) reported values between 0.5% BW and 1.4% BW for the spiny dogfish at 10° C and this is consistent with the slow metabolism, low growth rate, and lengthy gastric evacuation time of this shark. Kohler (1987) reported a mean value of 0.56% BW for the blue shark, *Prionace glauca*. Stillwell and Kohler (1982), found that the highly active, relatively fast growing (Pratt and Casey, 1983) shortfin mako shark, *Isurus oxyrinchus*, needed a daily ration of 3.2% BW to meet its energetic demands. This is consistent with the life history characteristics of lamnid sharks and other fast-swimming, active teleosts like tunas and billfishes, which maintain temperatures above ambient water temperature (Carey and Teal, 1969). This capacity to retain metabolic heat probably speeds up digestion and creates a greater demand for food uptake.

Medved et al. (1988) estimated the daily ration of the sandbar shark at around 1% BW, whereas Cortes and Gruber (1990) reported a value between 1.56% BW and

2.16% BW, for the lemon shark. They accounted for the difference by the slightly faster growth rate of the lemon shark (Henningsen and Gruber, pers. com.), lower metabolic rate and energy requirements of the sandbar shark, differences in ambient water temperature, and energy value of food consumed by both species. The gray smoothhound, by comparison, falls in the middle range of values reported by other studies.

GASTRIC EVACUATION

Examination of coefficients of variation, predicted initial meal sizes, and the proportion of the sum of squares explained by the regressions, indicates that the rate of gastric emptying is best described by the exponential model. Several factors are known to influence the rate of gastric emptying and must be considered when picking an evacuation model.

Increased temperature increases the rate at which food is evacuated from the gut of fish (Brett and Higgs, 1970; Tyler, 1970). However, temperature tends to lose its influence when approaching the thermal tolerance of a species (Molnár and Tölg, 1962a; Jobling and Davies, 1979). In this study, temperature could not be controlled but fluctuated only ~3°C throughout the experiment. It is doubtful that this small change in temperature had an important effect on rates of evacuation. Temperature changes of at least 4°C were

needed to change digestion rate in largemouth bass (Markus, 1932) and brook trout (Baldwin, 1957).

Both the amount of food and the process by which it is evacuated from the gut are affected by long periods (> 7 days) of food deprivation before feeding of the experimental meal (Windell, 1967; Elliott, 1972; Griffiths, 1976). Sharks used in this study were allowed 120 hours to completely empty their gut before being fed an experimental meal. The effect of this on gastric emptying is unknown but could be considered a factor on the total gastric evacuation time (TGET).

Shark size and meal type were nearly constant, and could not be considered a factor in affecting the TGET. Meal size, however, did vary and may affect (Hunt, 1960; Swenson and Smith, 1973) or not affect (Jobling and Davies, 1979) TGET. The time taken to evacuate the food from the stomach must be equal for all sizes of meal if one is fitting an exponential model to the gastric emptying curve (Jobling, 1981). If a volume-dependent model is fit to the data then one might expect an effect on TGET with differing meal sizes (Elliott, 1972; Swenson and Smith, 1973).

Jobling's (1981) review of the literature found that particle surface area is of minor importance in determining gastric emptying. However, his detailed analysis of the data, in the papers he reviewed,

apparently were not good tests of the effects of particle size on evacuation time. In cases where meals consisted of single particles of gradually increasing weight (Swenson and Smith, 1973), the surface area of a single meal will increase in proportion to its weight by a factor of 0.67. When meal sizes are increased by adding more food particles of more or less uniform size, as in this study, then surface area of the meal increased in proportion to meal size by a factor of 1.0. Therefore, the surface area is expected to have little or no influence on gastric evacuation time.

Increased volume of the ingested meal, on the other hand, is thought the most important factor determining shape of the gastric emptying curve. In this case, larger meals were associated with an increase in volume and may account for some variation in evacuation times of the various meals at specific times after ingestion. However, a plot of the residuals against meal size indicated little or no variation was associated with increased meal size. Therefore, I am confident that the exponential model, despite the different meal sizes, best represented gastric evacuation of gray smoothhounds.

BOMB CALORIMETRY

While many authors place great emphasis on the shape of the gastric evacuation curve and TGET, perhaps

a better indicator of a shark's digestive process is the change in energy content of its prey over time. In other words, it is not necessarily the total time taken to evacuate its gut that is important but the time to absorb the usable energy of the food. This study indicated that for gray smoothhounds, most energy is absorbed within the first third of its TGET. Very little change in caloric content occurs after this period. This suggests a rapid absorption of the high energy components and a slow break down of the lower energy components. The high energy protein in crab flesh is removed rapidly and the lower energy, harder to digest exoskeleton, is broken down slowly and passed to the intestine where maximum extraction of nutrients can take place. This is supported by the observation that very little morphological change occurs with a major change in caloric value.

ECOLOGICAL IMPLICATIONS

The ecology of the gray smoothhound in the ESNERR is one that involves a relatively safe, food rich, environment for the young and adults. The primary prey species appears to be in great abundance and based on the daily ration estimates and mean weight of crabs consumed may provide an average of 17.0 Kg of prey biomass per shark per year, while providing food for the young of the species and perhaps other predators as

well. Processes governing digestion in the gray smoothhound make it an efficient predator, losing almost nothing of its prey to the environment. The ESNERR may well be an important refuge as a nursery ground and food resource to the gray smoothhounds of Monterey Bay.

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Table 1. Models used to estimate daily ration in the gray smoothhound shark. Values are means $\pm$ 1 SE. Elliott and Persson (E&P), Thorpe (Th), Winberg (Wn), Field stomach contents (Fsc).

Method	Equation for estimating daily ration ^a	DR (n=69) $\pm$ SE*
E&P (1978)	$C_t = (S_t - S_o e^{-Rt}) Rt / 1 - e^{-Rt}$ DR = Sum of C_t	1.57 $\pm$ 0.57
Th (1977)	$C_t = S_t - S_o + 1/2 (S_o + S_t) (1 - e^{-Rt})$	1.53 $\pm$ 0.55
Wn (1956)	DR = 1.25(G + M)	1.53
Fsc	NA	1.32 $\pm$ 0.18

^a C_t : consumption between sampling periods; S_t amount of food in stomach at the end of the interval between catches;
 S_o : amount of food in stomach at the beginning of the interval between catches;

R: exponential rate of gastric evacuation; DR: daily ration;

B: time of gastric evacuation; G: energy for growth;

M: laboratory derived metabolic rate.

* error based on minimum and maximum values of S_t and R_t

Table 2. Equations fitted to gastric evacuation data of gray smoothhound sharks and the goodness of fit values.

Model	General equation	CV	Y-Intercept	%SS _{reg}
Linear	$Y = A + BX$	0.208700	93.7	85.1
Logistic	$Y(t) = K / \{1 + [(K - Y_0) / Y_0] \exp(-rt)\}$	0.000346	100.9	94.6
Exponential	$Y(t) = Y_0 * \exp(-rt)$	<u>0.000012</u>	<u>100.6</u>	<u>100.0</u>

Y(t): Amount of food remaining in the stomach at time t; t: time after feeding

CV: Coefficient of variation of the residuals

SS_{reg}: Sum of squares explained by regression of Y(t) on t, expressed as a percentage of the total sum of squares. Best fit values are underlined.

Table 3. Total numbers, and mean numbers per seine caught in Main Channels and Coves throughout the study. N refers to the number of seines made in each area.

SPECIES	MAIN CHANNEL N=32 TOTAL	COVE N=33 TOTAL	MAIN CHANNEL MEAN±SD	COVE MEAN±SD
SHARKS	84	240	2.6±1.2	11.1±4.5
BAT RAYS	29	34	1.1±0.7	1.3±0.8
GUITARFISH	9	11	0.4±0.2	0.5±0.4
THORNBACKS	7	4	0.4±0.3	0.03±0.2
ROUND RAYS	2	0	0.04±0.05	0.0

Table 4. Relative Importance of the various food items found in the guts of gray smoothhound sharks. The numbers are means $\pm$ 1 SD. N=70

PREY	%V	%W	%N	%FO	IRI
Crabs	98.8 $\pm$ 4.1	98.9 $\pm$ 4.4	98.7 $\pm$ 4.1	100.0	19750.0
<i>Loligo opalescens</i>	9.4 $\pm$ 8.9	9.2 $\pm$ 9.0	7.4 $\pm$ 8.0	4.2	70.6
<i>Emerita</i>	4.9 $\pm$ 2.8	4.8 $\pm$ 2.2	12.5 $\pm$ 5.9	2.8	49.0
<i>Urechis</i>	17.9 $\pm$ 0.9	18.3 $\pm$ 0.4	13.4 $\pm$ 7.2	2.8	88.0
Clam siphons	2.7 $\pm$ 2.5	2.9 $\pm$ 0.3	11.9 $\pm$ 6.8	2.8	41.0

Table 5. Amount of food found in the guts of gray smooth-hounds in grams (g) and percent of live body weight (%BW) between 0600 and 2100 hrs. N=71.

(mm) Shark TL	Amount of Food in Gut (g)			Percentage of Live Body Weight (%BW)	
	range	n	mean±SE	range	mean±SE
500-599	5.6-16.8	4	9.3±2.6	0.9-4.7	2.0±0.9
600-699	-	1	12.4	-	1.1
700-799	4.7-18.9	4	12.2±3.4	0.3-1.2	0.78±0.22
800-899	4.4-34.2	10	19.0±3.0	0.2-1.5	0.91±0.13
900-999	4.0-74.9	16	32.2±5.3	0.1-2.6	1.12±0.18
1000-1099	6.2-162.9	23	44.9±8.1	0.2-4.1	1.22±0.21
1100-1199	3.4-162.5	6	57.4±22.6	0.08-3.9	1.35±0.53
1200-1299	13.0-262.3	6	73.7±47.4	0.3-5.4	1.53±0.08
1300+	-	1	53.3	-	0.9

Overall mean; sharks < 1000 mm TL - 1.1±0.1% BW (n=35)
> 1000 mm TL - 1.3±0.2% BW (n=34)

Table 6. Qualitative descriptions of crabs after various hours in the gut of gray smoothhound sharks. The recency indices 1-4 are shown along with the hours of digestion required to get to that stage.

Recency Index	Eyes	Gills	Flesh within exoskeleton	Exoskeleton	Pigment
1 (21.5 h)	Present, undigested	Present, undigested	Not digesting	Normal, intact, slime covered	Normal-reddish
2 (37.5 h)	Digesting or absent	Present, undigested	Present, digesting	Limbs separating	Reddish
3 (72 h)	Absent	Present, undigested	Mostly removed	Limbs separated, main body broken, mostly mush	Bleached and translucent
4 (95 h+)	Absent	Digesting or absent	Absent	Mush, some identifiable limb segments	Bleached, transparent

Figure 1. Elkhorn Slough National Estuarine Research Reserve
(ESNERR) relative to Elkhorn Slough and Monterey
Bay.

Figure 2. Main sampling areas in ESNERR and areas in which tagged sharks were recaptured by beach seine or resighted from shore or in a boat.: 1) Boat Dock Cove; 2) Deadfall; 3) CIMC; 4) LVC. Sites 1, 2 and 4 were designated as shallow water coves and site 3 as a main channel. While other catches were made south of CIMC in the main channel most of the data is from CIMC. Site 4 was sampled with a beach seine only in 1992 and only at night. Visual surveys were made throughout the study in all areas. T designates where the shark was tagged, R designates where the shark was recaptured or resighted.

Figure 3. Number of sharks seen per hour of observation during preliminary visual surveys. Each data point represent one day of surveying. Total number of sharks seen per day was divided by the number of hours observed. The mean time observed per day was 2.5 ± 0.5 h. Eight and one half hours of observation were at high tide, while 9 hours of observation were at low tide.

Figure 4. Mean catch per unit effort (± 1 SE) of gray smoothhound sharks throughout the study period. No sampling was done in January or December. N is the number of sets made in each season. One unit of effort equals one beach seine.

Figure 5. Mean catch per unit effort (± 1 SE) of gray smoothhound sharks during four six hour time intervals. N represents the number of sets made during that time interval. Data is from entire study period.

Figure 6. Length frequency distribution for 312 gray smoothhounds, *Mustelus californicus*, captured in the ESNERR from April 1990 to September 1992.

Figure 7. Mean size, range and standard deviation of Young-of-the-Year gray smoothhounds captured in the ESNERR from June 1991 to September 1992.

Figure 8. Number of gray smoothhound stomachs examined for feeding habits in proportion to the number of sharks captured during the months shown.

Figure 9. Relationship between crab carapace width and total length of shark for the two most represented genera of crabs found in the diet of the gray smoothhound, *Mustelus californicus*. Data are from those stomachs which contained measurable prey (n=40).

Figure 10. Amount of food found, in grams (solid line), and expressed as % live body weight (dashed line), in the stomachs of gray smoothhounds, *Mustelus californicus*, 500-1300mm total length. Values are means $\pm$ SE (n=72).

Figure 11. Diel variation in mean ratio of wet stomach weight to wet weight of shark (g/kg) for 69 gray smoothhounds, *Mustelus californicus*. Each value represents the mid-point of a given time interval. Vertical lines designate ± 1 SD.

Figure 12. Exponential curve fit to the gastric evacuation data with 95% confidence intervals for 4 gray smoothhound sharks. The different symbols represent individual sharks. Regression parameters are listed in Table 2.

Figure 13. Caloric value (cal/g) of experimental meals at various hours after feeding. Meals consisted of whole, live shore crabs, *Pachygrapsus* sp., which were recovered from the guts at prescribed intervals after feeding. Different symbols represent individual samples.

Figure 14. Caloric value (cal) of experimental meals at various hours after feeding. Different symbols represent individual samples.