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GROWTH OF THE GIANT PACIFIC OCTOPUS
OCTOPUS DOFLEINI MARTINI
ON THE WEST COAST OF BRITISH COLUMBIA

by

Shawn Michael Charles Robinson
BSc(Honors) Acadia University 1979

THIS IS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE
in the Department
of
Biological Sciences

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April 1983

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ABSTRACT

During the summer of 1980 and from May 1981 to May 1982 a tag-recapture growth study on Octopus dofleini martini (Wulker) was conducted on an inshore, shallow water (2-15 m), octopus population in Clayoquot Sound, Vancouver Island. The objective was to describe the growth of an average O. dofleini individual in the field and to look for growth differences related to sex, season or location. Monthly collections of octopuses provided information on maturation. Growth and feeding experiments were carried out on captive O. dofleini.

In total, 211 octopuses were tagged and 87 of these were recaptured, some up to 8 times. Octopuses ranged in weight from 1.6 to 18.8 Kg and the sex ratio was skewed towards females. O. dofleini had a high growth rate in the field which was comparable to many smaller, warm water species of octopuses. The growth rates were variable for all sizes studied and there was an inverse relationship between size and the specific growth rate (SGR). No difference was found in growth rates between sexes or between study sites. There were two distinct growth seasons for O. dofleini in Clayoquot Sound, a slow period from January to June and a faster period from July to December. These two seasons correspond with the yearly water temperature cycle.

Male O. dofleini matured at a smaller size than females and spermatophores were found in males over 12.5 Kg. No mature females were found although a wide size range was sampled. There was no seasonal reproductive cycle for males in the shallow

water population in Clayoquot Sound.

Laboratory studies showed an inverse relationship between octopus weight and the percent body weight of food eaten per day. Food conversion efficiency was high with a mean of 58%.

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A. Introduction

Octopus dofleini (Wulker, 1910), is a member of the phylum Mollusca, class Cephalopoda and order Octopoda. It is commonly known as the giant Pacific octopus and is distributed in the northern Pacific Ocean from California to Alaska, among the Aleutian Islands and down the Asian coast to northern Japan and Korea (Pickford, 1964). There are three recognized subspecies: O. dofleini martini from the west coast of North America, O. dofleini apollyon from the Pacific far north and O. dofleini dofleini from Japan and Korea (Pickford, 1964).

Female O. dofleini generally lay and brood their eggs on the roof of their dens until the eggs hatch or the female dies of starvation. Mottet (1975) reports that female ovaries from octopuses in Japanese waters contain 30,000 to 100,000 eggs. These eggs are laid in strands and take approximately 6.5 months to hatch or an accumulated water temperature of 2,300 to 2,700 °C days. This agrees with Gabe (1975) who reports hatching after 5 to 6 months for eggs in British Columbia. Newly hatched larvae are planktotrophic but the duration of this planktonic stage is unknown. The only estimates available are those of Itami et al. (1963) who raised planktonic Octopus vulgaris larvae on various species of crustacean larvae until settling. They found that at a mean water temperature of 24.7°C, the larvae took 33 to 40 days to pass from the planktonic to the benthic stage.

Very little information exists on the early benthic stage of O. dofleini. Yamashita (1975) suggests that very young octopuses reside in inshore waters because small octopuses (5 cm in total length) are occasionally caught in small inshore octopus traps. This view is supported by the discovery of a 5 g juvenile in a tidepool in Barkley Sound on the west coast of Vancouver Island (personal observation). The ecology of animals weighing more than 1 Kg is better known. Hartwick et al. (1981) have described O. dofleini as primarily a nocturnal, refuging predator. Their analysis of the food remains at den entrances indicates that the diet of the octopus includes: red rock crabs (Cancer productus), Dungeness crabs (C. magister), kelp crabs (Pugettia producta), littleneck clams (Protothaca staminea), cockles (Clinocardium nuttalli), abalone (Haliotis kamtschatkana), and moon snails (Polinices lewisii). In addition, Japanese studies have shown that O. dofleini also consumes flatfish, sand lance, bullhead (sculpin), shrimp, fish eggs, sea cucumbers, sea squirts, starfish, squid and other octopods (Mottet, 1975; Yamashita, 1975). O. dofleini has several predators which include harbor seals (Phoca vitulina) (Spalding, 1964), sea otters (Enhydra lutris) (Kenyon, 1965; 1975), dogfish (Squalus acanthius) (Brocklesby, 1927), ling cod (Ophiodon elongatus) (Hartwick et al., 1978) sea lions (Eumetopias jubata) (Spalding, 1964), flatfish (Yamashita, 1975) and larger octopuses (pers. obs.). In northern Japan, fishing and tagging studies indicate that immature octopuses make four migrations in total a year

(Mottet, 1975), with the animals in deep water from February to April and August to October and in shallow water from May to July and November to January. Reports also reveal that these animals are capable of swimming in the water column during these migrations and covering distances of 4 Km a day (Kanamaru and Yamashita, 1967, from Mottet, 1975). Abundance of O. dofleini in an area has been suggested to be related to the number of suitable dens available (Kanamaru and Yamashita, 1967; Mottet, 1975; Hartwick et al., 1978) and this is one of the premises on which the oriental, Mediterranean and African trap fisheries are based.

O. dofleini is thought to reach maturity at two (Mottet, 1975) or three years (Yamashita, 1975). Mature males contain approximately 8 spermatophores which are deposited with the hectocotylus into one or more females. The inseminated females are generally immature and thus store the sperm in the oviducal balls until the eggs are mature (Mottet, 1975). The peak spawning season in Japan is thought to be May and June (Yamashita, 1975). Egg laying takes approximately 15 days (Gabe, 1975) and afterwards, the female aerates, cleans and protects the eggs until they hatch or the female dies of starvation. This sequence of events is identical to that reported on other species such as O. vulgaris (Nixon, 1969; Mangold and Boletzky, 1973), O. joubini (Thomas and Opresko, 1973) and O. cyanea (van Heukelem, 1976).

Growth in animals has been described by von Bertalanffy (1950) as "the quantitative increase in a living system which results from the prevalence of anabolism of building blocks over catabolism". Studies on growth characteristics of aquatic animals have centered on fish and many of the techniques presently used to describe growth have been derived from these studies (see Ricker, 1975 for review). In the case of invertebrates, the growth of molluscs, in particular bivalves, has received much of the attention (see Wilbur and Owen, 1964 for review).

The growth of an organism is usually represented in graphic form as a plot of size versus age, commonly known as a growth curve. These growth curves are often sigmoid or logarithmic in shape and are described mathematically in order to model the growth of the animal. One of the most common growth curves or growth models used is the von Bertalanffy growth curve. This has been used on many types of aquatic animals including: salmon (Ricker, 1969), ciscoes (Bayley, 1977), bivalves (Brousseau, 1979), sea urchins (Ebert, 1980) and abalone (Breen, 1980). However this model has been criticized (Knight, 1968; Roff, 1980) because of its use of a theoretical size maximum and the lack of statistical testability. Originally, it was devised around a physiological basis of anabolic and catabolic processes, but these assumptions have proved to be untestable so far. Other growth curves which have been used are: the logistic, exponential, Gompertz, power and parabolic curves. Recently,

powerful computer programs have been developed which incorporate most of the common growth curves and allow a researcher to quickly test their applicability to his data (Ebert, 1980; Schnute, 1981).

In order to construct a growth curve for an animal, an age for at least one size must be known. The shape of the growth curve can be determined by analyzing the growth rates but in order to position the growth curve on a time axis, it is essential to have an estimate of age. In many animals, age can be estimated from growth lines occurring on hard parts but these are often lacking in soft bodied invertebrates. As a solution to this problem, Fabens (1965) proposed a physiological age based on the time required for an animal to achieve half of its remaining linear growth to a theoretical asymptote. Kaufmann (1981) approached the problem by giving the smallest animal of the group he was studying an arbitrary age of zero and constructing his model from that point.

There are basically two means of studying growth in animals, longitudinal methods and cross sectional methods (Kaufmann, 1981). Longitudinal methods follow the growth of a single animal over a long time interval and are most often carried out in laboratories where relatively constant conditions can be maintained. Cross sectional studies follow the growth of a number of different sized individuals over a short time period and are applicable to field situations where animals may be studied on an individual basis with tag-recapture programs or

indirectly through a series of size-frequency histograms. Both of the above methods have been used on octopuses.

In the laboratory, very little growth work has been done on O. dofleini except for some preliminary studies by Hartwick et al. (1981). However, in Europe and Africa, extensive work has been done on the growth and feeding of O. vulgaris (Nixon, 1966; 1969; 1971; Mangold and Boletzky, 1973; Smale and Buchan, 1981). In Australia, growth and feeding of O. tetricus has been studied by Joll (1976; 1977) who fit a von Bertalanffy growth curve to the data. Laboratory studies on growth and feeding have also been conducted with Eledone cirrhosa (Boyle and Knobloch, 1982), O. joubini (Mather, 1980; Forsythe, 1981), O. briareus (Borer, 1971) and O. cyanea (Boucher-Rodoni, 1973; van Heukelem, 1973; 1976).

Field studies are not as abundant as the above longitudinal laboratory studies. For O. dofleini, Hartwick et al. (1981) gave some preliminary results from their tag-recapture studies while Mottet (1975) reports on some recapture results from Japanese studies. A minor tag-recapture study was also done on O. cyanea (van Heukelem, 1976). However, the animals were in poor condition when they were released and so the results are suspect. Most of the field studies have used the indirect, size frequency analyses in conjunction with existing fisheries and have had varying degrees of success. This has been done for O. vulgaris (Mangold-Wirz, 1963; Guerra, 1979; Hatanaka, 1979), Eledone cirrhosa (Boyle and Knobloch, 1982) and O. cyanea (van

Heukelem, 1976).

In spite of the importance of octopus as a fisheries resource in other parts of the world and the large size of our west coast form, there is no detailed growth information on O. dofleini. Therefore, I decided to begin a tag-recapture program with octopus in a coastal, shallow water habitat to: 1) describe the growth of an average Octopus dofleini martini individual in the field, 2) look for growth differences related to sex, season, or location, and 3) provide a description of the resident octopus population in this area. Concurrent with the field tagging program, monthly octopus collections were done to determine when O. dofleini became sexually mature. In addition, longitudinal studies were conducted on larvae, juveniles and adults to monitor growth and feeding in the laboratory.

B. Materials and Methods

Tag-Recapture Program

During June, July and August of 1980 and from May 1981 to May 1982, octopuses were captured and tagged using SCUBA at two major study sites on Vancouver Island in Clayoquot Sound near Tofino, British Columbia (Figure 1). The two sites, Moser Point and MacIntosh Rock (Table 1), are semiprotected and experience strong currents (0.62 m/sec) three to four times daily as Tofino has a mixed semidiurnal tide pattern. The substrate in both areas is composed mainly of large boulder rubble and the octopus dens found in this ranged from three to eleven meters deep. Benchmarks were placed at each study site above the high tide mark for permanent identification of the sites. Water temperature and salinity obtained at a depth of 10 m over the year may be seen in Figure 2.

Animals were initially located by searching for food remains discarded by an octopus at the entrance to the den and the presence of an animal was verified using an underwater light. A small amount of bleach solution was introduced into the den and the emerging individual was captured, carefully put in a mesh bag, and taken to the surface where it was examined for scars and deformities, a previous tag, and its sex. The mantle cavity and funnel of the octopus were drained of retained water

Figure 1. Location of the study sites used in this project in Clayoquot Sound, Vancouver Island. 1.) Moser Point 2.) Moser Point-north 3.) Vargas Island II 4.) Meares Island 5.) MacIntosh Rock 6.) MacIntosh Channel.

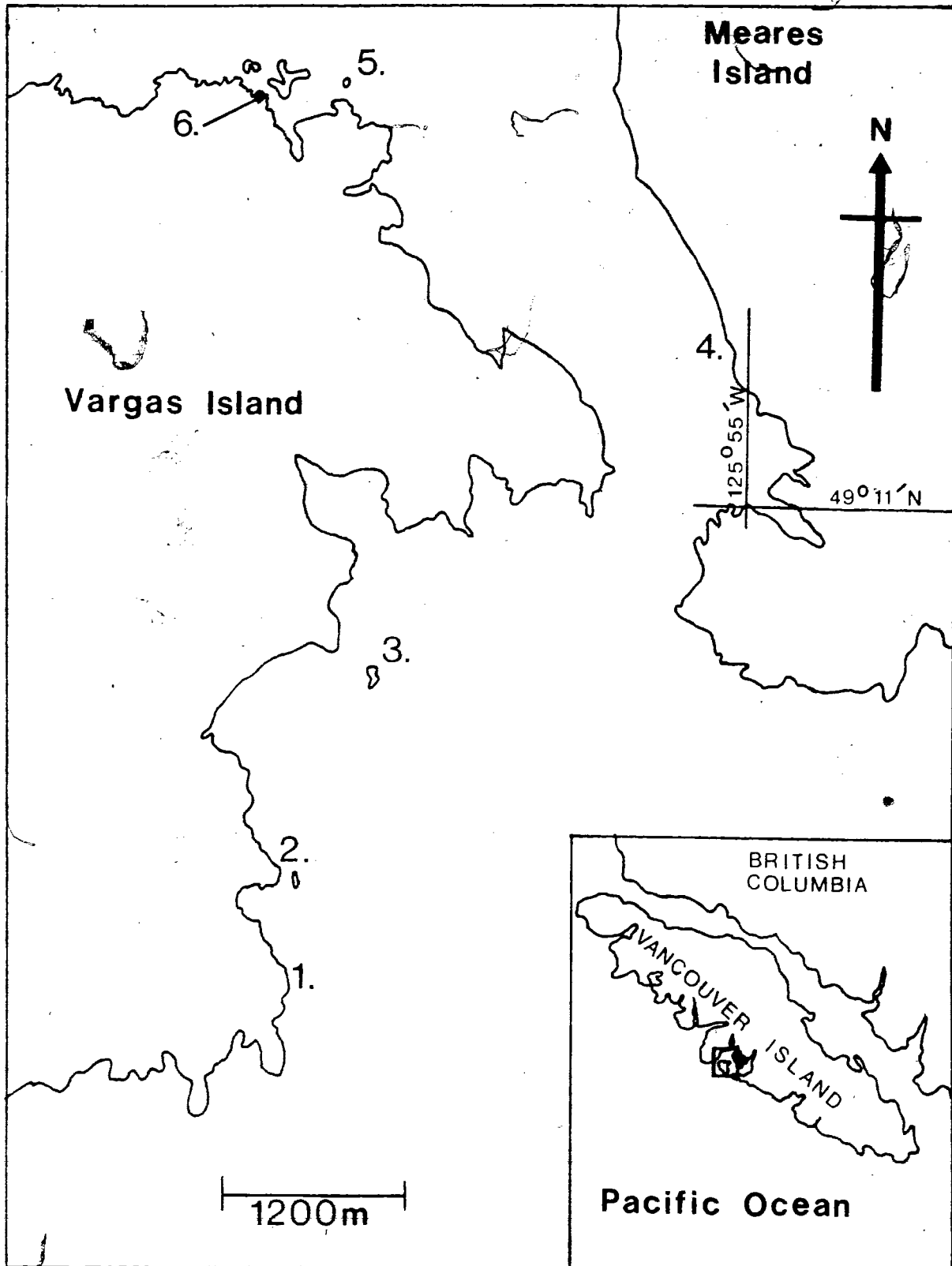
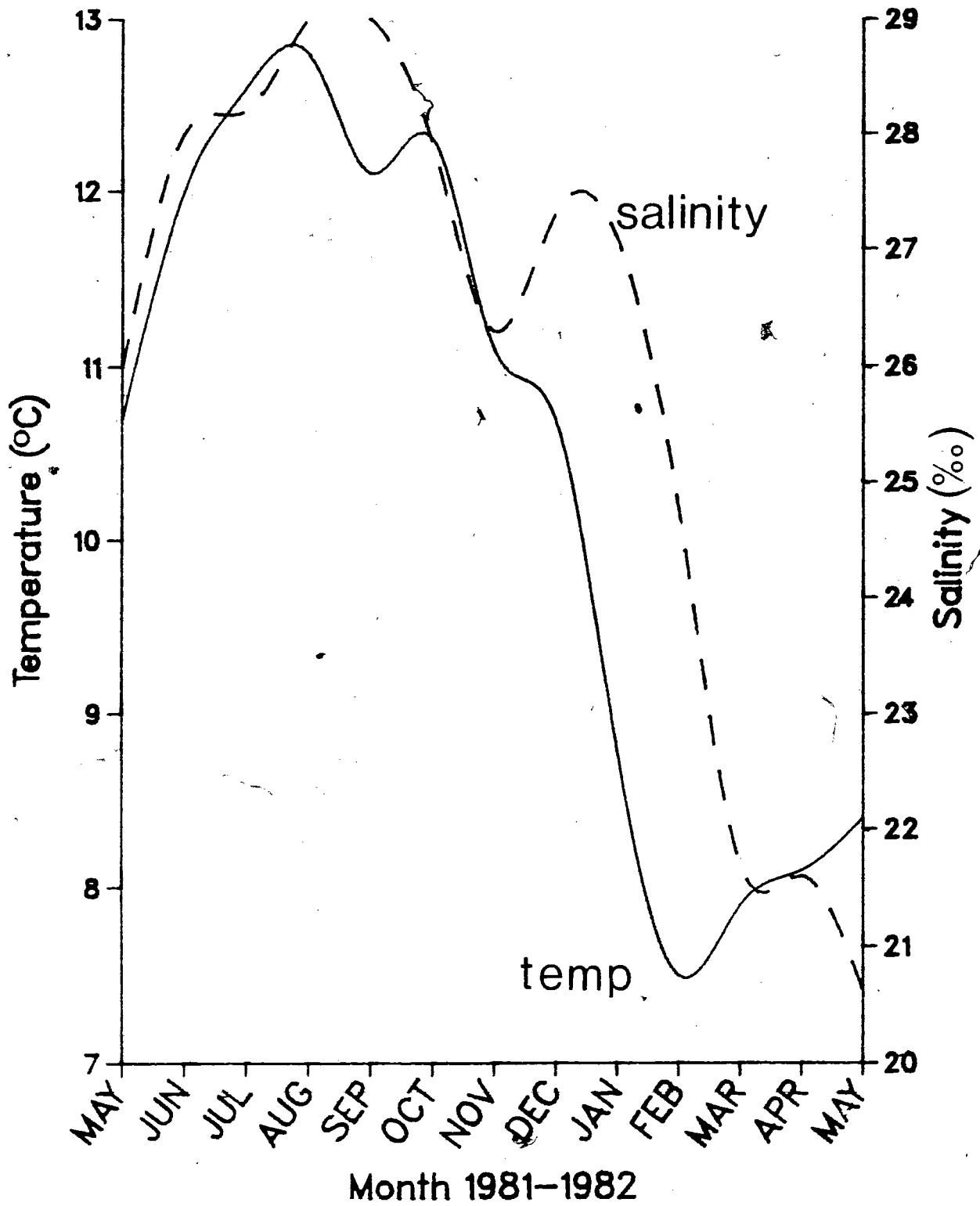


Table 1. List of the octopus study sites used in this project with their respective latitudes and longitudes. *=local names

| Site | Latitude and Longitude |
|--------------------|-------------------------------|
| Moser Point | 49° 9' 5" N, 125° 57' 10" W |
| MacIntosh Rock* | 49° 12' 38" N, 125° 57' 16" W |
| Cliff Cove | 49° 22' 38" N, 123° 17' 17" W |
| Wizard Islets | 48° 51' 30" N, 125° 9' 27" W |
| Dixon Island | 48° 51' 9" N, 125° 7' 15" W |
| Ragged Islets | 49° 22' 40" N, 123° 26' 48" W |
| MacIntosh Channel* | 49° 12' 36" N, 125° 57' 46" W |
| Moser Point-north* | 49° 9' 46" N, 125° 57' 12" W |
| Vargas Island II* | 49° 10' 27" N, 125° 56' 38" W |
| Meares Island | 49° 12' 14" N, 125° 55' 46" W |

Figure 2. The mean temperature and salinity per month at 10 m from May 1981 to May 1982. Both study sites, Moser Point and MacIntosh Rock, are combined.



and the octopus was weighed in the mesh bag on a brass spring scale to the nearest 0.25 Kg. Length measurements were not taken to measure growth as Nixon (1966, 1969) showed that change in weight is the most accurate growth indicator. Length is more of a function of the state of muscular contraction at the time of measurement. Animals smaller than 3 Kg were weighed on a brass scale to the nearest 0.025 Kg. Untagged octopuses were tagged on the third left arm using a numbered, yellow, plastic Peterson disc, 2 cm in diameter and held in place with a 6 cm nickel pin. Tagged animals were then taken back to their dens, released and the dens marked using white 100 cm plastic numbered squares. The entire capture procedure took approximately five to ten minutes and the octopuses re-entered their dens with no obvious difficulties. All the marked dens were mapped and checked at approximately two week intervals for recaptures and new immigrating individuals. This method of sampling was biased in that octopuses weighing 0.5 Kg or heavier had a greater probability of being captured because their dens were easier to locate.

O. dofleini Larval Studies

Using SCUBA, egg strands were carefully collected from a den containing a brooding Octopus dofleini female at Cliff Cove (Table 1) near Horseshoe Bay, British Columbia, and were then transported in seawater to the Vancouver Public Aquarium where they were placed in a 1000 liter hexagonal tank under the

care of Dr. Jeffrey Marliave. The tank was supplied with a flow-through seawater system and had an airlift in each corner which provided aeration and a downwelling current in the middle of the tank. The water temperature fluctuated from 9.0 to 9.5°C and the salinity remained constant at 27.75‰.

Upon hatching, the larvae were fed daily in excess with flakes of frozen krill (Euphausia pacifica) and Aminoplex (Clark Rogers Ltd.), a mixture of essential amino acids and electrolytes. Subsamples of the population (n = 5-13 larvae) were taken approximately every ten days and weighed on a Mettler H10 analytical balance to the nearest 0.5 mg. Two methods were used to measure wet weight: 1) each animal was weighed in seawater in a 0.5ml beaker, and 2) each one was weighed in a small weighing boat after being placed on a piece of Whatman No. 1 filter paper for five seconds. Dry weights were taken of each individual after it had been dried in an oven for three days at 85°C. Dimensions of larvae and eggs were measured from known-scale photographs taken during the study.

Laboratory Studies

Two sets of laboratory experiments were carried out on octopuses in enclosed tanks where the animals were fed with weighed amounts of food. These experiments took place at the Bamfield Marine Station in Barkley Sound on Vancouver Island and at the Vancouver Public Aquarium.

At Bamfield, in the fall of 1980, animals were captured in Trevor Channel at Wizard Islets and at Dixon Island (Table 1) where the water depth ranged from 4.6 to 13.7 meters. Four octopuses were captured and immediately transported to the station where they were housed in tanks with flow-through seawater systems. Two experiments were run.

In the first experiment, three octopuses (2 females and 1 male) were placed in a large tank with separate compartments, each having dimensions of 61 cm x 122 cm x 122 cm (906 liters). Each compartment had its own water flow. The mean water temperature was $11.4^{\circ}\text{C} \pm 0.5$. Clay pipes were placed on the bottom of each compartment to act as "dens", but the animals did not utilize them and spent their time in a corner just below the air-water interface. Animals were exposed to a natural photoperiod from fluorescent lights controlled by an external light sensor. The octopuses were fed daily with a weighed amount of crabs, mainly kelp crabs (Pugettia producta) but occasionally red rock crabs (Cancer productus). Food levels were kept ad lib (i.e. in excess). Food was readily accepted as the animals would attack the crabs as soon as they were placed in the tank. One week prior to the start of the experiment, all animals were tagged using a yellow plastic numbered Peterson disc with a nickel insertion pin. After draining the mantle cavity and siphon, octopuses were weighed at 14 day intervals in a preweighed mesh bag on a brass spring scale to the nearest 0.25 Kg. Food remains were collected and weighed to the nearest gram

after excess moisture was dried off with blotting paper. The amount eaten was determined by subtraction of the remains from the amount of food given to the octopus.

In the second experiment, a large male octopus was kept in a 61 cm x 61 cm x 210 cm (780 liter) tank with a flow-through seawater system. The top of the tank was covered to prevent escape. Water temperatures (mean 11.4°C) were taken daily and feeding was done every two days with preweighed amounts of frozen scrap fish obtained from a local shrimp trawler. Food levels were kept ad lib. The families of fish used as food were mainly: Pleuronectidae, Bothidae (flatfish), Cottidae (sculpins) and Agonidae (poachers). Some Sebastes spp. were also included. Food remains were collected and weighed. The octopus was weighed as described above after a 61 day period.

For the studies at the Vancouver Aquarium, two male octopuses were captured, in the spring of 1981 at the Ragged Islets (Table 1) off southwest Bowen Island in water depths of 9.1 and 13.7 meters. These animals were transported to the Aquarium in seawater where they were placed in two 164 liter oval fiberglass tanks with flow-through seawater systems. Light screens were placed on top of the tanks to reduce light input. The animals were fed every two to three days with measured amounts of thawed, fresh-frozen Pacific herring (Clupea harengus pallasii). Food levels were kept ad lib. Food remains were collected from the previous feeding and weighed on a double beam balance to the nearest 0.1 g before new food was added. The mean

water temperature was $9.4^{\circ}\text{C} \pm 0.1$ and the salinity remained constant at 27%. Octopuses were weighed at three week intervals as described above.

Field Cage Studies

During the summer of 1980 and the summer and fall of 1981, cage studies were conducted at two study sites in the Tofino area using small O. dofleini captured locally during the tag-recapture study. A very small individual was obtained from the Bamfield Marine Station.

Plywood boxes, with 1 mm mesh size screens at each end for ventilation, were used to house the octopuses. These were of two sizes: 30 cm x 30 cm x 61 cm (57 liters) and 30 cm x 61 cm x 122 cm (227 liters). The cages were weighted with cement blocks on the seabottom and hollow construction bricks were placed inside to act as "dens". The cages were located at MacIntosh Rock in 8.25 m of water and at MacIntosh Channel (Table 1) in 3.7 m. Six animals (2 males and 4 females) were studied for different lengths of time due to escape and mortality. Octopuses were weighed at approximately weekly intervals on spring scales to the nearest 0.002 Kg for animals less than 0.25 Kg and to the nearest 0.025 Kg for animals heavier than 0.25 Kg. Feeding was carried out ad lib at weekly intervals using a mixed, preweighed diet of live food consisting of some or all of the following: red rock crabs (Cancer productus), purple shore crabs (Hemigrapsis nudus), porcelain crabs (Petrolisthes eriomerus), littleneck

clams(Protothaca staminea, Tapes japonica), cockles(Clinocardium nuttalli), butter clams(Saxidomus giganteus) and soft shelled clams(Mya spp.). Mean water temperature was 13.3°C.

Maturation Studies

Samples were taken approximately every 30 days from May 1981 until May 1982. Sample sizes ranged from 3 to 10 per month and were obtained from four sampling sites: 1) Moser Point-north, 2) Vargas Island II, 3) Meares Island and MacIntosh Channel (Table 1 and Fig. 1). The first animals encountered were captured using the technique described for the tag-recapture study. After the animals had been brought aboard the boat, wet weight, sex, general condition and water depth at capture were noted for each animal. Gonads were removed and placed in labelled jars containing 10% formalin in seawater for later analysis in the laboratory.

Preparation of the samples consisted of trimming the connective tissue away from the gonads and for the female samples, removal of the oviducts. Measurements for the males were composed of: volume of the gonadal bag, volume of the testes, weight of the gonadal bag and weight of the testes while for the females, volume and weight of the ovary was taken. Volume measurements of the gonads were done with a water displacement method to the nearest 0.1 ml while weights were determined on an analytical balance to the nearest 0.1 mg for gonads under 160 g and on a top loading digital balance to the

nearest 0.1 g for gonads over 160 g.

The state of maturity for males was determined by checking Needham's sac for the presence of spermatophores. Female maturity was determined by visually examining the size and condition of the eggs in the ovary.

Data Analysis

Computer analysis of the data was done using the MTS system at Simon Fraser University and statistical analysis was performed using one of the statistical program packages (MIDAS).

In describing growth, the specific growth rate (SGR) was used because it fits into later growth model descriptions more easily than an average daily growth rate (for example, Hartwick et al., 1981). The SGR is defined as::

$$SGR = (\ln WT2 - \ln WT1) / t$$

where WT2 is weight at time 2, WT1 is weight at time 1 and t is the time interval in days between the two weights (Kaufmann, 1981).

A few other terms also need some clarification:

1. Mean* Weight of Recaptured Octopuses. As animals are weighed at two time intervals, there are three possible weights one could use for description: an initial weight, a final weight or a mean weight. The most appropriate one to use for the purposes of growth analysis is the mean weight. If a number of measurements were taken, one could obtain a mean of the mean weights. For simplicity, the mean of the mean weights

will be referred to as the mean* weight.

2. Food conversion efficiency is a gross, non-physiological measurement of the amount of measured weight gain per weight of food eaten. The formula for calculation is:

$$\text{EFFICIENCY} = (\text{WTg}/\text{WTf}) \times 100$$

where WTg is the wet weight change of the octopus(Kg), and WTf is the wet weight of the food ingested.

3. The measurement of the percent body weight eaten per day was taken from van Heukelem(1976) and is defined as:

$$\% \text{ EATEN} = (\text{WTf}/\text{WTo}) \times 100$$

where WTf is the weight of food eaten per day and WTo is the wet weight of the octopus.

4. The gonadal index for an octopus in this study was defined as:

$$\text{INDEX} = (\text{Gwt}/\text{Owt}) \times 100$$

where Gwt is the gonad wet weight(Kg) and Owt is the wet weight of the octopus(Kg).

Growth Curve Analysis

Kaufmann(1981) has shown that most of the traditional growth curves that are used(i.e. the exponential, the power, the logistic, the Gompertz, the Bertalanffy) are all mathematically related. Therefore the parameters for these curves can all be calculated using the same method and can thus be compared. Kaufmann's method involves calculating an SGR for the mean weight of an individual over a certain time period. The mean

weight and the SGR are plotted against each other with the mean weight as the independent variable. By changing the scale (i.e. logarithmic) on one or both axes, to correspond to a specific growth model, various correlation coefficients, slopes and y-intercepts can be obtained, the latter two values are the growth curve parameters. After choosing the appropriate model, a third value, which positions the curve on the time axis, is calculated by giving the smallest size in the analysis an arbitrary age of zero and back calculating to determine the time parameter.

There is no reason that an animal has to grow according to any one model and so, in this study, a growth curve was chosen strictly on the basis that it described the data "best", based on the correlation coefficient between the mean weight and the SGR. In addition, two methods were developed to plot the data on the growth curve in order to observe the scatter. The first method involved using the growth curve to assign an age to an octopus when it was first captured and then calculating the age at recapture as the capture age plus the time interval of the recapture. By plotting only the size and age at recapture an estimate of how closely the octopuses follow the curve can be gained by observing the scatter around the line. The second method is similar to the first except that it uses multiple recaptures of a few octopuses. Again an age at capture is determined from the growth curve but the successive ages are determined by the time intervals of the recaptures. These sizes

and ages at each recapture interval are plotted around the curve in order to observe the scatter and to see how closely the line is followed. Obviously the above two methods do not test the accuracy of the curve as these data were used to derive the curve but, they do give some insight into the variation involved.

C. Results

I. Tag Recaptures

Population Information

From June 1980 to May 1982 211 individual octopuses were located, captured and tagged. They had a male:female ratio of 1:2.9 for newly captured octopuses and 1:3.2 for recaptures. The percentage of males per month from June 1980 to May 1982 at both sites combined is shown in Figure 3. This is a combination of all new captures and recaptures. There are two periods, April-May and August-December when males make up 30% or more of the sample.

The total number of animals captured at each study site from May 1981 to May 1982 is shown in Figure 4. During the months August to January, there were more animals captured than during the period February to July. These two periods are significantly different ($p < 0.01$) based on a Student t-test. Generally, there were more octopuses captured per month at Moser Point than MacIntosh Rock.

The mean weights of the newly captured octopuses may be found in Table 2. The mean capture weights for the months May 1981 to May 1982 at both study sites combined are given in Table





Figure 3. The percentage of male O. dofleini captured per month from June 1980 to May 1982 in Clayoquot Sound.

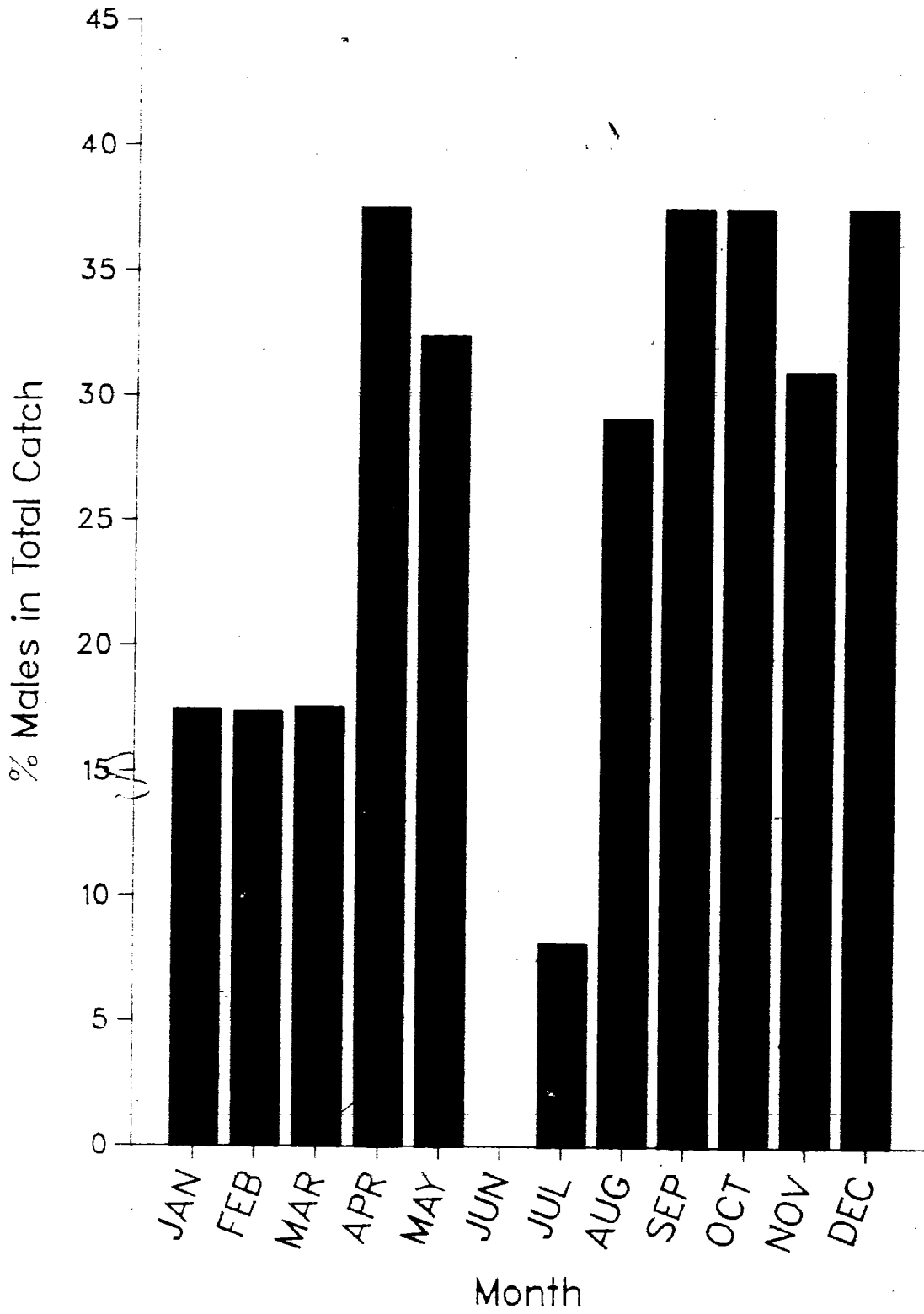
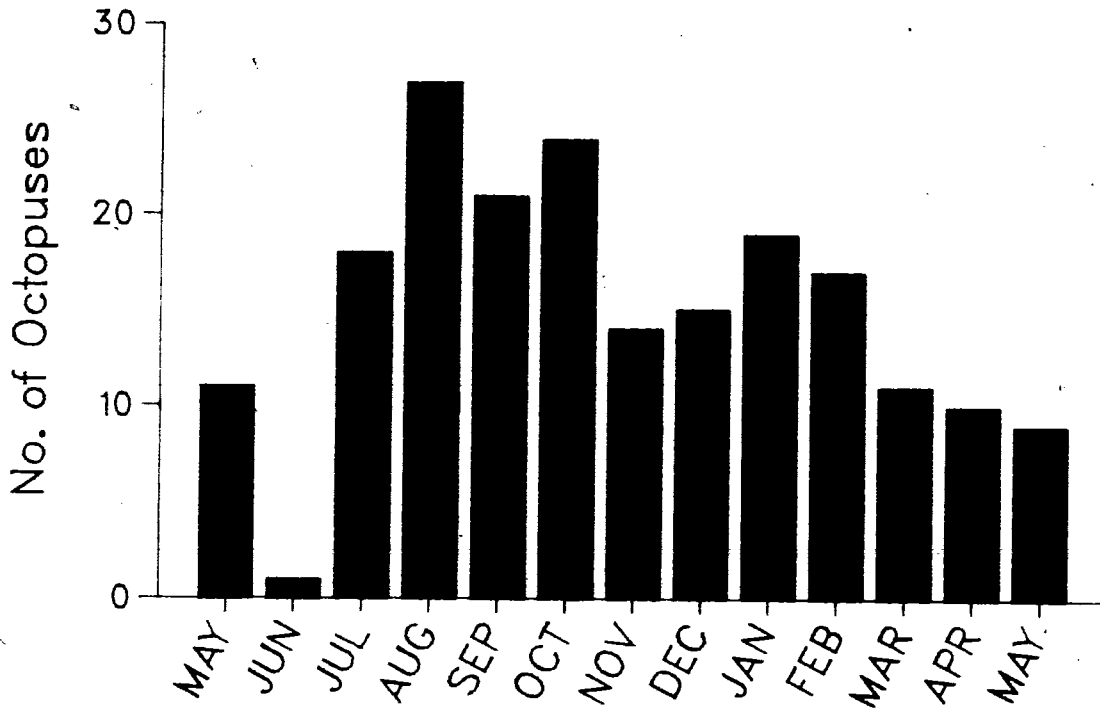


Figure 4. The number of O. dofleini captured per month at Moser Point
and MacIntosh Rock from May 1981 to May 1982.

Moser Point 1981-82



MacIntosh Rock 1981-82

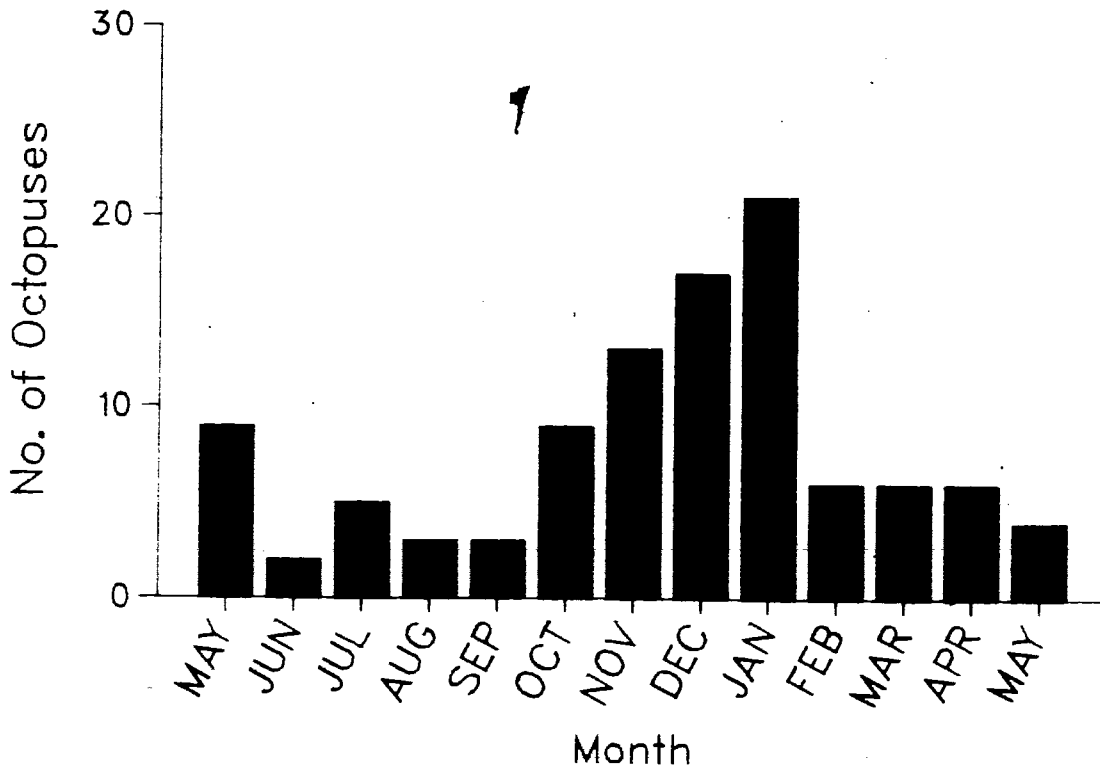


Table 2. The mean weight of octopuses captured in Clayoquot Sound from June 1980 to May 1982.

| Octopuses | n | Wet Weight (Kg) | |
|----------------|-----|-----------------|------|
| | | \bar{x} | s.d. |
| all captures | 211 | 8.43 | 4.97 |
| males | 54 | 8.96 | 5.36 |
| females | 157 | 8.25 | 4.84 |
| Moser Point | 115 | 8.19 | 4.94 |
| MacIntosh Rock | 86 | 8.44 | 5.18 |

3. No clear pattern was displayed although in some months, octopuses have almost double the mean weights of those in other months. There is a fairly large variation in the size of the animals as one standard deviation is equal to at least 50% of the mean in most cases.

A total of 211 octopuses were tagged and of these, 87(41.2%) were recaptured. Some of these 87 animals were recaptured up to 8 times, giving a total number of 184 recaptures. The frequency of multiple recaptures of an octopus decreased rapidly in a curvilinear fashion as shown in Figure 5.

The mean* weights of the recaptures may be seen in Table 4. The mean* weight per month for recaptures during the period May 1981-May 1982 for both study sites combined is given in Table 5. There is not as much variation in the means per month as for the newly captured animals and also the means are larger while the standard deviations are smaller. When the number of octopuses at each size interval that have been captured for the first time and those that have been recaptured at least once are studied, the percent recaptured was greater in the 6 to 10 Kg range. (Fig. 6).

Growth

In order to analyze the data, it was necessary to test various groups to determine if they could be combined. Therefore, a Student t-test was used to test for differences between sexes, study sites or the same months of different

Table 3. The mean weights per month for octopuses captured in Clayoquot Sound from May 1981 to May 1982. The study sites Moser Point and MacIntosh Rock are combined.

| Month | n | Wet Weight(Kg) | |
|--------------|----|----------------|------|
| | | \bar{x} | s.d. |
| May 1981 | 21 | 9.62 | 2.21 |
| June | 6 | 6.08 | 3.64 |
| July | 20 | 7.60 | 3.89 |
| August | 20 | 7.66 | 3.87 |
| September | 8 | 5.61 | 5.20 |
| October | 15 | 4.63 | 3.13 |
| November | 16 | 6.34 | 3.62 |
| December | 13 | 6.98 | 4.05 |
| January 1982 | 12 | 4.77 | 3.26 |
| February | 8 | 6.07 | 3.07 |
| March | 7 | 11.22 | 7.22 |
| April | 4 | 7.56 | 5.83 |
| May | 5 | 10.71 | 2.88 |

Figure 5. The frequencies of multiple recaptures for O. dofleini at both study sites, Moser Point and MacIntosh Rock, combined.

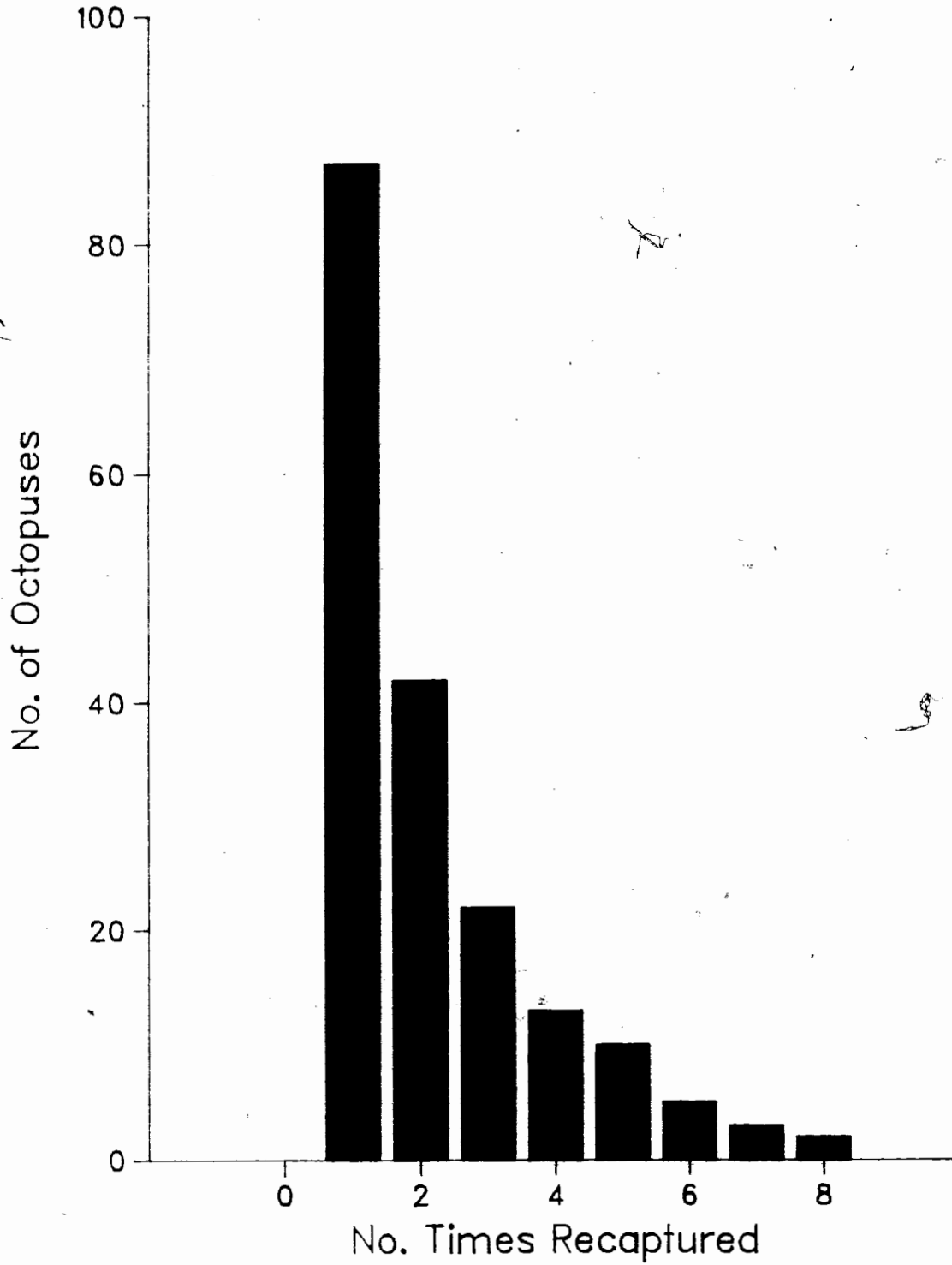


Table 4. Mean* weights of all octopuses recaptured, including multiple recaptures, in Clayoquot Sound from June 1980 to May 1982.

| Octopuses | n | Wet Weight(Kg) | |
|----------------|-----|----------------|------|
| | | \bar{x} | s.d. |
| all recaptures | 184 | 9.07 | 3.69 |
| males | 44 | 9.10 | 4.15 |
| females | 140 | 9.06 | 3.55 |
| Moser Point | 108 | 9.21 | 3.63 |
| MacIntosh Rock | 76 | 8.86 | 3.81 |

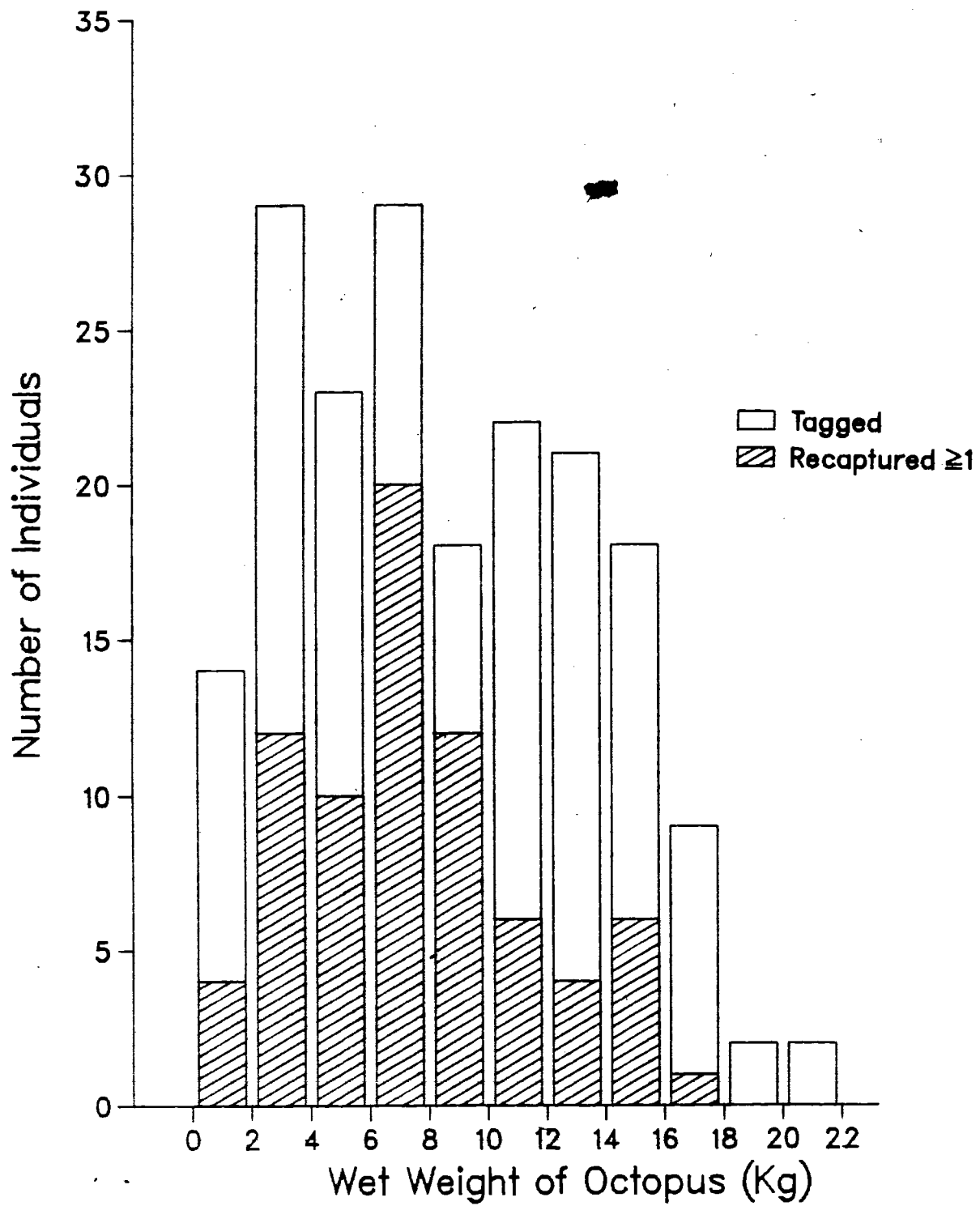
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Table 5. Mean* weights per month for all octopuses recaptured in Clayoquot Sound from May 1981 to May 1982. The study sites Moser Point and MacIntosh Rock are combined.

| Month | n | Wet Weight(Kg) | |
|--------------|----|----------------|------|
| | | \bar{x} | s.d. |
| May 1981 | 3 | 9.63 | 2.21 |
| June | 1 | 7.50 | * |
| July | 13 | 7.98 | 3.48 |
| August | 14 | 7.84 | 3.64 |
| September | 16 | 9.27 | 3.92 |
| October | 21 | 8.96 | 3.42 |
| November | 11 | 8.32 | 3.53 |
| December | 19 | 9.43 | 4.65 |
| January 1982 | 28 | 8.83 | 3.87 |
| February | 15 | 9.51 | 5.04 |
| March | 10 | 10.20 | 2.71 |
| April | 12 | 8.06 | 2.70 |
| May | 8 | 10.72 | 2.88 |

Figure 6. The size frequency of O. dofleini recaptured at least once
(weight at tagging) and newly tagged octopuses.

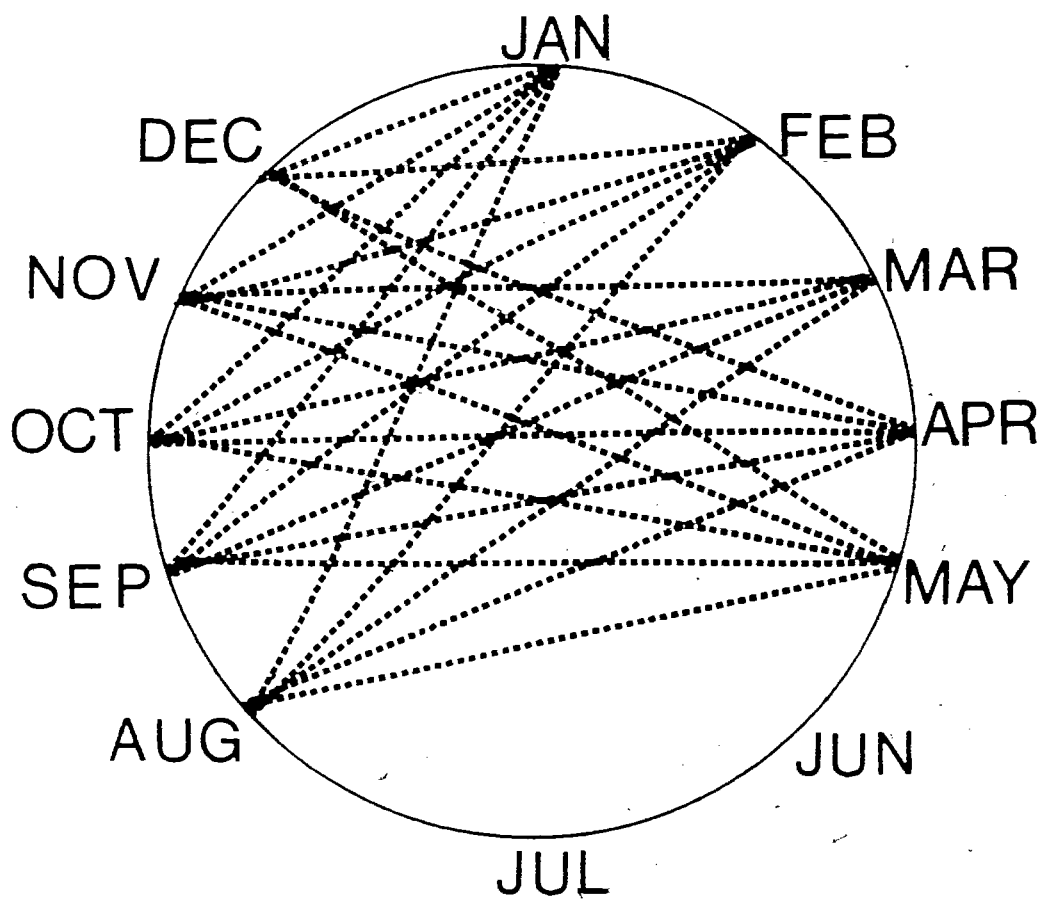


years. No significant differences ($p > 0.05$) were found in mean* weight or SGR between males and females and so they were combined in the growth analysis. Similarly, when study sites and months of different years (i.e. August 1980 vs August 1981) were tested, no significant differences ($p > 0.05$) were found in mean* weight or SGR and these data were also pooled. To test whether mean* weight or SGR varied over the year, a Kruskal-Wallis one way analysis of variance was performed on the entire data base. No significant differences ($p > 0.05$) in mean* weight among months were found but there was a significant difference ($p < 0.05$) in SGR. A Mann-Whitney U-test was done on all possible pairs of months and a schematic representation of the results of this test was produced (Fig. 7). The results in Figure 7 show a division of two periods, January to May and August to December. The month of June had only one recapture and therefore could not be included in the separation test. However, the SGR for June was very low compared to the other months and so it was included in the January to May group. Similarly, the mean SGR for July appeared to be more closely related to the August to December group and so it was grouped with that period.

When the months January to June are combined, the mean* weight was $9.23 \text{ Kg} \pm 3.68$ and the SGR ranged from -0.0168 to 0.0139 with a mean of 0.0042 . During this period, 22.1% of the animals recaptured either lost weight or did not grow. For July to December, the mean* weight was $8.95 \text{ Kg} \pm 3.71$ and the SGR ranged from -0.0154 to 0.0241 with a mean of 0.0081 . Only 6.5%

Figure 7. Schematic representation of the results of the Mann-Whitney U test on the SGR between all possible pairs of months. The dotted lines indicate a significant difference in the SGR between months ($p < 0.10$).

MEAN SGR
per MONTH



.....
($p < 0.10$)

of the animals in this period either lost weight or did not grow.

The SGR was related to the mean* weight of the octopus in a negative curvilinear fashion, with a large amount of variation. The relationships for the slow growing season (January-June) and the fast growing season (July-December) may be seen in Figure 8. For the slow season, the line of best fit is:

$$\text{SGR} = \ln\text{WT}(-0.001313) + 0.008921$$

where SGR is the specific growth rate and WT is the mean weight(Kg). This relationship has a correlation coefficient of -0.203 which is not significantly different from zero($p > 0.05$). For the faster season, the line of best fit is:

$$\text{SGR} = \exp(\text{WT}(-0.07098) - 4.2116)$$

This derived curve has a correlation coefficient of -0.440 and is significantly different from zero($p < 0.01$).

Using the above relationships, growth curves can be produced for the two growth seasons based on Kaufmann's technique described above. The curve of best fit for the January-June season is described by an Exponential growth curve:

$$\text{WT} = \exp(0.00533(t + 88.18))$$

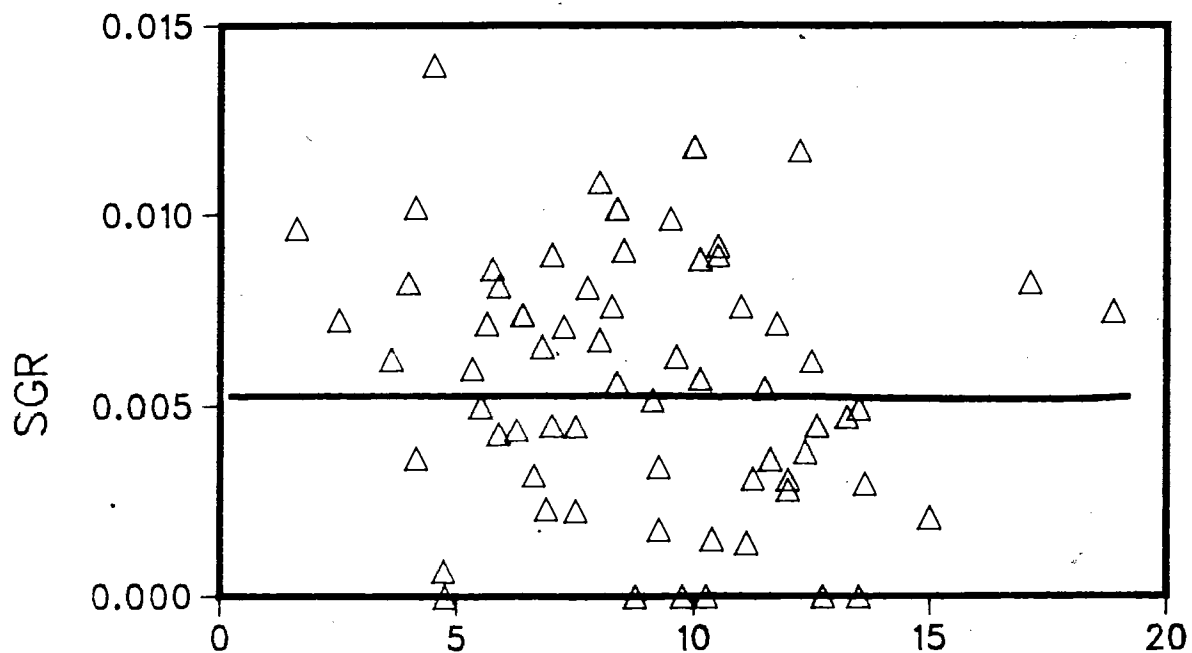
where WT is the weight of the octopus(Kg) at time t and t is the age(days). The July-December season is best described by a Logistic growth curve:

$$\text{WT} = 26.87(1 + \exp(-0.013592(t - 203.032)))^{-1}$$

(Figs. 9 and 10). The plotted points around the curves indicate a uniform variation along the curves and that the variation is

Figure 8. The relationship between the SGR and the mean weight of O. dofleini for the seasons January to June and July to December. The fitted lines are the result of least squares regression after the appropriate logarithmic transformations.

January to June



July to December

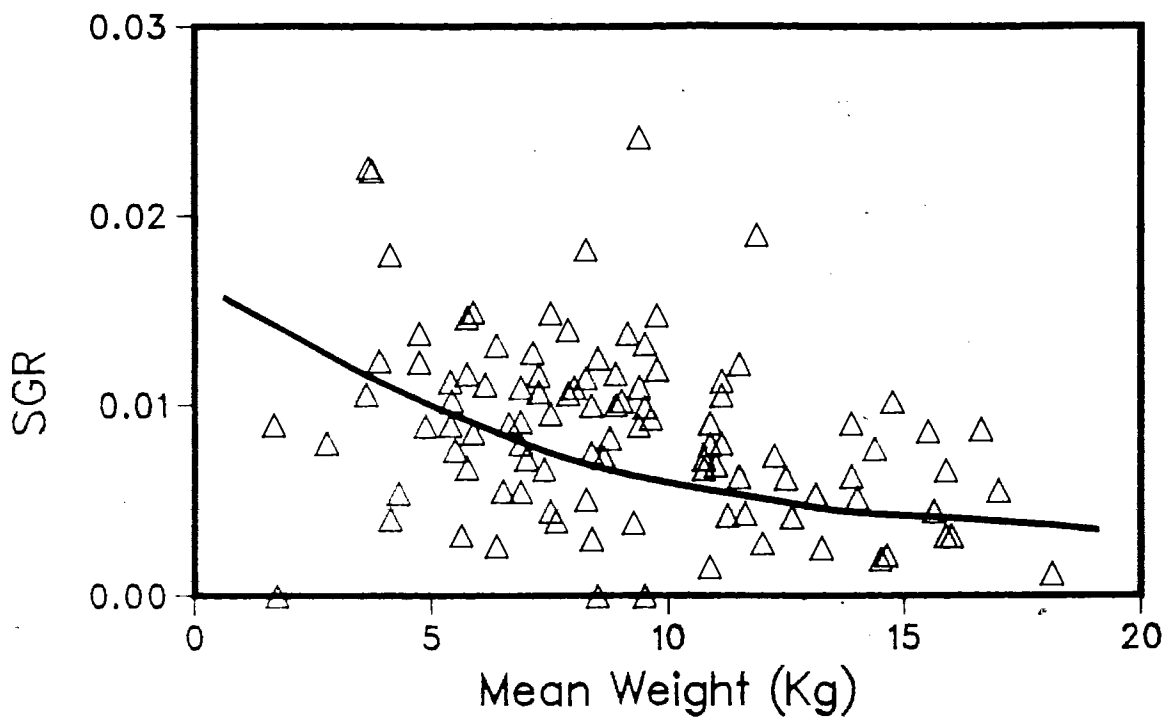


Figure 9. Generated Exponential growth curve for the slow growth season, January to June. Time 0 is defined as the time when the octopus weighs 1.6Kg. Points are fitted using Method 1.

7
January - June

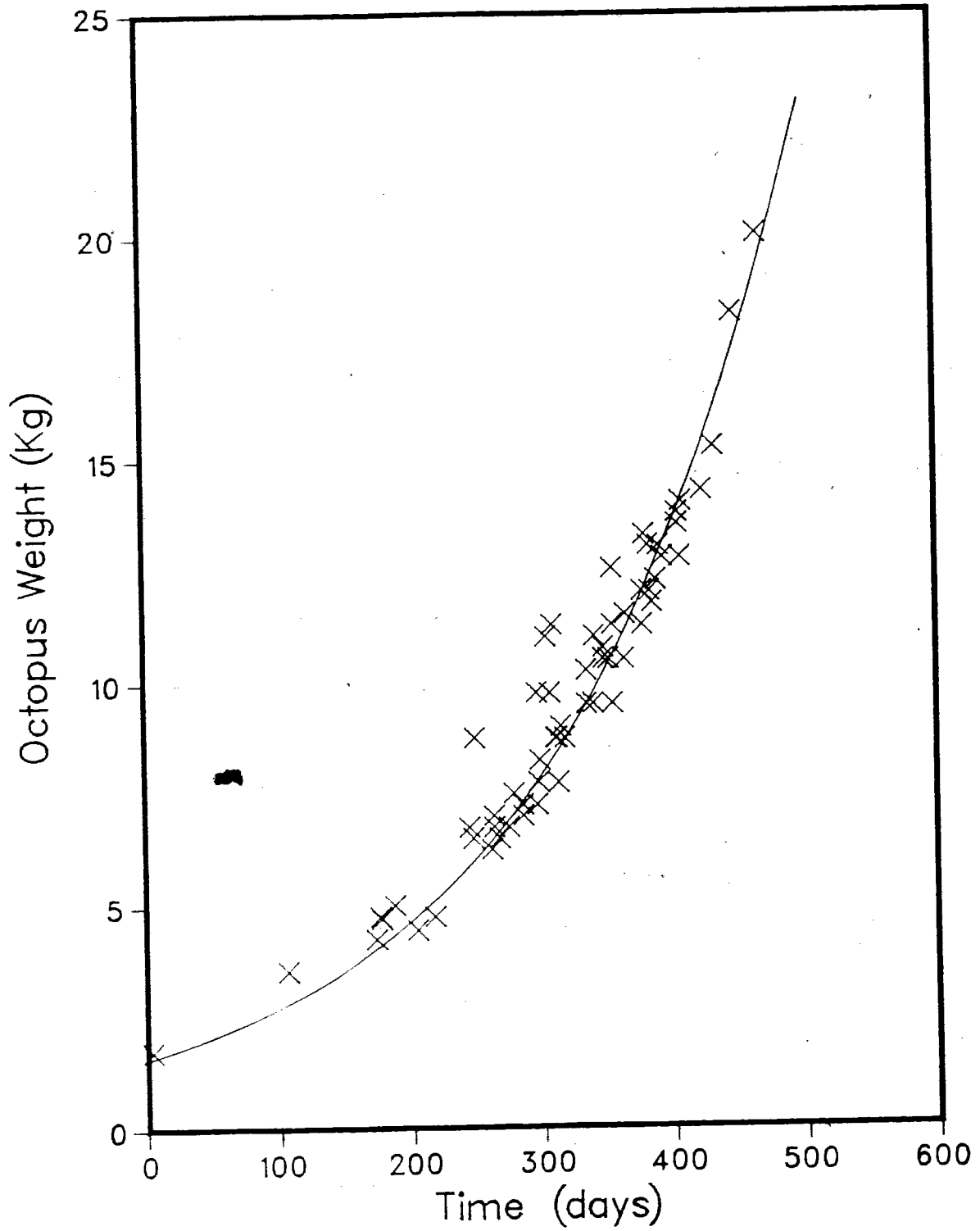
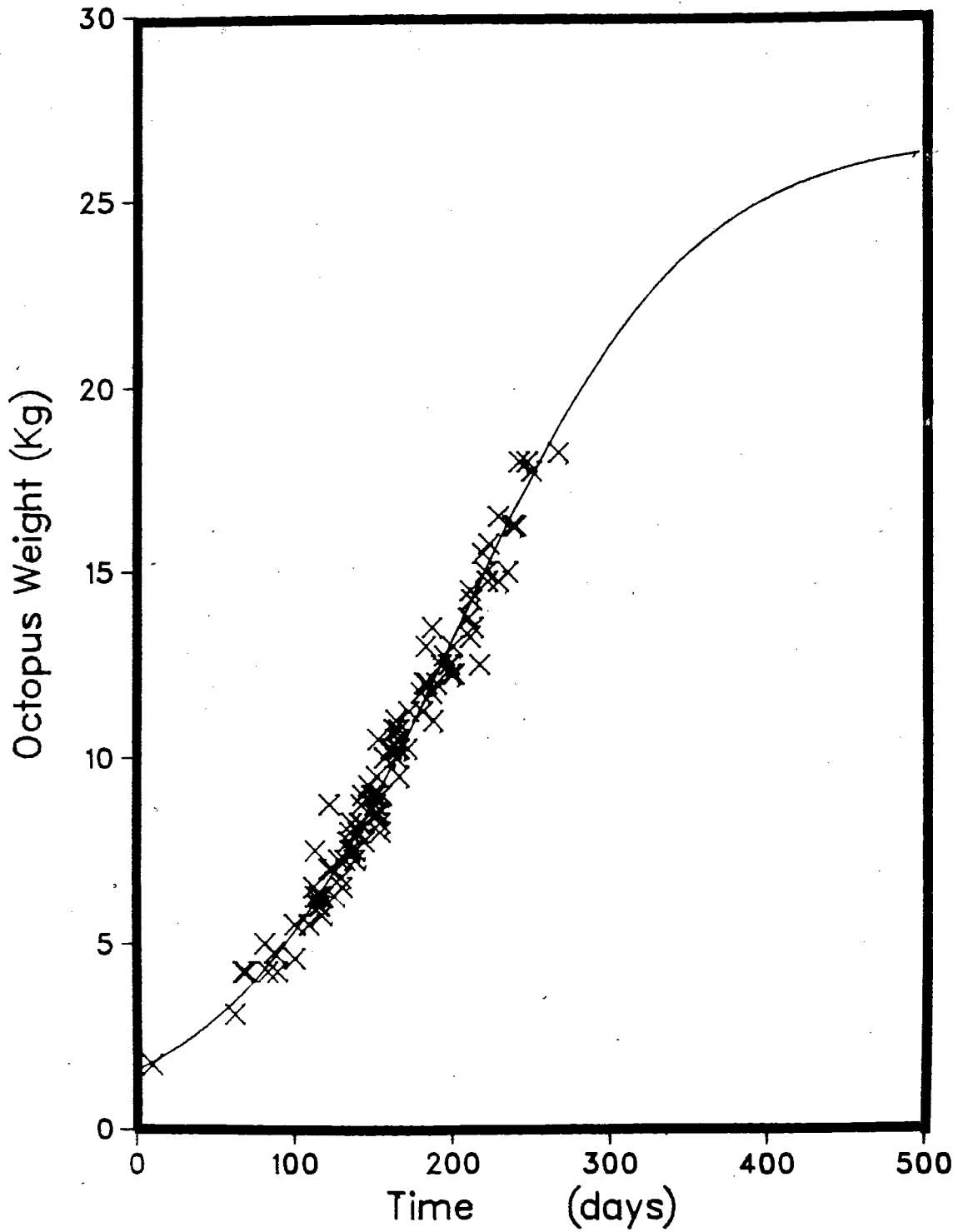


Figure 10. Generated Logistic growth curve for the fast growth season, July to December. Time 0 is defined as the time when the octopus weighs 1.6Kg. Points are fitted using Method 1.

July to December



larger in the slow season.

The second method used to examine the fit of the growth curves may be seen in Figures 11 and 12. The individual octopuses follow the curves fairly closely and do not consistently stay to one side.

II. Larvae

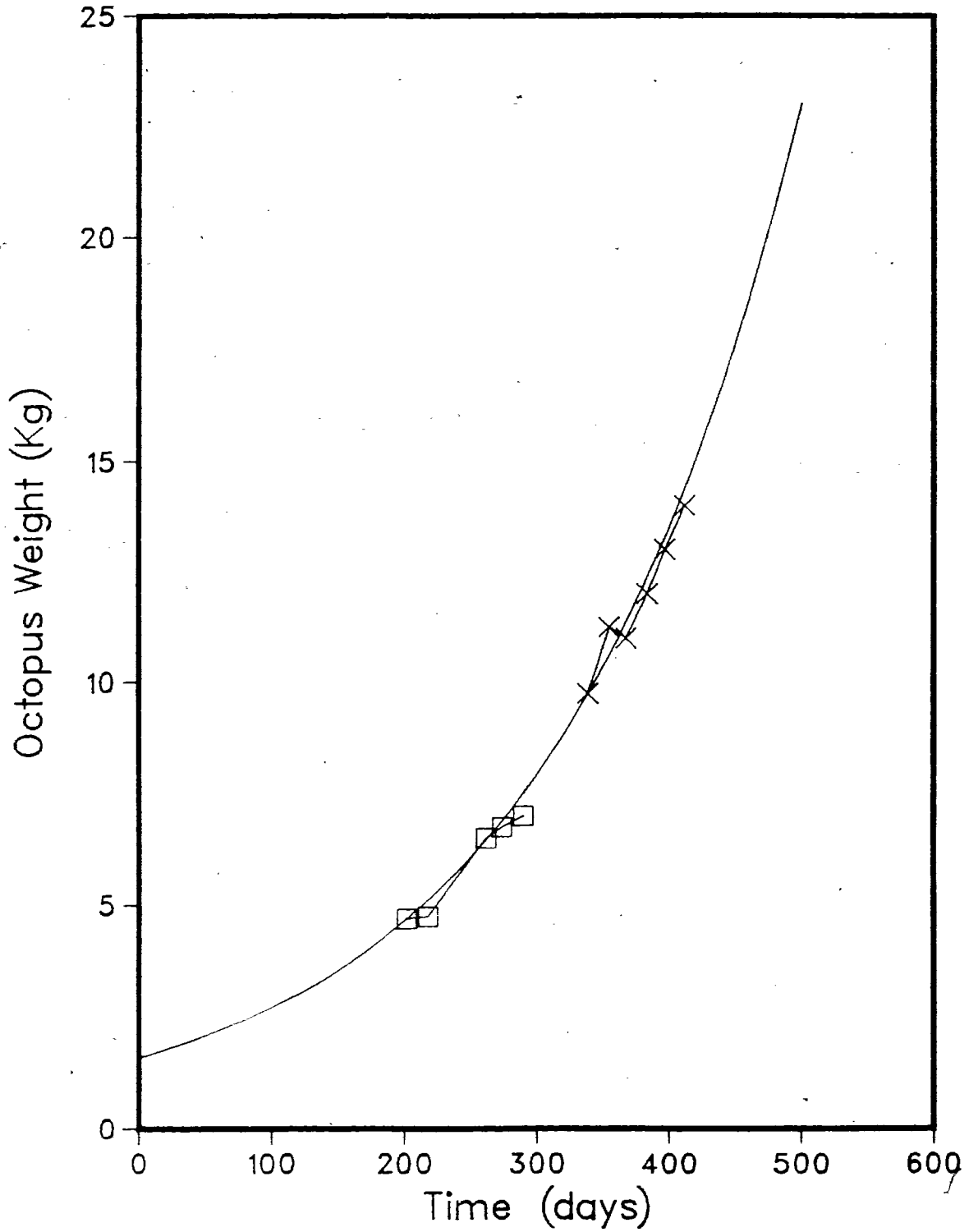
Observations

The egg of Octopus dofleini is similar in appearance and shape to that of Octopus vulgaris, described by Wells (1978). A newly laid egg was an elongated teardrop shape, creamy white in color with a length of 7.5 mm, a width of 2.3 mm and a strand length of 15.8 mm. The eggs were woven into clusters with a mean of 252 ± 21 eggs per cluster. A total of 73 clusters collected at Cliff Cove (January, 1981) was estimated to contain 18,396 eggs. This was approximately 25% of the eggs present in the den.

Just prior to hatching, the larvae was plainly visible inside the egg and the egg shape changed to a more normal teardrop shape with a mean length of $6.6 \text{ mm} \pm 0.2$ and a mean width of $3.2 \text{ mm} \pm 0.08$ ($n=10$). The larvae hatched from the egg capsules with the application of a physical stimulus, such as a vibration to the cluster, and would swim to the water surface. They had a mean total length of $6.9 \text{ mm} \pm 0.5$, mean dorsal mantle length of $3.4 \text{ mm} \pm 0.5$, mean arm length of $2.7 \text{ mm} \pm 0.2$ and a

Figure 11. Generated Exponential growth curve for the slow growth season,
January to June, with multiple recaptures of two animals.
Points are plotted using Method 2.

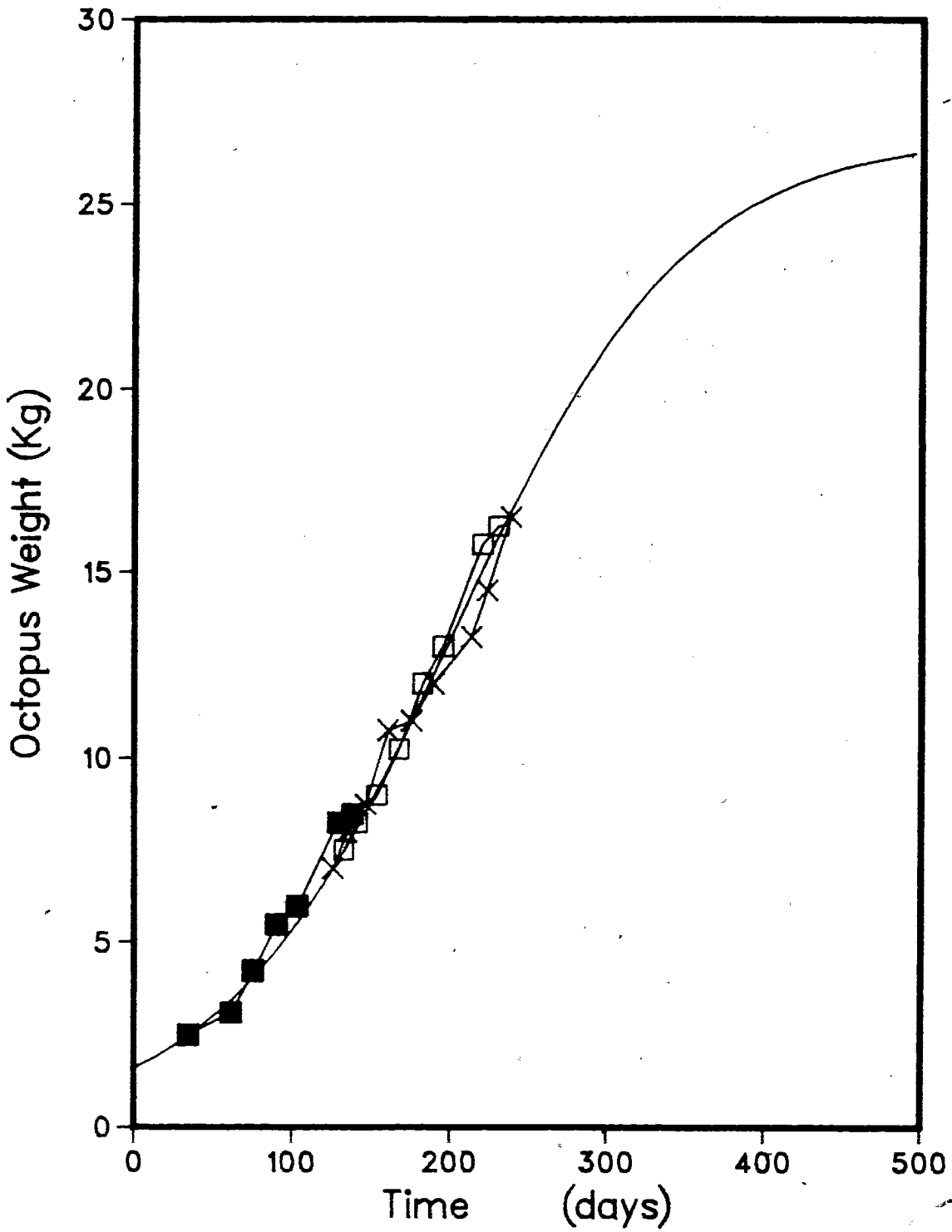
January - June



3

Figure 12. Generated Logistic growth curve for the fast growth season, July to December, with multiple recaptures of three animals. Points are plotted using Method 2.

July - December



mean interocular width of $1.4 \text{ mm} \pm 0.3$ ($n=3$). The mantles of the larvae were transparent and the siphon, located ventrally, was very large in proportion to the rest of the body. Reddish chromatophores could be seen on the apex of the visceral mass through the mantle, and small suckers were noted on the short arms. The larvae were observed to have functional ink sacs. They were more dense than the seawater as they would sink to the bottom of the tank if they stopped swimming. Neustonic feeding was observed (Marliave, 1981) and food could be seen in the gut as the animals fed on the krill and Aminoplex mixture.

Growth

A paired Student t-test was done to test for differences in the techniques used to measure larval wet weights. No significant difference was found ($p > 0.05$) so the weighing boat technique was used for the subsequent analyses.

A linear relationship existed between larval wet weight and dry weight with a correlation coefficient (r) of 0.87 ($p < 0.05$) ($n=36$). The equation of the line was:

$$DW = WW \times 0.1501 + 0.0806$$

where DW is dry weight (mg) and WW is wet weight (mg) (Fig. 13).

The growth pattern of the larval octopuses was followed on a wet and a dry weight basis (Tables 6 and 7). The larvae were studied for 40 days at which time the last of the population died. Specific growth rates were very variable ranging from 0.00314 to 0.0325 for wet weights and from -0.01019 to 0.0354

Figure 13. The relationship between the wet weight and the dry weight of O. dofleini raised at the Vancouver Aquarium. The fitted line was derived using least squares regression.

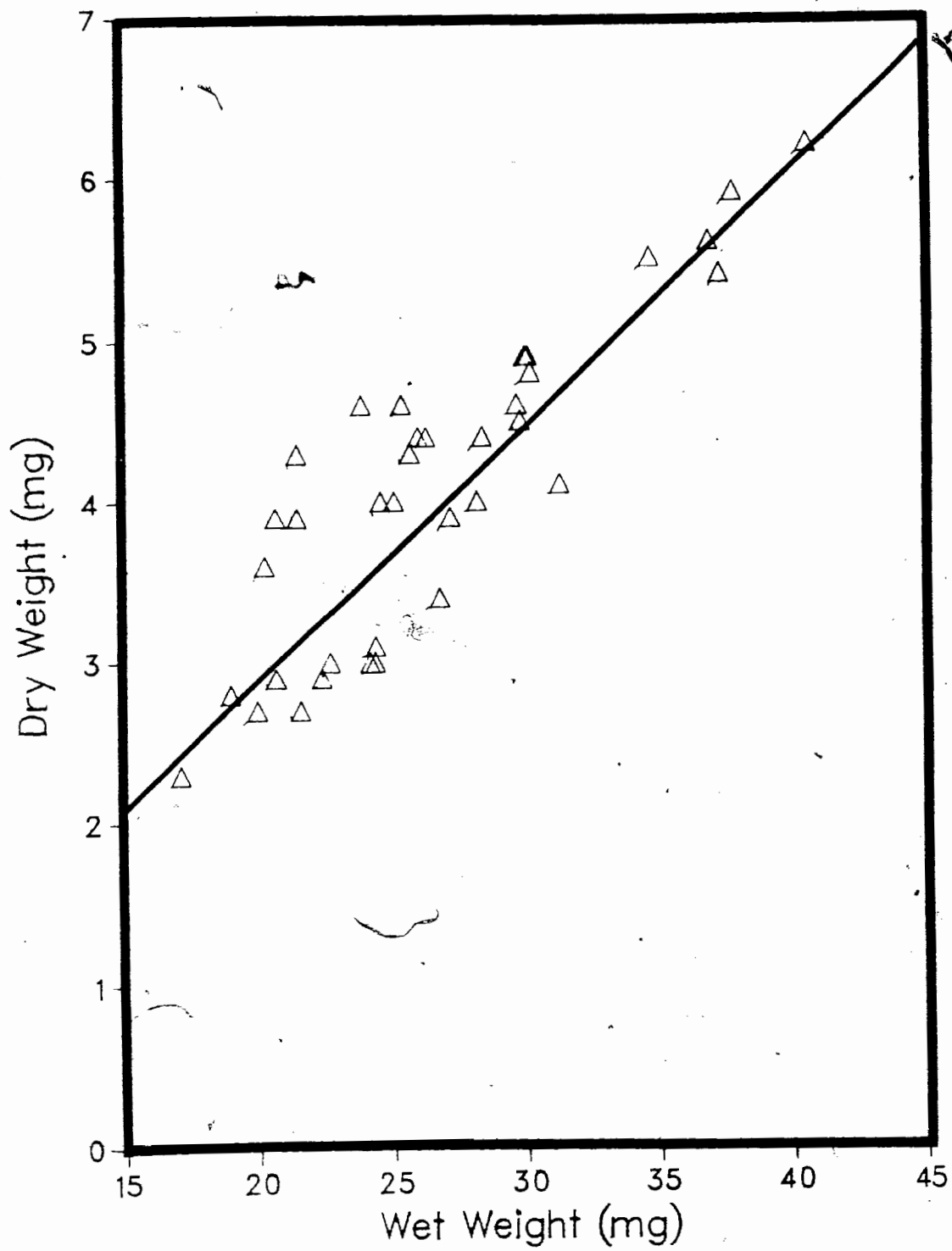


Table 6. The growth of larvae using average wet weights to measure the change in weight of the population. N=number of larvae in the sample, SGR=specific growth rate.

| Age (days) | N | Average Wet Weight(mg) | s.d. | SGR (x 100) |
|------------|----|------------------------|------|-------------|
| 2 | 10 | 21.65 | 2.87 | 0.31 |
| 12 | 5 | 22.34 | 1.55 | 1.16 |
| 26 | 6 | 27.75 | 3.86 | 0.44 |
| 33 | 13 | 28.61 | 3.59 | 3.25 |
| 40 | 6 | 35.92 | 3.84 | |

Table 7. The growth of larvae using average dry weights to measure the change in weight of the population. N=number of larvae in the sample, SGR=specific growth rate.

| Age (days) | N | Average Dry Weight (mg) | s.d. | SGR (x 100) |
|------------|----|-------------------------|------|-------------|
| 2 | 10 | 2.93 | 0.37 | 3.54 |
| 12 | 4 | 4.18 | 0.34 | -1.02 |
| 26 | 5 | 3.62 | 0.53 | 3.32 |
| 33 | 12 | 4.57 | 0.42 | 2.71 |
| 40 | 5 | 5.52 | 0.65 | |

for dry weights. The water content of the larvae appeared to affect the accuracy of weighing so dry weight was used for further analysis.

The growth curve of the larvae is shown in Figure 14. The exponential equation for the dry weight curve is:

$$DW = \exp(0.0139(Ti) + 1.0665)$$

where DW is dry weight(mg) and Ti is time(days). The correlation coefficient for the line of best fit to dry weight is 0.82. This is significantly different from zero($p < 0.01$).

III. Laboratory Studies

The results of the growth studies of Octopus dofleini in the laboratory may be seen in Table 8. Octopuses in the Bamfield study had significantly higher mean* weights($p < 0.05$), SGR's($p < 0.05$) and feeding rates($p < 0.05$) than those animals in the study at the Vancouver Aquarium. There was no significant difference($p > 0.05$) in mean feeding efficiencies for octopuses between the two studies. All of these variables were tested using a Student t-test.

There was no clear relationship between the SGR and the mean weight(Fig. 15). If each location is considered separately, there is a slight negative trend as shown by the correlation coefficients; -0.260 for Bamfield and -0.475 for Vancouver, but neither is significantly different from zero ($p > 0.05$). The equations for the lines are, for Bamfield:

$$SGR = \ln WT(-0.00113) + 0.0103$$

Figure 14. Generated Exponential growth curve of larval O. dofleini
raised at the Vancouver Aquarium in January 1981.

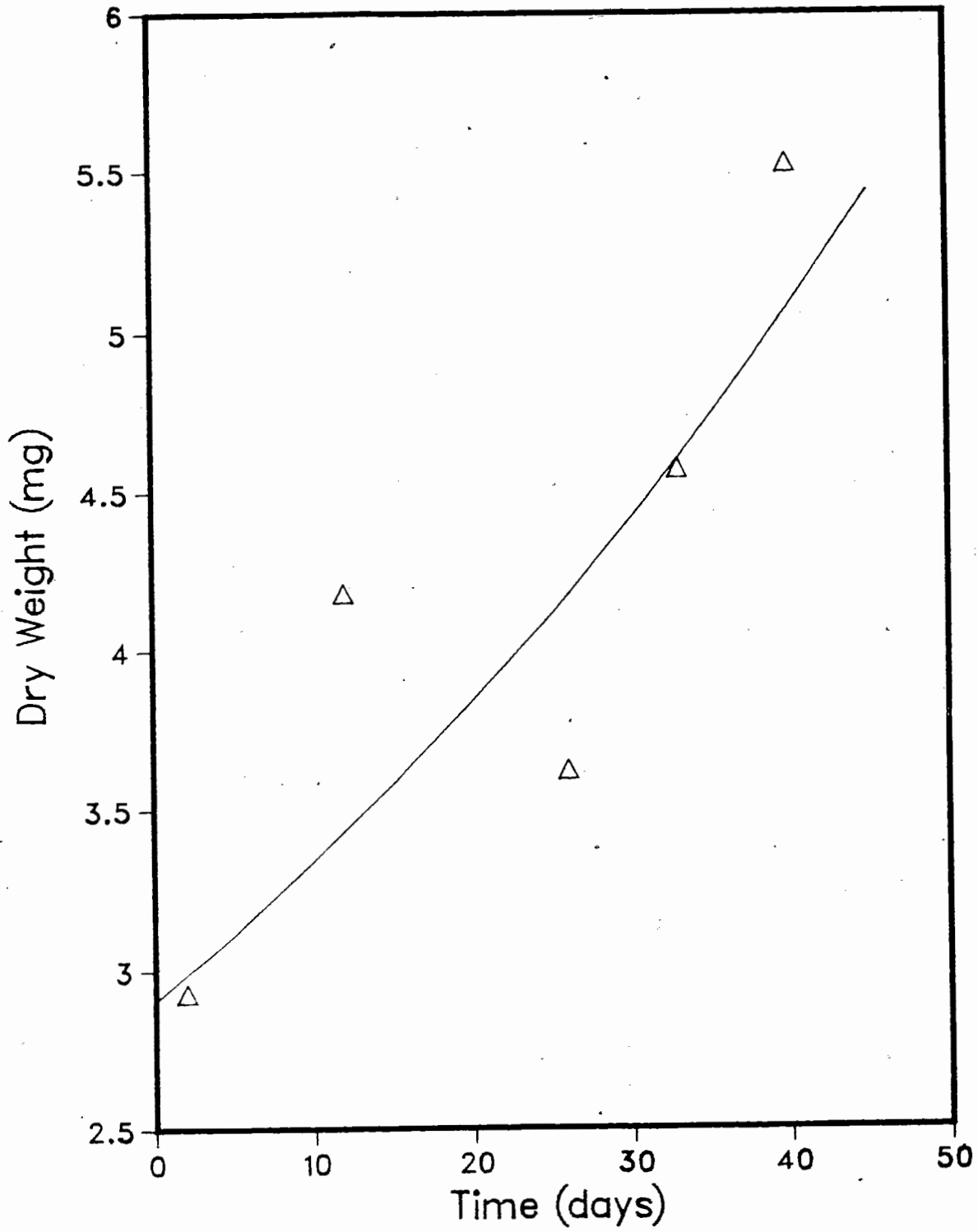
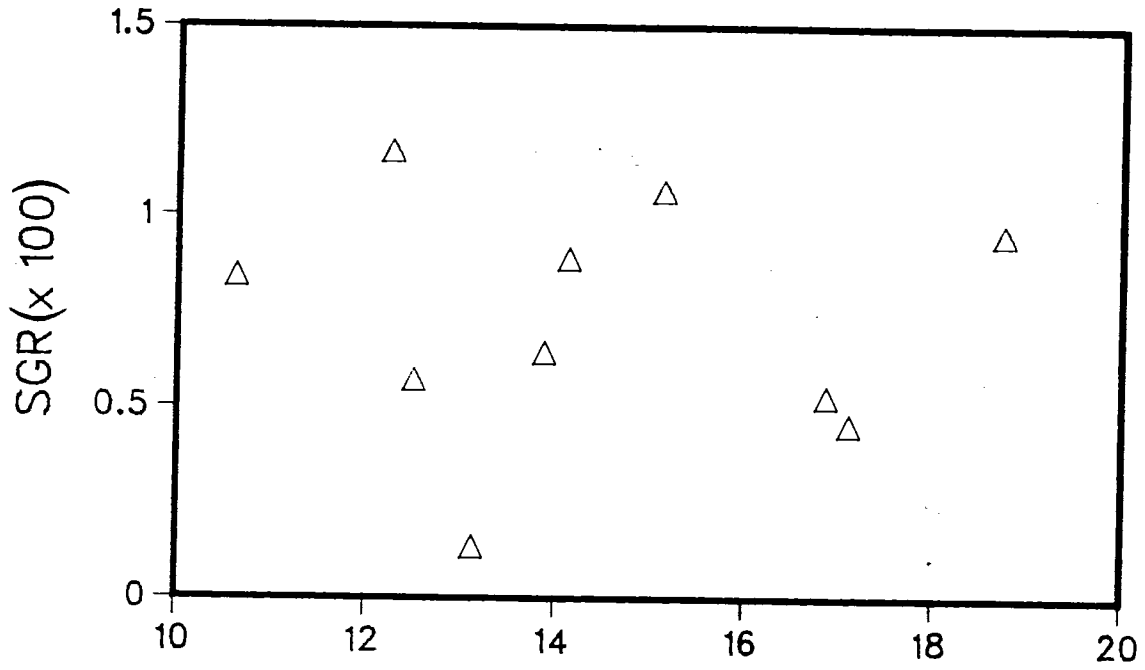


Table 8. Summary of the laboratory growth and feeding experiments at the Bamfield Marine Station and the Vancouver Public Aquarium. N=number of weighing sessions, SGR=specific growth rate, %Eaten=the %body weight of food ingested, Efficiency=food conversion efficiency. Brackets denote ranges.

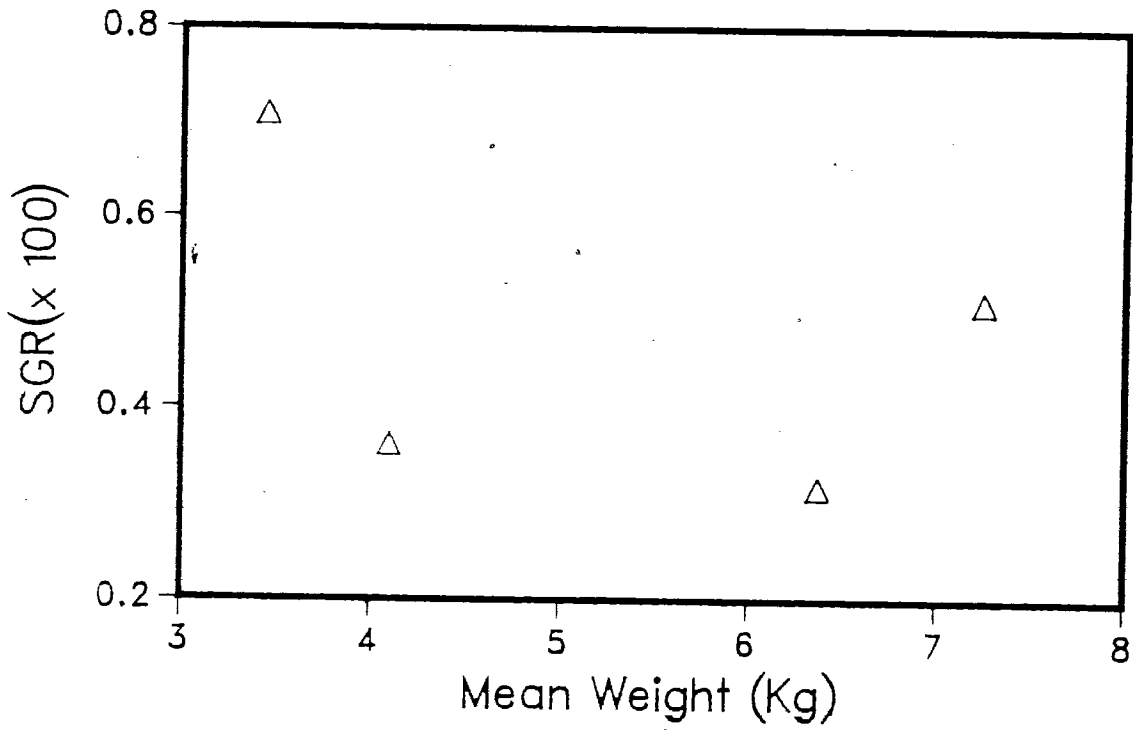
| Octopus No. | N | Sex | Site | Average Wet Weight (Kg) | Food | SGR (x 100) | %Eaten | Efficiency (%) |
|-------------|---|-----|-----------|-------------------------|-------|---------------------|---------------------|---------------------|
| 1 | 3 | F | Bamfield | 13.25 (12.0-15.0) | crabs | 0.53 (0.14-0.89) | 1.19 (0.86-1.51) | 45.2 (11.8-66.1) |
| 2 | 3 | F | Bamfield | 12.25 (10.0-14.5) | crabs | 0.89 (0.64-1.17) | 1.55 (1.26-1.76) | 58.2 (36.7-71.4) |
| 3 | 3 | M | Bamfield | 16.92 (14.0-20.0) | crabs | 0.85 (0.53-1.07) | 1.15 (1.09-1.23) | 72.7 (48.4-86.4) |
| 4 | 1 | M | Bamfield | 17.13 (14.8-19.5) | fish | 0.46 | 0.71 | 64.5 |
| 5 | 2 | M | Vancouver | 3.78 (3.0-4.3) | fish | 0.54 (0.36-0.71) | 1.02 (0.93-1.11) | 54.4 (32.6-76.1) |
| 6 | 2 | M | Vancouver | 6.81 (6.0-7.8) | fish | 0.42 (0.32-0.51) | 0.71 (0.52-0.91) | 59.0 (56.3-61.7) |

Figure 15. The relationship between the SGR and the mean weight of O. dofleini raised at the Bamfield Marine Station and the Vancouver Aquarium.

Bamfield



Vancouver



and for Vancouver:

$$\ln SGR = \ln WT(-0.433) - 4.697$$

where SGR is the specific growth rate and WT is the mean weight(Kg).

When food relationships are examined, there are no clear patterns displayed. The mean weight vs % body weight eaten/day shows a negative curvilinear relationship with a correlation coefficient for Bamfield of 0.38 and for Vancouver of 0.53(Fig. 16). Neither of these coefficients is significantly different from zero($p > 0.05$).

An analysis of covariance showed no significant difference in the relationship between the % body weight eaten per day and the SGR for the two study locations($p > 0.05$). Therefore the data from the two studies were pooled. The equation for the line was:

$$SGR = \ln EAT(0.00486) + 0.00616$$

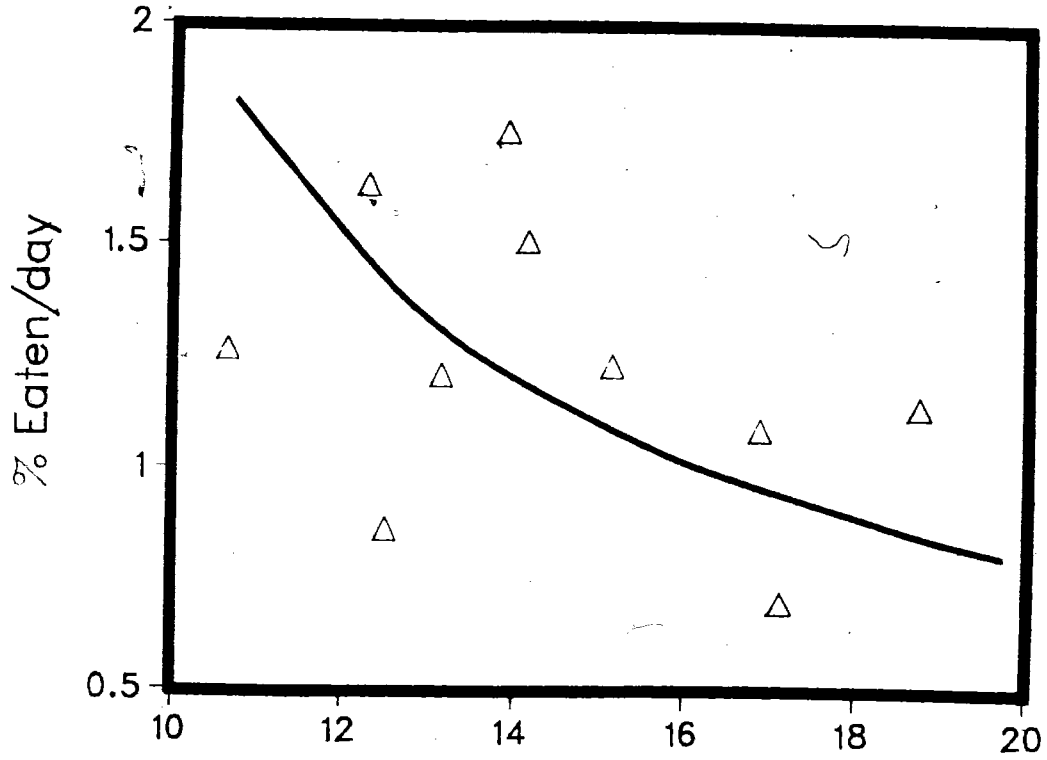
where SGR is the specific growth rate and EAT is the % body weight of food eaten per day(Fig. 17). The correlation coefficient(0.54) was significantly different from zero($p < 0.05$).

IV. Field Cage Studies

A summary of the growth of the juvenile O. dofleini raised in the underwater cages at MacIntosh Rock and MacIntosh Channel may be seen in Table 9. The octopuses fed readily on the food offered and would select crabs over bivalves as food items. Of the bivalves eaten, those with the thinner shell were taken first and were generally broken apart as opposed to being

Figure 16. The relationship between the percent body weight of food eaten per day and the mean weight of O. dofleini raised at the Bamfield Marine Station and the Vancouver Aquarium. The fitted lines are the result of least squares regression after the appropriate logarithmic transformations.

Bamfield



Vancouver

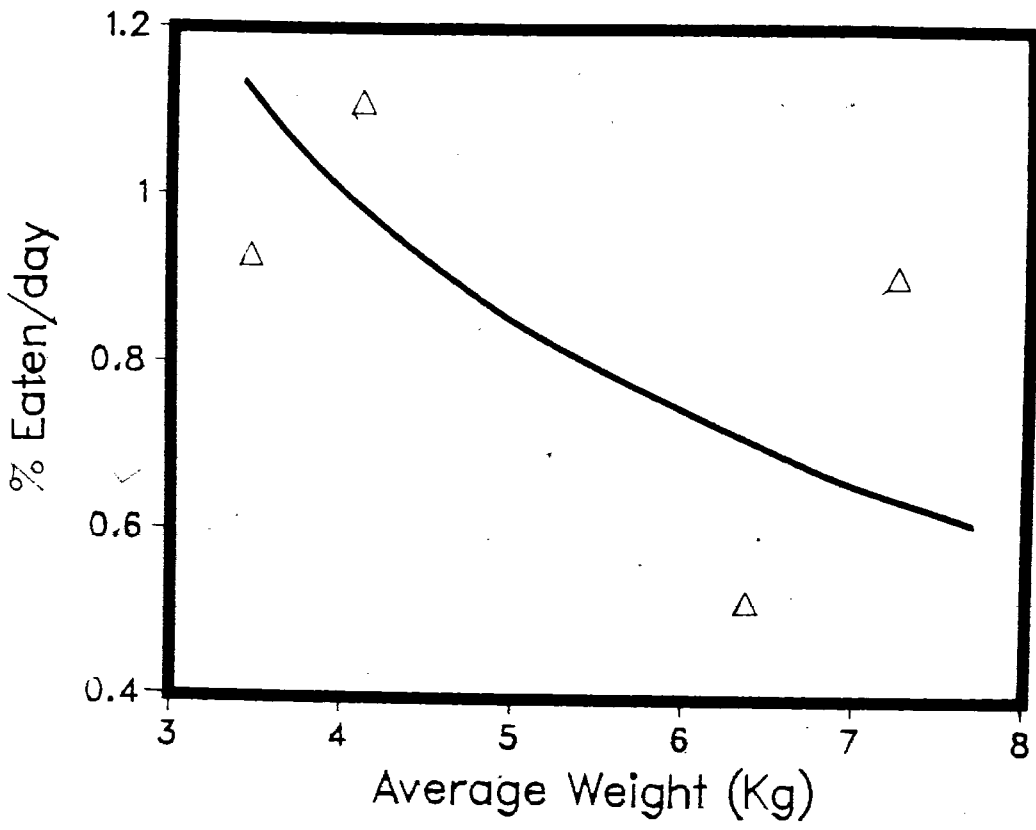


Figure 17. The relationship between the SGR and the percent body weight of food eaten per day. Data from Bamfield and Vancouver are combined. The fitted line is the result of least squares regression after the appropriate logarithmic transformations.

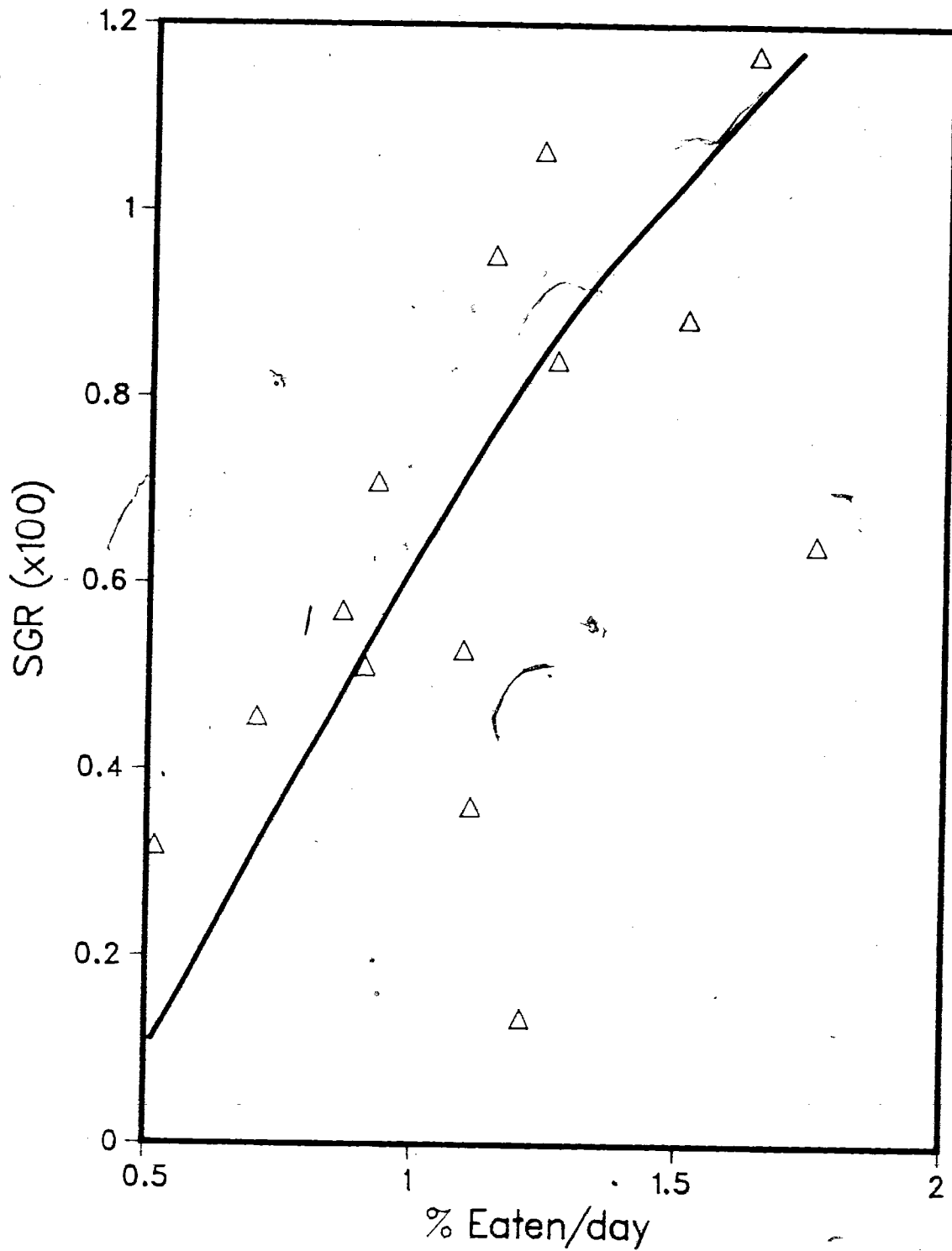


Table 9. Summary of growth experiments in the field cages, at MacIntosh Rock and MacIntosh Channel.

N=number of weighing sessions, Time=length of time the octopus was monitored, SGR=specific growth rate. Brackets denote ranges.

| Octopus No. | N | Sex | Site | Average Wet Weight (Kg) | Time (days) | SGR (x 100) |
|-------------|---|-----|-------------------|-------------------------|-------------|---------------------|
| 1 | 5 | F | MacIntosh Rock | 0.0128 (0.005-0.037) | 35 | 3.06 (0.87-3.98) |
| 2 | 5 | M | MacIntosh Rock | 1.40 (0.875-1.85) | 24 | 1.69 (1.04-3.56) |
| 3 | 1 | M | MacIntosh Rock | 1.69 (1.60-1.78) | 6 | 1.73 |
| 4 | 4 | F | MacIntosh Rock | 0.36 (0.25-0.55) | 24 | 1.69 (1.21-2.28) |
| 5 | 2 | F | MacIntosh Channel | 3.29 (2.73-3.85) | 11 | 1.90 (1.40-2.39) |
| 6 | 5 | F | MacIntosh Channel | 0.47 (0.30-0.83) | 24 | 1.98 (1.33-3.24) |

drilled.

In the growth curve analysis, Octopus No. 1 was analyzed separately as it was the smallest specimen examined during the study (there was a tenfold weight difference between it and the next largest octopus). Octopus No. 1 grew exponentially during the 65 day study period. Growth was described by the exponential growth curve:

$$WT = \exp(0.0310(t) + 1.609)$$

where WT is the octopus wet weight (g) and t is time (days). The derived growth curve and data points may be seen in Figure 18.

A Mann-Whitney U test was used to test for differences in the SGR and the mean weight of octopuses (No. 2 to 6) between MacIntosh Rock and MacIntosh Channel. No significant difference was found ($p > 0.05$) and so the data were pooled. No clear pattern was displayed between the SGR and the mean weight for octopuses No. 2 to 6. The slope was negative and the correlation coefficient (-0.058) was not significantly different from zero ($p > 0.10$). No growth curve was generated for these animals.

V. Maturation Studies

The results of the gonad collections taken from May 1981 to May 1982 may be seen in Table 10. A strong linear relationship existed between the weight of the gonad and the volume of the water it displaced. This relationship was found to be significantly different ($p < 0.05$) between males and females using an analysis of covariance. For males the line of best fit was:

Figure 18. Generated Exponential growth curve with fitted data points
for the 5 g juvenile O. dofleini(No: 1) raised in an
underwater cage at MacIntosh Rock during the summer of 1981.

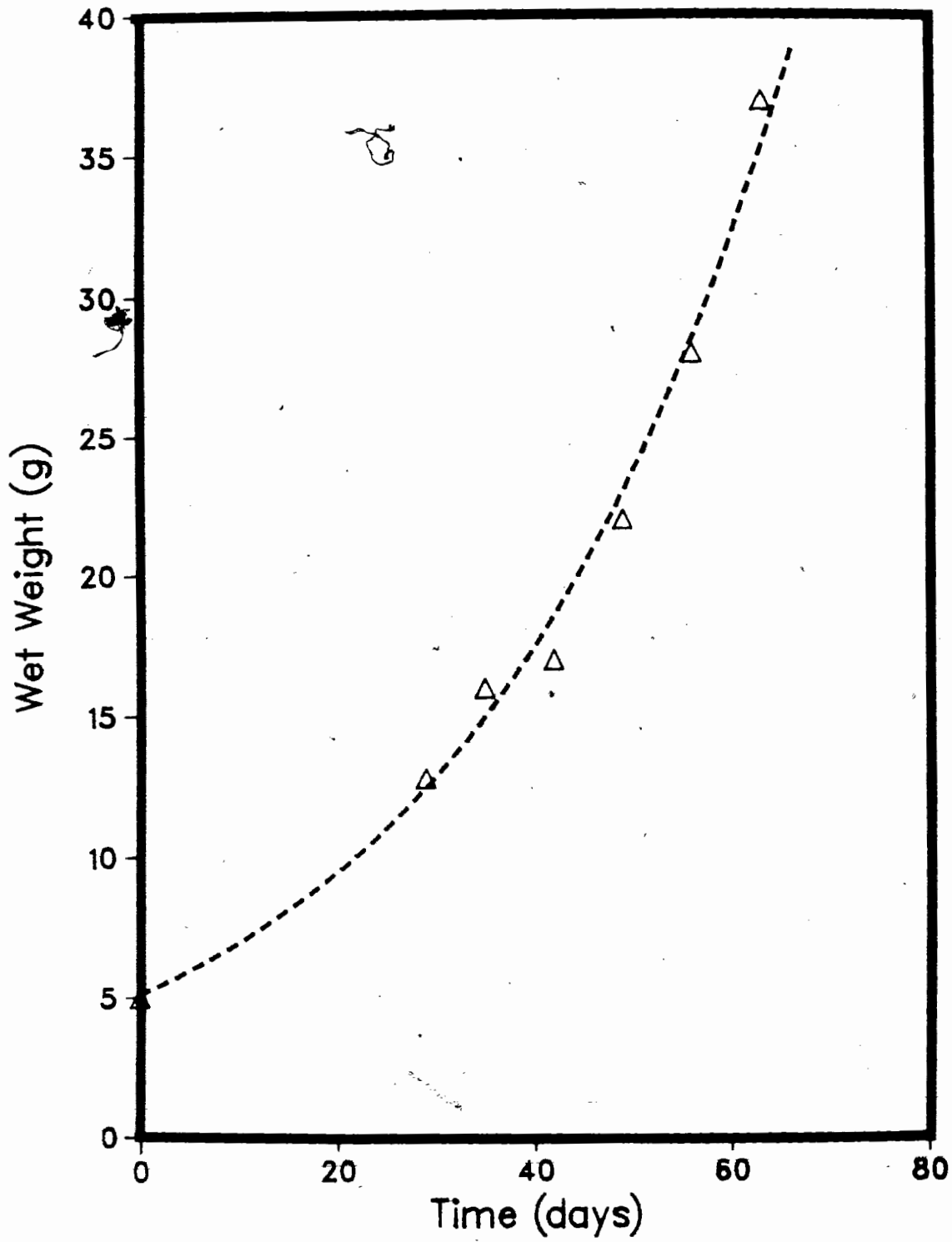


Table 10. Weights of the octopuses captured in Clayoquot Sound for reproductive studies from May 1981 to May 1982 and the gonad weights.

| Octopuses | n | Wet Weight(Kg) | | Gonad Weight(Kg) | |
|--------------|----|----------------|------|------------------|--------|
| | | \bar{x} | s.d. | \bar{x} | s.d. |
| all captures | 94 | 8.16 | 4.25 | 45.02 | 104.12 |
| males | 25 | 9.11 | 3.94 | 73.19 | 78.85 |
| females | 69 | 7.82 | 4.33 | 14.76 | 43.40 |

$$GVOL = GWT(1.038) - 2.856$$

where GVOL is gonad volume(ml) and GWT is gonad weight(g). The correlation coefficient for this relationship was 0.999 and was significantly different from zero($p < 0.001$). The line of best fit for the females was:

$$GVOL = GWT(1.015) + 0.068$$

The correlation coefficient was 0.999 and was significantly different from zero($p < 0.001$)(Fig.19).

When the mean gonadal index was examined on a monthly basis for males and females, it did not appear as though there was any clear breeding season (Table 11). For males, there was some variation in the index per month but no pattern was obvious. No samples were obtained during the months December to February, June and September. The index for females stayed fairly constant throughout the year at a low level except for the month of February when one female octopus had a large gonadal index.

The relationship between the gonadal index and the live wet weight of the octopus may be seen in Figure 20. It would appear that males and females are following two different curves and this is confirmed by an analysis of covariance($p < 0.001$). Males appear to experience an increase in testes weight at a body weight of approximately 7.5 Kg while the ovaries in the females start to increase at approximately 16 Kg. The line of best fit for the males is:

$$INDEX = \exp(WT(0.209) - 0.393)$$

where INDEX is the gonadal index and WT is the wet weight of the

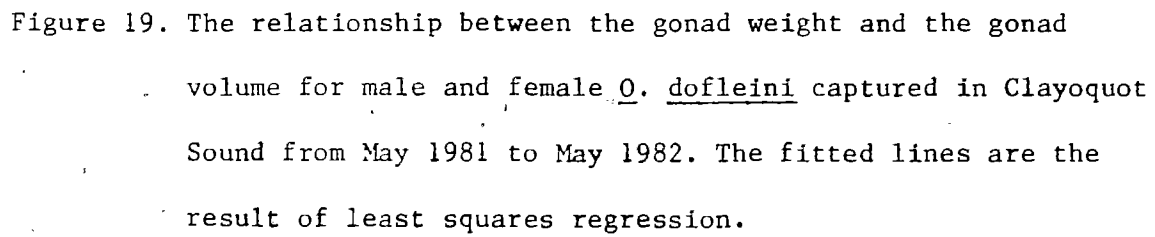


Figure 19. The relationship between the gonad weight and the gonad volume for male and female O. dofleini captured in Clayoquot Sound from May 1981 to May 1982. The fitted lines are the result of least squares regression.

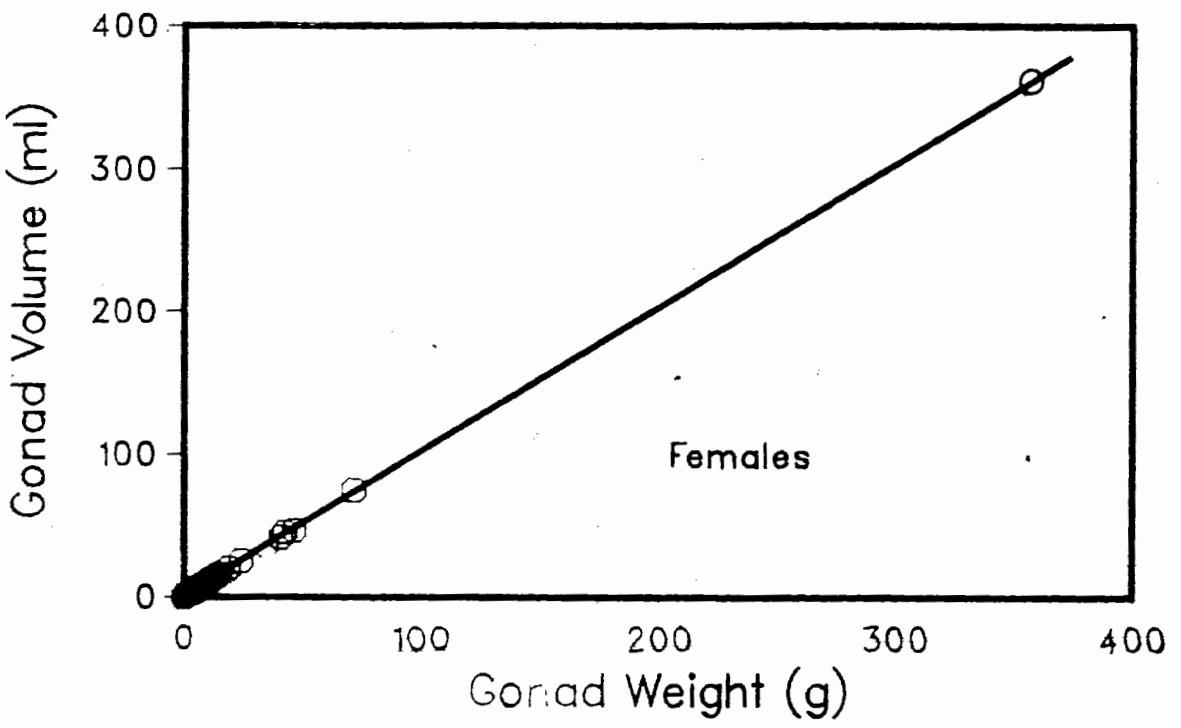
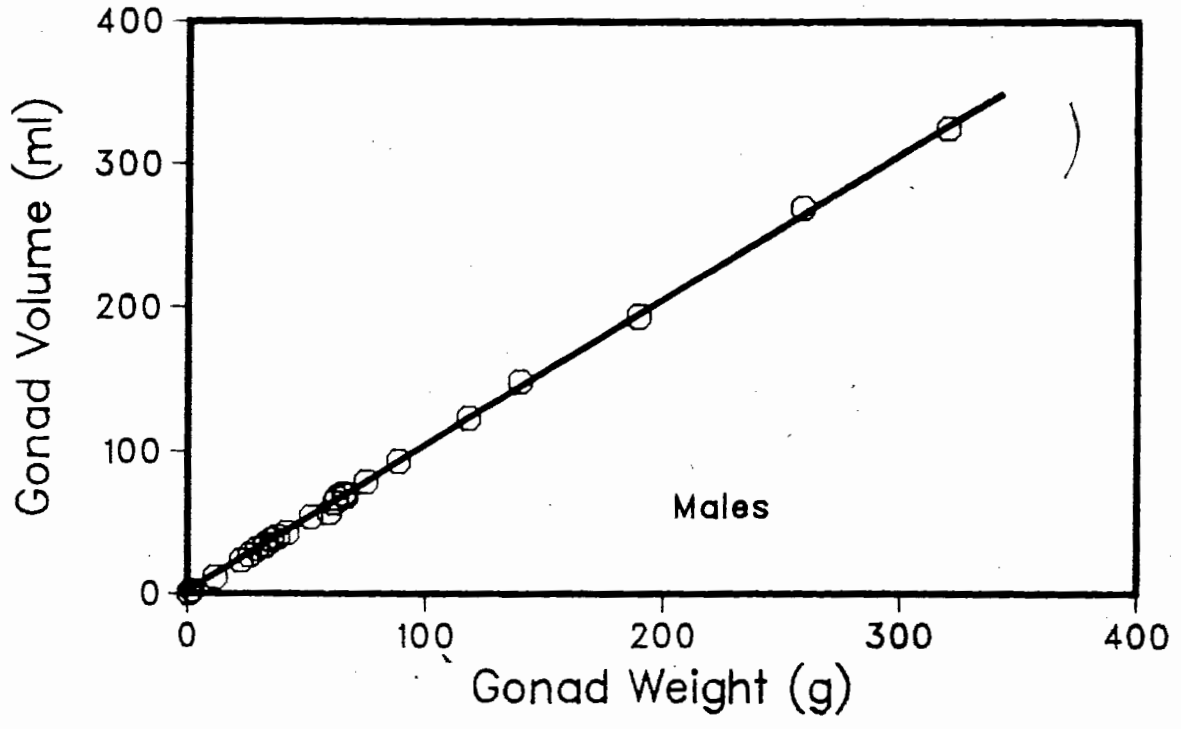
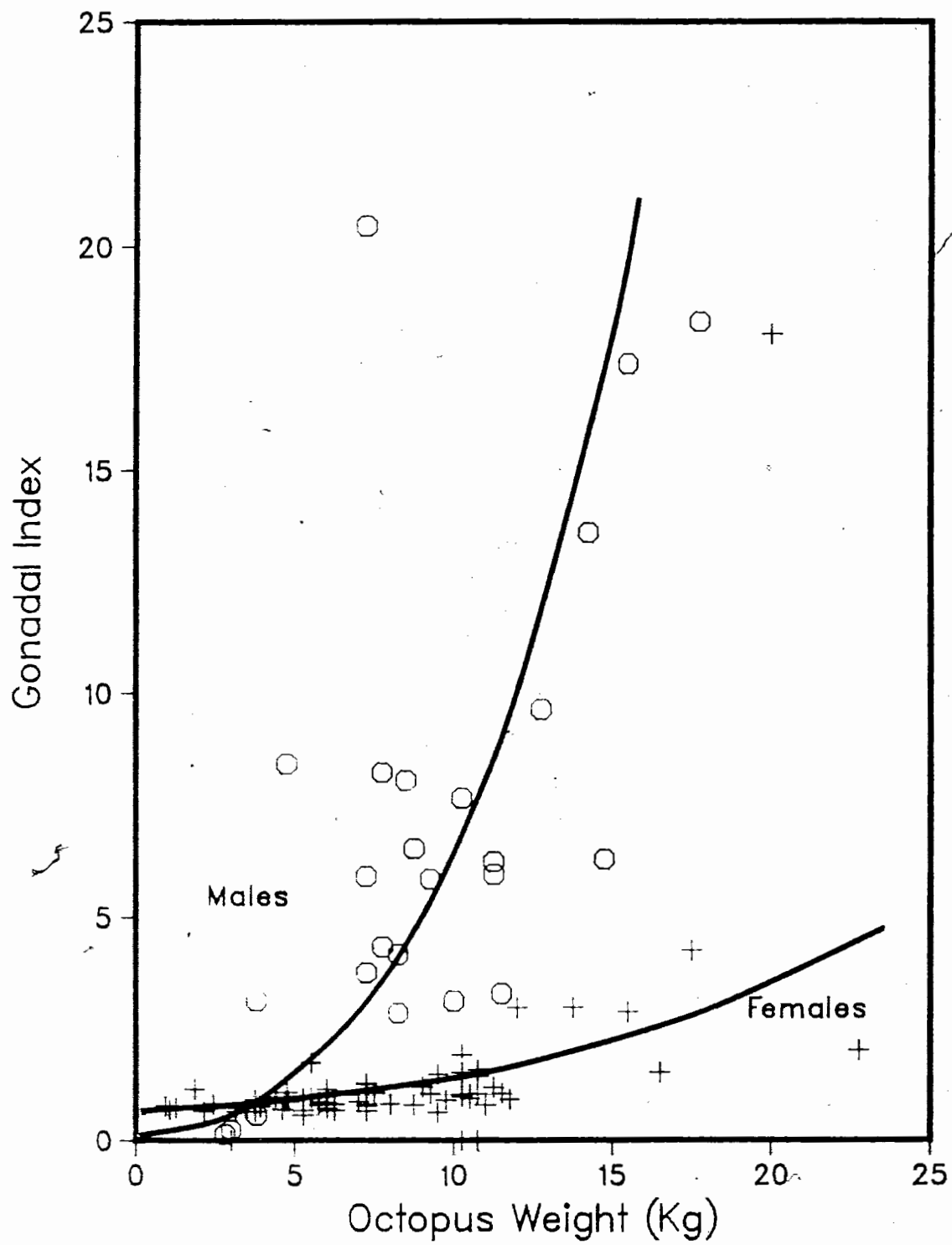


Table 11. Mean gonadal indices per month for octopuses captured in Clayoquot Sound for reproductive studies from May 1981 to May 1982.

| Month | n | Males | | n | Females | |
|--------------|---|-----------|------|----|-----------|-------|
| | | \bar{x} | s.d. | | \bar{x} | s.d. |
| May 1981 | 1 | 4.17 | - | 4 | 1.06 | 0.23 |
| June | 0 | - | - | 9 | 0.79 | 0.51 |
| July | 1 | 13.59 | - | 4 | 1.16 | 0.23 |
| August | 2 | 5.45 | 1.55 | 7 | 0.62 | 0.45 |
| September | 0 | - | - | 0 | - | - |
| October | 6 | 4.01 | 3.62 | 16 | 1.44 | 1.05 |
| November | 5 | 7.57 | 7.78 | 14 | 1.02 | 0.42 |
| December | 0 | - | - | 3 | 1.08 | 0.59 |
| January 1982 | 0 | - | - | 3 | 0.77 | 0.08 |
| February | 0 | - | - | 2 | 10.52 | 10.64 |
| March | 4 | 10.54 | 8.45 | 2 | 0.88 | 0.08 |
| April | 2 | 6.11 | 0.20 | 2 | 1.26 | 0.47 |
| May | 4 | 7.37 | 1.70 | 3 | 0.99 | 0.17 |

Figure 20. The relationship between the gonadal index and the wet weight of O. dofleini males and females. The fitted lines are the result of least squares regression after the appropriate logarithmic transformations.



octopus(Kg). The correlation coefficient(0.68) for this line was significantly different from zero($p < 0.01$). For the females, the line of best fit was determined to be:

$$\text{INDEX} = \exp(W(0.0888) - 0.618)$$

The correlation coefficient(0.72) was significantly different from zero($p < 0.01$).

Upon examination of the state of maturity of the gonads, the smallest male found to have produced spermatophores weighed 12.5 Kg and had a gonadal index of 9.65. Six males were captured which weighed 12.5 Kg or more and of these, only one weighing 14.75 Kg did not have any spermatophores. It had a gonadal index of 6.31. Mature males were found in March, May, July and November. The largest gonadal index for females observed was 18.05 from a 20.0 Kg female. A large number of eggs were present which could easily be seen with the naked eye, but they were still in a developing stage.

D. Discussion

Population Information

In Clayoquot Sound, the sex ratio of Octopus dofleini is strongly skewed toward females in the shallow water inshore region. This trend agrees with Hartwick et al. (1981) who found a significantly different male:female sex ratio of 1:3.3 among O. dofleini caught in the same area. The males of this species appear to spend much of their time in deeper water as a trapping experiment in deeper water showed a sex ratio skewed towards males (Hartwick et al., 1982). The sexual partitioning of habitat is not absolute as males are found inshore, although the reasons for this separation of sexes are not understood. Possible explanations may relate to mortality from predation and sexual differences in behaviour.

No density measurements were calculated for either Moser Point or MacIntosh Rock because of the difficulty in getting an accurate measurement of the area involved. However, the same discrete areas were surveyed at each two week interval and it was apparent that Moser Point encompassed a larger area. Therefore, more animals were captured there. If the assumption is made that the catchability of octopuses is the same for all months of the year and that the number captured accurately reflects the number of octopuses present, then two periods of

abundance occurred at both study sites, a period from August to January when the animals were common and from February to July when they were less abundant. This trend suggests a seasonal movement or migration or possible seasonal mortality rates. While migration patterns have not been demonstrated for this species in North America, Japanese studies have shown two roundtrip migrations a year off the island of Hokkaido (Mottet, 1975).

The wide range of sizes encountered in this study implies that at least two benthic year classes of animals are present at any one time in the shallow water inshore area. This view is based on the growth curves derived in this study. While the weights are skewed towards the lower end of the distribution, the presence of animals in all size classes suggests that the growth rates of the octopuses may be very variable or that recruitment into the population is continuous. The idea of continuous recruitment has been reported for O. dofleini in Japan (Mottet, 1975).

Growth Aspects

In this study the specific growth rates were not significantly different between male and female O. dofleini. This conclusion agrees with a study on O. cyanea (van Heukelem, 1976), but differs from results on O. joubini (Forsythe, 1981) and on O. vulgaris (Smale and Buchan, 1981). The reasons for sexual growth differences were unclear in the latter studies but

the difference may have been due to differential maturation times between the sexes. If there is a sexual growth difference in O. dofleini it will probably have to be determined in carefully controlled laboratory experiment.

The growth of O. dofleini did not differ significantly between locations despite differences in exposure. Judging from the food remains at den entrances in the two sites, octopuses were feeding on the same basic prey items.

I discovered two distinct growth periods for O. dofleini, a period of slow growth from January to June and a period of more rapid growth from July to December. The existence of growth seasons has been suggested for O. dofleini by Hartwick et al. (1981) and has been reported for O. cyanea (Wells and Wells, 1970) and Eledone cirrhosa (Boyle and Knobloch, 1982). The mean SGR per month was observed to drop at the same time that the drop in the water temperature and salinity occurred. The effect of a drop in the temperature of the water on O. vulgaris has been examined by Mangold and Boletzky (1973) and Wells (1978). Both studies found that a decrease in water temperature decreased the growth rate by reducing the daily food intake. No work has been done on the effects of changes in salinities.

The only information available on seasonal food availability in Clayoquot Sound comes from a study by Hartwick et al. (1982). They show incidental captures of Cancer productus, one of the major food items of O. dofleini, in octopus traps in Clayoquot Sound from December 1981 to June 1982

(Fig. 21). The mean number of crabs per trap decreased rapidly after December and did not approach December levels again until June, closely following the seasonal water temperature patterns. Unfortunately, the data only covered this six month period and therefore fluctuations in the other months are unknown. The use of this data to measure the abundance of C. productus in this area is unwarranted as the trapping is only a measure of the crab catchability. However, if it is assumed the catchability is related to the ease of an octopus obtaining food, then the decline in crab catchability may help to explain the seasonal growth separation (i.e. less food in the winter).

In this study, O. dofleini was found to have rapid growth and was comparable to many smaller, warm water species of octopuses at approximately the same stage in the life cycle (Table 12).

With respect to planktonic octopus larvae, very little comparable literature exists. The sizes of eggs and larvae at hatching agree with Mottet's (1975) report although her measurements are not as detailed. The only source of planktonic octopus growth rate information comes from a study on O. vulgaris (Itami et al., 1963). Using their data I calculated that for the first 30 days, the specific growth rate was 0.1253 at 24.7°C. This value is approximately four times higher than the growth rate found in this study (0.0325) and is probably due to better quality food and higher water temperatures.

Figure 21. Incidental red rock crab (Cancer productus) captures in experimental octopus traps in Clayoquot Sound from December 1981 to June 1982. (data from Hartwick et al., 1982).

Total Incidental Captures of *Cancer productus*

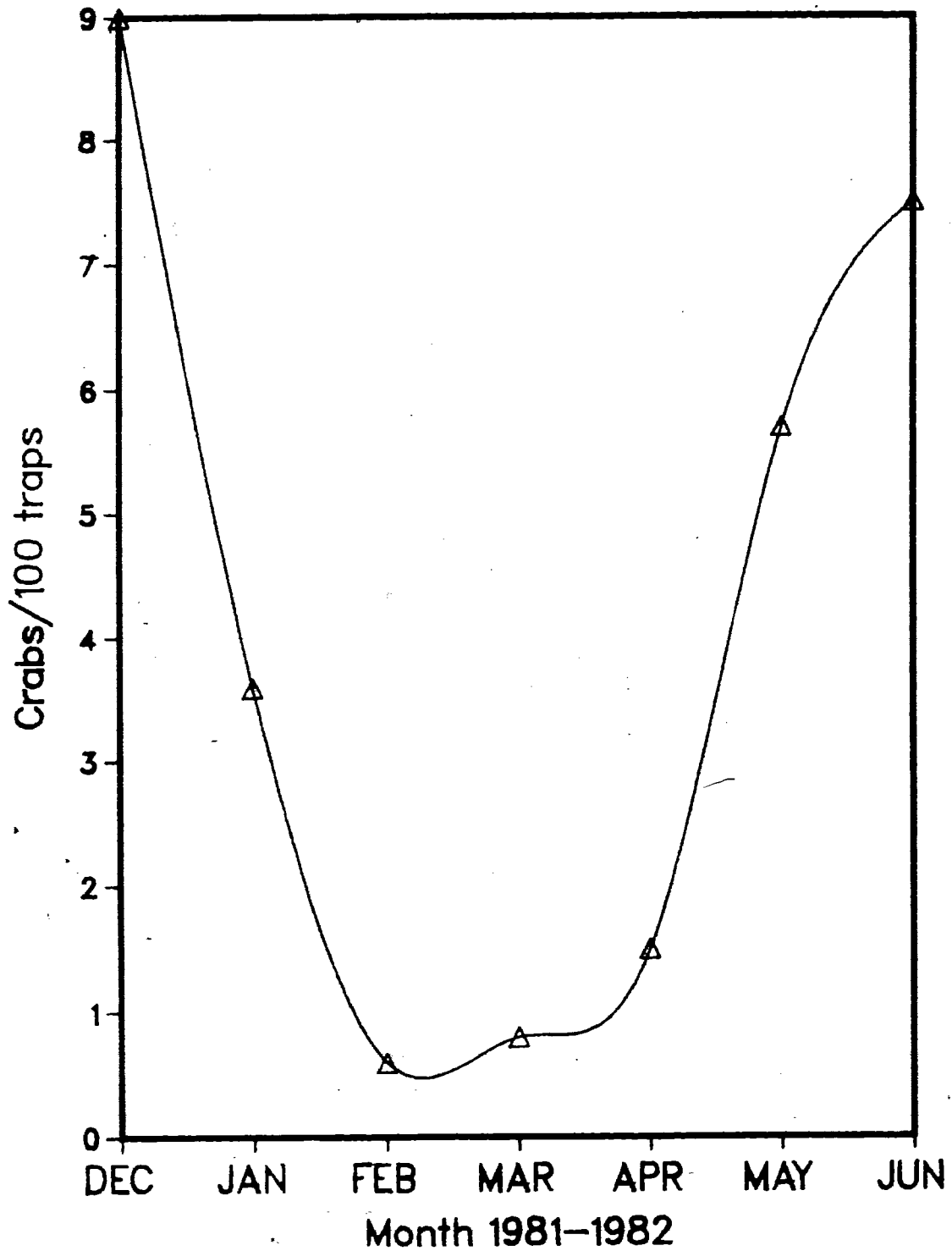


Table 12. Comparative table showing growth rates of O. dofleini in this study and the growth rates found in laboratory studies on other warm water octopus species. SGR=specific growth rate, Time=the duration of the study(days), Temp=water temperature.

| Octopus Species | Weight Range | SGR (x 100) | Time (days) | Temp. (°C) | Source |
|-------------------------|--------------|-------------|-------------|------------|-------------------------------|
| LARVAE | | | | | |
| <u>Octopus dofleini</u> | 22-36mg | 0.3-3.3 | 40 | 9.4 | *** |
| <u>O. vulgaris</u> | ?? | 12.5 | 30 | 24.7 | Itami <u>et al.</u> (1963) |
| JUVENILES | | | | | |
| <u>O. dofleini</u> | 5.0-830g | 1.3-4.0 | 11-35 | 12.0 | *** |
| <u>O. cyanea</u> | 4.0-49g | 5.5-5.6 | 45 | 22-27 | vanHeukelem(1976) |
| <u>O. joubini</u> | 5.3-9.2g | 1.9-2.7 | 20 | 20-26 | Forsythe(1981) |
| <u>O. vulgaris</u> | 47-1930g | 0.8-4.4 | 20-208 | 15-25 | Nixon(1966) |
| <u>O. tetricus</u> | 200-800g | 1.9-5.0 | 42 | 20.0 | Joll(1977) |
| ADULTS (FIELD) | | | | | |
| <u>O. dofleini</u> | 1.6-18.8Kg | 0.2-2.5 | 14-210 | 7.5-13 | *** |
| <u>O. dofleini</u> | 2.9-8.9Kg | 0.6-1.8 | 14-67 | ? | Hartwick <u>et al.</u> (1981) |
| ADULTS (LABORATORY) | | | | | |
| <u>O. dofleini</u> | 3.0-20.0Kg | 0.1-1.2 | 42 | 9.0-11.0 | *** |
| <u>O. dofleini</u> | 2.5-4.0Kg | 0.6-1.1 | 40-45 | 10-13 | Hartwick <u>et al.</u> (1981) |
| <u>O. cyanea</u> | 1.2-6.4Kg | 1.3-2.1 | 15-75 | 22-27 | vanHeukelem(1976) |
| <u>O. vulgaris</u> | 0.5-1.8Kg | 0.9** | 139 | 20-25 | Smale and Buchan (1981) |

=mean weight, *=this study.

My results show that larval O. dofleini are capable of growth at an exponential rate. However, I think that my highest observed growth rate of 0.0325 underestimates the growth of larvae in the field. This is because none of the larvae reached the settling stage, and both the food source and the water currents experienced by the larvae were unnatural. It is possible that octopus larvae may have an innate feeding response to certain planktonic prey species and that the frozen krill was a poor substitute. The ability to grow rapidly would be advantageous to the larval octopuses in that it would allow them to quickly pass through many predators' prey size ranges and eventually into a possible size refuge. There are no good estimates for the duration of the planktonic phase of O. dofleini in the Pacific Northwest but in Japan, Itami et al. (1963) report that settling was observed for O. vulgaris at 32 days after hatching at a water temperature of 24.7°C. This planktonic phase may be longer for O. dofleini in British Columbia because of the colder water temperatures.

Newly settled benthic octopuses also appear to be capable of exponential growth based on the field cage results for Octopus No. 1. The highest observed growth rate of 0.0398 is lower than those of O. vulgaris where rates of 0.0885 for animals 6.7 to 39.4 g were found (Itami et al., 1963).

The results from the field work on adult and subadult (>0.5Kg) O. dofleini indicate that the specific growth rate is size related, with smaller octopuses having higher

growth rates (although, there was a large amount of variation in all size classes studied). This negative curvilinear relationship is common and is exhibited in many animals. Van Heukelem (1976) refers to Medawar (1945) who states that tissue gradually loses its ability to replicate itself at the rate it was formed. This trend has been reported for O. tetricus (Joll, 1977), O. vulgaris (Nixon, 1966), Eledone cirrhosa (Boyle and Knobloch, 1982), O. joubini (Opresko and Thomas, 1975; Forsythe, 1981), and O. cyanea (van Heukelem, 1976). The same large amounts of variation in growth rates with respect to size were also found in these studies. In a review on molluscs in general, Wilbur and Owen (1964) concluded that the remarkable thing about mollusc growth was the variability in its rates. For O. dofleini, this variation could be caused by differing amounts of food ingested, tagging disturbances, genetic differences in digestive rate and/or food conversion efficiency, and intra or interspecific competition. O. dofleini has a high rate of growth and therefore the annual production of the animals must be considerable. The laboratory and field cage studies support the conclusions of the field study and show that growth at ad lib feeding conditions in a captive situation is equal to the field situation. The apparent contradictory results from the laboratory studies (octopuses at Bamfield being larger and having higher SGR's than those at the Vancouver Aquarium) are the result of the food type fed to the animals. If each location is examined separately, the smaller octopuses had higher SGR's

than the larger ones.

Growth Model Evaluation

While many growth curves and methods of describing them have been developed, some problems become apparent when they are applied to invertebrates. The major difficulty in this study was associated with my inability to age the octopuses although I examined many octopus beaks for growth lines during a morphometrics study (Robinson and Hartwick, 1983). Without age indicators, it is impossible using standard techniques, to back calculate to determine equation parameters and to examine the growth model for the degree of fit to the data. I therefore used Kaufmann's (1981) technique and generated two growth models: an Exponential curve for January to June and a logistic curve for July to December. The two methods used to place the data points on the growth curves show that the derived curves are not unreasonable and that the variation in growth is relatively uniform around the curve.

The model used for the growth description of the fast season is an model. This is somewhat misleading as no animals were found in the asymptotic weight range (27 Kg). Therefore extrapolation to this region is unwarranted. It is the lower part of this model which gives a satisfactory fit to the data. The topic of asymptotic growth models and their applications to octopus has been considered by van Heukelem (1976) in a study on O. cyanea. He has hypothesized that because the animal reaches

its final size when it is mature, and that growth will be reduced if the octopus is experiencing hardships, then there will be no single final size or asymptote that the animals will reach. This then, van Heukelem argues, invalidates the use of asymptotic models and he subsequently used a power curve to describe growth. The objective of this study was to describe the growth of O. dofleini as best as possible and so I chose not limit the number of growth models available for growth description.

While the growth of octopuses over 2 Kg can be seen in the two growth curves, some estimate of the actual age at approximately 2 Kg is needed in order to fully utilize the curves. The only source of information on age comes from Mottet's (1975) review of various Japanese studies on O. dofleini, in which she reports that a 1 Kg octopus would unlikely be older than 1 year. If we assume that an octopus hatched in January, and then one year later it weighed 1 Kg, then, using the two growth curves, it could weigh almost 20 Kg at the end of December in the second year. This final size is double that given by Mottet(1975) who reports that O. dofleini can increase in weight from 1 to 10 Kg in a year.

Feeding Aspects

Food consumption was examined during the laboratory experiments and while definitive relationships were not obtained, certain trends were evident. I think that two factors were primarily responsible for the lack of statistical significance: the low sample numbers (in conjunction with the inherent variability in growth of the octopus) and the fact that the animals were stressed by being in an unnatural situation. Nixon (1966) noted that some retardation in O. vulgaris growth was caused by frequent handling and I noticed a brief reduction in feeding after weighing sessions.

I found an inverse relationship between the % body weight eaten/day and the mean weight of the octopus. Although this relationship was not found to be statistically significant, it does agree with other octopus feeding studies on O. tetricus (Joll, 1977), O. joubini (Forsythe, 1981), Eledone cirrhosa (Boyle and Knobloch, 1982), O. cyanea (van Heukelem, 1976) and O. vulgaris (Mangold and Boletzky, 1973; Smale and Buchan, 1981). The % body weight eaten/day was somewhat higher in the other studies, (2 to 5%/day compared to 1.3%/day in this study) but I feel this may be due in part to a smaller body size in the above species and higher water temperatures. This trend of larger octopuses eating proportionately less may help explain why the specific growth rate decreases with increasing weight. I also found there was a significant positive relationship ($p < 0.05$) between the % body weight eaten/day and the specific growth rate.

If this relationship is extrapolated back to where the specific growth rate becomes zero (based on a technique by van Heukelem (1976)), an estimate of the maintenance ration of the octopus can be obtained. I determined it to be 0.28% body weight/day. This figure is much lower than that cited by van Heukelem (1976) of 1.8% for O. cyanea.

The food conversion efficiency was found to be quite high in this study with a mean of 59% and 57% for Bamfield and Vancouver respectively. These figures closely agree with a study by Hartwick et al. (1981) who report a food conversion efficiency of 59%. O. dofleini appears to have a higher food conversion efficiency than other species; for example: 40% for O. cyanea (van Heukelem, 1976), 40% for O. joubini (Forsythe, 1981), and 50% for O. vulgaris (Mangold and Boletzky, 1973). The observed higher efficiency for O. dofleini may be caused by lower water temperatures resulting in lower metabolic expenditures which would allow more energy to be put into growth. Food conversion efficiency does not seem to fluctuate significantly with changes in the octopus weight. This consistency of food conversion over a wide range of octopus weights has been found in other studies on O. vulgaris (Nixon, 1966; 1969; Mangold and Boletzky, 1973) and on O. cyanea (van Heukelem, 1976).

Maturation

I found that male O. dofleini mature at a smaller size (12.5 Kg or greater) than do females in the shallow water population. Although there is no information on differential maturation for this species, this trend is found in O. tetricus (Joll, 1976) and in O. vulgaris (Smale and Buchan, 1981). The differential maturation may occur because spermatophores may be energetically "cheaper" to produce than eggs and therefore females may have to be larger. Females also undergo a period of starvation while they brood their eggs (Wells, 1978) and thus need large energy reserves. If the growth curves derived in this study are used and an assumption of an age of 1 year at 1 Kg is made, an age of approximately 1.5 years at maturation is obtained for males. This agrees with Mottet (1975) who reports that, in Japan, O. dofleini is mature at 1.5 to 2 years. However, the male octopuses in this study reached maturity at a smaller size (12.5 Kg) than those reported by her (15-20 Kg). She found that females matured at approximately 20 Kg.

I found no evidence of distinct seasonal reproductive cycles in this study, but this may be an artifact as only shallow water, inshore animals were sampled. In Japan, the peak spawning season is in May and June and probably occurs at depths of 50 m (Mottet, 1975). More work involving a wider range of samples needs to be done before any conclusions can be reached on this aspect for the British Columbia population.

E. Summary

1. Octopus dofleini martini had a high growth rate in the field comparable to those of many smaller warm water species of octopus at approximately the same stage in the life cycle.
2. Growth rates were very variable in all size classes examined and may have been a result of the animals being very sensitive to changes in environmental conditions.
3. There was no observed difference in the mean specific growth rate between sexes or locations.
4. There appear to be two distinct growth seasons over the year in the study areas. The first one is from January to June and the second one is from July to December. A growth curve has been drawn for each. These seasons, which were separated on the basis of observed growth rates, correspond with the yearly cycle fluctuations and a possible seasonal octopus prey availability.
5. Laboratory studies indicate that captive O. dofleini in ad lib feeding conditions grow as fast as O. dofleini in the field. There was an inverse relationship between the weight of an octopus and the percent body weight of food it ate. The food conversion efficiency was found to be generally quite high in all octopuses studied, with an overall mean of 58%.
6. Maturation results indicate that males mature sooner than

females at approximately 12.5 Kg. No mature females were found although a wide size range was sampled. There does not appear to be any distinct seasonal reproductive cycle in the observed shallow-water inshore population.

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