

THE POPULATION DYNAMICS AND ENERGY BUDGET OF *Notothenia neglecta* Nybelin AT SIGNY ISLAND, SOUTH ORKNEY ISLANDS

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ABSTRACT. The demersal fish population around Signy Island is composed of 13 species, three of which are common. The population dynamics of *Notothenia neglecta*, the most abundant and one of the largest species, has been investigated. Growth is slow and natural mortality is high. The mean biomass is 19.4 g./m.² and the annual production is low, 0.34 g./g. The results have also been considered as an energy budget. The efficiency of transformation of energy to production is low (5 per cent), because of the effect of cold adaptation and because food may be energy limiting. Consideration of *N. rossii*, an allied species, suggests that krill may be utilized as food more efficiently than benthos.

MARINE biological research based at the British Antarctic Survey station on Signy Island began in 1962 with a general ecological survey of the inshore waters of the island. Much of the taxonomy required for this work had already been published by the Discovery Investigations so that the initial work consisted of community analysis. The emphases of the initial survey have now been changed slightly to the autecology of selected groups, e.g. Amphipoda (Thurston, 1968), Isopoda (White, 1970) and fish (Everson, 1968, 1969).

Research on the population ecology of Antarctic fish has been restricted and only three workers have investigated this at all (Olsen, 1954, 1955; Wohlschlag, 1962; Hureau, 1964); they found that, for the species worked on, the growth rates were not very different from those of morphologically similar Arctic species. Because of obvious logistic difficulties, none of these programmes was extended to determine the biomass or annual production of the populations in question.

Research on the inshore fish of Signy Island has been in progress since 1964 and this paper presents the results of work on the population dynamics of the most abundant of the larger fish, *Notothenia neglecta*, and their evaluation in terms of biomass and annual production in relation to the ecosystem and in the form of an energy budget.

THE EXPERIMENTAL AREA

The South Orkney Islands form part of the Scotia arc, which extends from the Andes to the Antarctic Peninsula. The sea depth in their vicinity varies greatly; depths of 5,000 m. have been recorded 60 km. to the north. To the south the descent is far more gradual; a shelf extends for about 150 km. before the 1,000 m. depth contour is reached (Marr, 1935; Adie, 1964).

Signy Island, one of the smallest in the group, lies 1.5 km. south of Coronation Island and it is used by the British Antarctic Survey as the centre for its main biological programmes. The Survey's station is situated on the shore of Factory Cove, an inlet in Borge Bay on the east coast of the island. Part of this bay was chosen for the population study as it was typical of inshore waters in the area and conveniently accessible by small boat in most weathers.

Borge Bay has mostly rocky shores, although there are beaches of pebble and coarse sand, and several groups of rocks and shoal areas. The sea bed is very uneven, as is indicated by the irregularity of the contour lines on the chart (Fig. 1), and the substrate varies from sand and pebbles to boulders or bedrock. The transition from one substrate to another is quite rapid so that habitats in a relatively small area are likely to be very varied.

The hard rock faces form attachment surfaces for large algae, e.g. *Phyllogigas* and *Pontogeneia antarctica*, and also Gastropoda, e.g. *Margarella* sp. The sandy areas, while colonized by the large brown algae there is generally a sparse covering of red algae, *Myriogramme*, *Plocamium*, etc.

The large algae harbour quite an extensive fauna, mainly Amphipoda, e.g. *Bovallia gigantea*, *Pontogeneia antarctica*, and also Gastropoda, e.g. *Margarella* sp. The sandy areas, while not having any attached algae, frequently contain populations of free-floating *Desmarestia* while the sand itself supports large numbers of the Amphipoda *Cheiromedon femoratus* and *Tryphosa kerguelensis*, both of which scavenge in enormous numbers on animal remains.

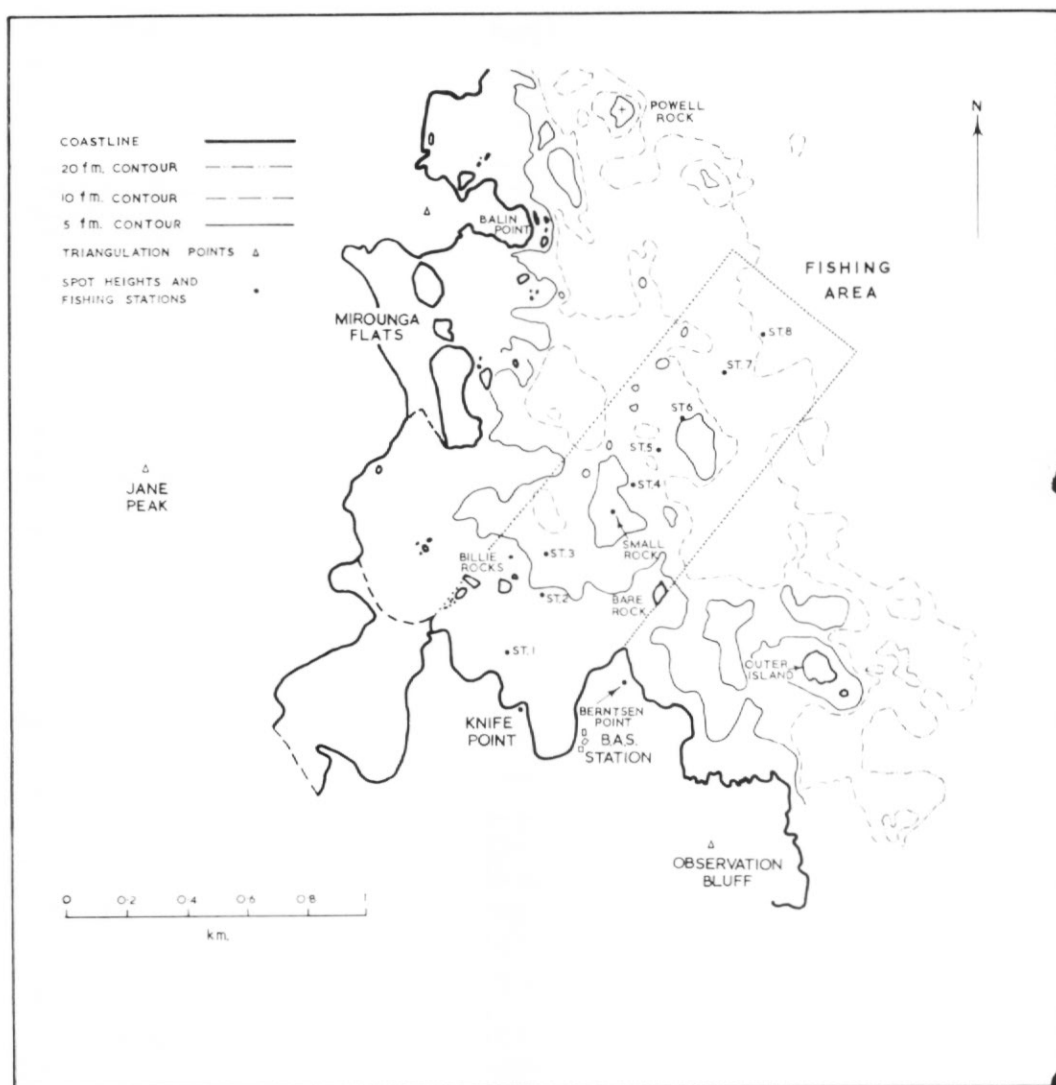


Fig. 1. Bathymetric map of Borge Bay, Signy Island, South Orkney Islands. (From soundings by Cdr J. Bradley, R.N., in December 1964–February 1965. Reproduced from British Admiralty Chart No. 1775 with the sanction of the Controller of H.M. Stationery Office and the Hydrographer of the Navy.)

In view of the size and shape of the bay, it was decided to limit the main work to an experimental area 550 m. wide extending seawards for 1,650 m., a total area of 907,500 m.². This transect was arbitrarily divided into eight zones as shown in Fig. 1. Each zone also had a station for oceanographic and quantitative benthos sampling. Uniform sampling over the whole of this area was attempted throughout the period of the investigation.

The results of monthly temperature and salinity measurements at station 8 are shown in Fig. 2. The range of only about 2.5°C, which probably represents an average seasonal cycle, is typical of an area south of the Antarctic Convergence. The salinity, although uniform for most of the period, showed a sudden drop in December 1966 after a sudden very warm spell on land which melted a lot of the previous winter's fall of snow.

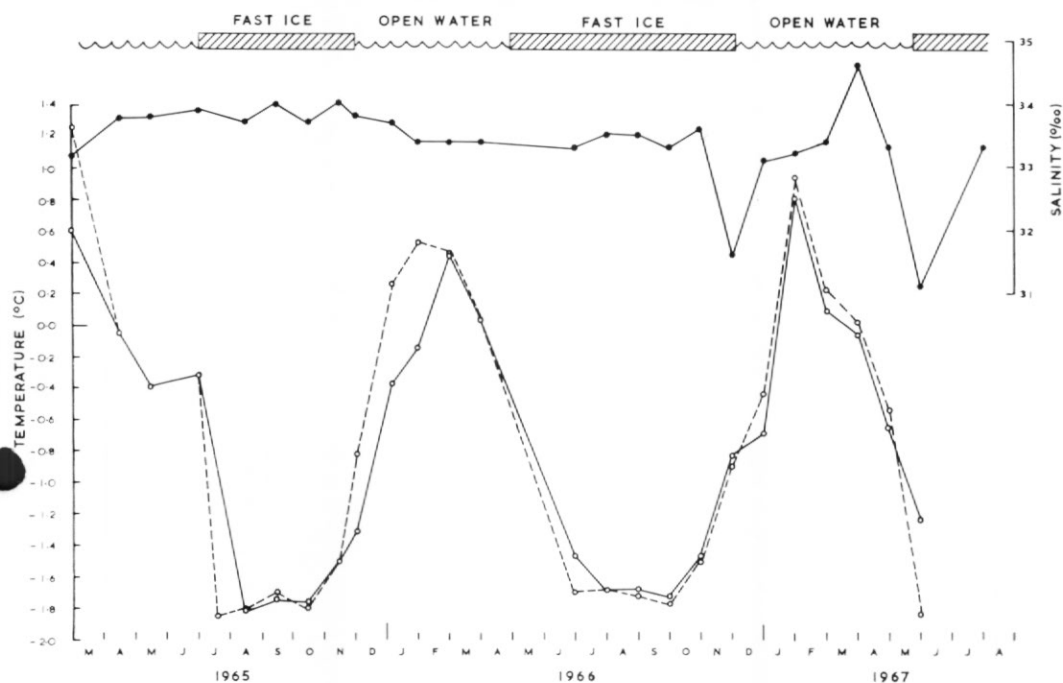


Fig. 2. Surface salinity (‰), surface temperature (pecked line) and temperature at 30 m. depth (solid line) in successive months at station 8. (Data from unpublished results of D. G. Bone, I. Everson, A. J. M. Walker and M. G. White.)

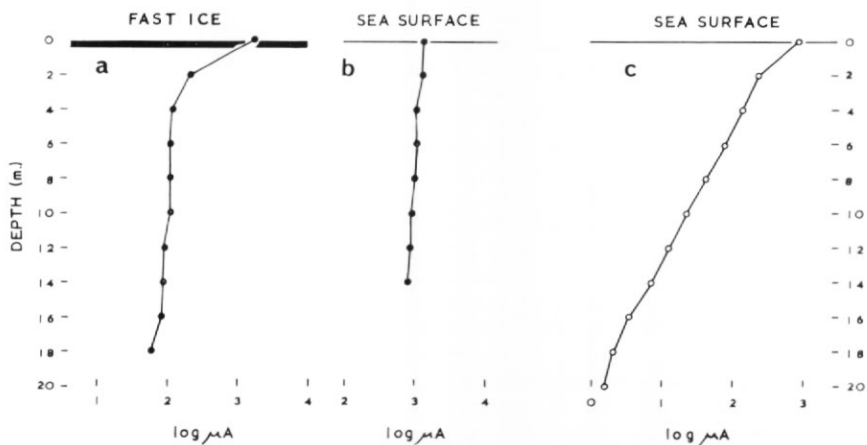


Fig. 3. Light-intensity readings at successive 2 m. depth intervals at different times of the year.
 a. 9 December 1966. The area was covered by fast ice.
 b. 14 November 1966. Through a lead about 5 m. wide.
 c. 11 December 1966. No fast ice but 5/10 pack ice.
 The steepness of the line indicates the clarity of the water.

During the winter, fast ice in the bay reduced turbidity by reducing turbulence and therefore the amount of light entering the sea. At this time the light intensity is low but the water is very clear (Fig. 3a). In the summer when there is no ice, turbidity is greatest due to the swell, and phytoplankton growth occurs because the light entering the sea is above the minimum necessary for photosynthesis.

Divers of the British Antarctic Survey and also American workers in other areas (Ray, 1970) benefit from the extreme clarity of the water at certain times of the year. It is probable that the clarity of the water is positively correlated with the amount of fast-ice cover as is shown in Fig. 3.

SUMMER FISHING

Fishing was carried out from a 16 ft. (4.9 m.) dinghy, greenheart sheathed up to the water line. Power was supplied by a small outboard motor, which was found to permit fishing when the station anemometer registered wind speed up to force 8 on the Beaufort Scale. Work was suspended when pack ice approached as even small pieces of ice were capable of dragging marker floats, and thus the gear, for quite considerable distances.

Line fishing in two forms was found to be a very effective method. Long lines, made up in 50 fathom (91 m.) lengths of Stockholm-tarred codline each having 50 No. 3 or No. 5 whiting hooks attached to Corlene snoods, were baited with penguin meat and laid along the sea bed in the evening from a drifting boat. Each line had generally caught about ten fish when lifted the following morning. Hand lines made from mono-filament nylon with two or three hooks baited with penguin meat were used successfully. They were wound on to 12 in. (30 cm.) diameter reels mounted with a fair lead on to the gunwale of the boat.

Traps of a similar design to those used by other workers (Pirie, 1908; Wohlschlag, 1962) were used extensively. They were box-shaped, 1 m. long and 0.5 m. \times 0.5 m. in cross-section, with a funnel narrowing at one end to about 15 cm. at its inner extremity. The complete upper surface, a removable hatch, was held in position with a turn button or codline lashing. The body of the trap was made from 5 cm. \times 2.5 cm. wood or "Dexion" and the whole covered with 2.5 cm. mesh chicken netting. The penguin carcasses used as bait soon became full of amphipods and it was probably the presence of the latter that induced the fish to enter the traps. Dredges and trawls, which were quite effective for some of the smaller species, caught very few larger fish, probably because *N. neglecta* tends to inhabit dense weed patches.

WINTER FISHING

The presence of fast ice over the experimental area made it possible to use sledges for the transport of fishing gear. Fishing holes were cut with a woodman's axe in the ice when it was new and still quite soft, and when it was well formed by means of a petrol powered Homelite chainsaw.

The hand lines which had been used from the boat were also very effective when mounted on the handlebars of a Nansen sledge and catches of up to 50 fish an hour were obtained. Long lines produced insignificant catches through fast ice.

Traps were quite effective during the early winter months, catching about four fish a day, but from September onwards catches were almost entirely of the isopod *Glyptonotus*.

Because of the changing weather and ice conditions, none of the fishing methods was consistently effective throughout the year. However, the size of fish caught in the same month in the same zone by different fishing methods did not vary significantly, as shown in Table I. The catches by the three methods may therefore be considered together.

The larger fish species present in the experimental area have been described in a separate paper (Everson, 1969) which did not consider bathymetric distribution. Catches were composed of the following species: *Notothenia neglecta*, *N. rossii*, *N. gibberifrons* and *Chaenocephalus aceratus*. The latter was caught occasionally in zones 7 and 8 and very rarely further inshore; it was caught more commonly in water deeper than that at zone 8. Histograms showing the percentage of *N. rossii* and *N. gibberifrons* in the total catch are shown summed for all zones plotted against the months of the year (Fig. 4a and b), and summed for all months plotted against the fishing zones (Fig. 4c and d). The results for *N. rossii* show no definite trend with either the month or the fishing zone and, since *N. rossii* is known now to be fairly active and

TABLE I. COMPARISON OF STANDARD LENGTHS OF *Notothenia neglecta* CAUGHT BY DIFFERENT FISHING METHODS

Date	Zone	Size range (cm.) (Number of fish caught)		
		Hand line	Long line	Trap
February 1965	2 and 3	35.0-43.5 (20)	34.6-43.4, 52.6 (25)	
March 1965	2 and 3	34.0-42.0 (18)	34.0-40.0 (8)	
March 1966	2 and 3	37.5-43.5 (5)	22.6-45.4 (30)	23.9-40.8 (46)
July 1966	2 and 3	24.5-40.2 (16)		26.1-43.1 (19)
October 1966	8	22.4-34.4 (4)		20.1-36.5 (14)

when older than 5 years pelagic, this is not unexpected. *N. rossii* is known to be a shoaling species (Permitin, 1970) and so catches are likely to be very sporadic. *N. gibberifrons*, on the other hand, shows a very marked trend with respect to the fishing zones and was only caught in the deepest stations; it is possible that the species becomes dominant at even greater depth.

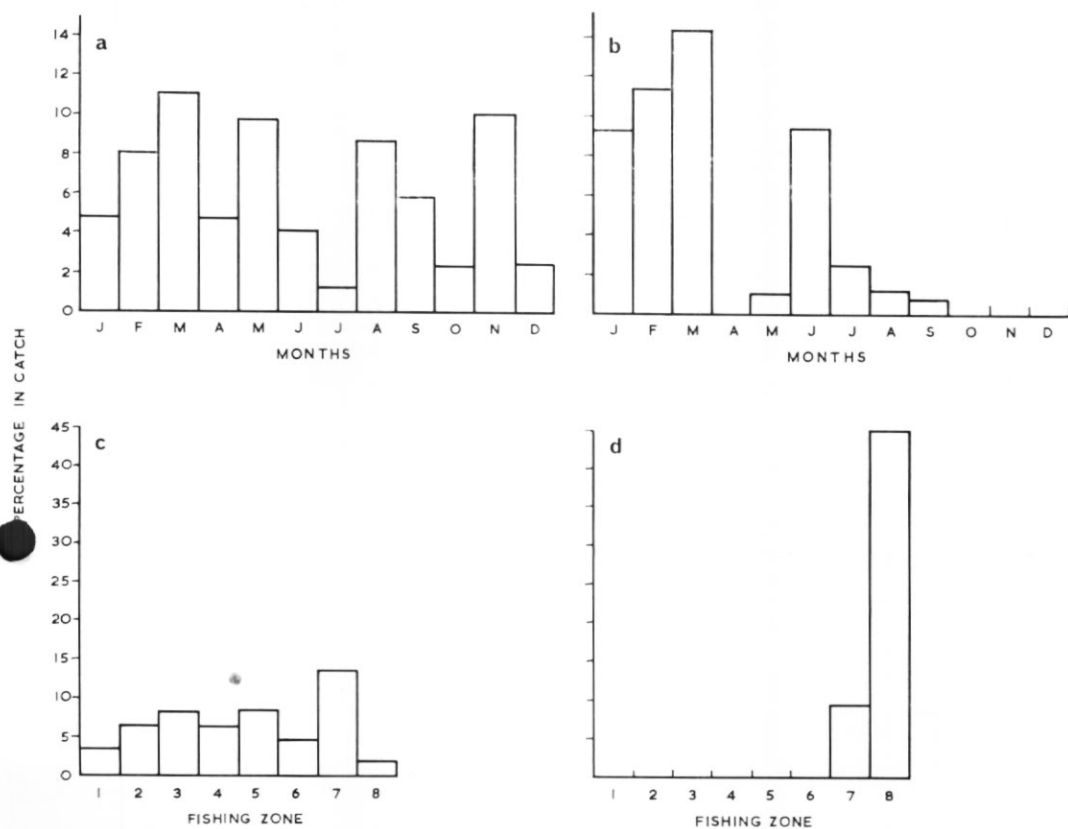


Fig. 4. a. and b. Number of *Notothenia rossii* and *N. gibberifrons* caught, expressed as a percentage of the total fish caught in each month.

c. and d. Number of *N. rossii* and *N. gibberifrons*, respectively, expressed as a percentage of the fish caught at each fishing zone.

The monthly results for *N. gibberifrons* reflect the difficulty in fishing zones 7 and 8 when sea ice is forming (April and May) and also when the ice is breaking out at the end of the year.

In shallow water there is a presumed stable population of *N. neglecta* feeding on the benthic epi- and in-fauna, whilst in the deeper water *N. gibberifrons* becomes dominant along with the necrophagous *Chaenocephalus aceratus*. However, *N. rossii* is a far more active species, feeding on benthos until 5 years old and on krill later on (Olsen, 1954).

SEASONAL MOVEMENTS

During the field work it became apparent that there was a variation in the mean size of fish caught; smaller fish predominated during the winter months (Fig. 5). There are two possible reasons for this:

- i. There is a tendency for larger fish to migrate from the area under investigation during the winter and return for the summer, or
- ii. The larger fish are not susceptible to capture during the winter.

Since *N. neglecta* is a totally demersal species, except for 2 years after hatching, a migration would have to be offshore and take fish to a depth greater than 40 m., the deepest area regularly sampled. The existence of an offshore migration could not be proved directly from the evidence available since Borge Bay was the only area fished.

The most effective fishing methods were hand lines, long lines and baited traps which, although not fished in the same effort ratio, produced more comparable results than the marked difference shown above. Each of these methods, although assumed to be unbiased seasonally with regard to the size of fish caught, requires for its effectiveness that the fish are feeding and also that they will take the bait offered. The change in the mean size of the fish caught can be related to the feeding habits of the fish; the larger fish tend not to go actively in pursuit of food during the later winter months. If the larger fish are not feeding at this time, they must be utilizing some other form of energy source, probably carbohydrate stored in the liver (Fig. 6). The mean relative liver size from June onwards shows a similar trend for both sexes. From June to September there is a gradual increase in the liver size of mature fish followed by a drop to a little more than two-thirds of this size in October, followed once again by a build-up prior to spawning for females and a levelling-off in the pre-breeding season for males. The cycle for immature fish is indistinct in both sexes. The late winter reduction in liver size of mature fish may be due to reduced feeding activity.

This semi-fast is coincident with the return to the inshore waters of Weddell, elephant and leopard seals, all of which are known to feed on fish for at least part of the time. The water at this time is very clear and so the larger fish probably do not venture far to feed but rather wait in algal tangles for suitable prey.

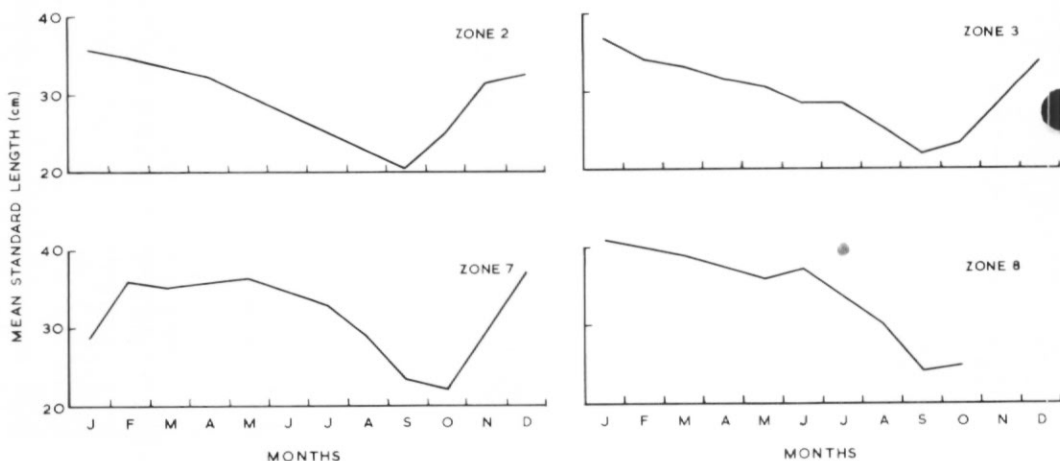


Fig. 5. The mean standard length of all *Notothenia neglecta* caught in each month at fishing zones 2, 3, 7 and 8.

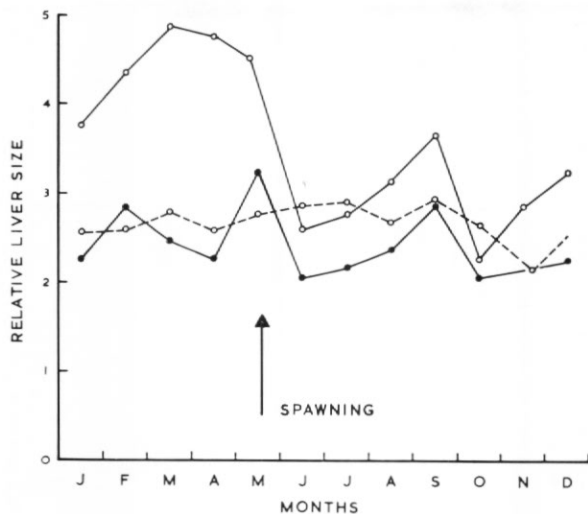


Fig. 6. The mean relative liver size ($\frac{\text{liver weight}}{\text{total weight}} \times 100$) for *N. neglecta* in each month of the year: ○—○ females, ●—● males, ○---○ immature fish. Spawning occurs in late May.

TAGGING

Confirmation of estimates of growth and determination of population size in the experimental area was attempted using mark and recapture techniques. Fish were marked with serially lettered Petersen discs attached by stainless steel wire through the dorsal musculature at about the level of the second dorsal fin. Observations on recaptured marked fish showed very little damage in the region of insertion of the wire pin, or infection of any kind. The discs themselves did not remove any of the scales.

No note was made of the condition of marked fish when released as other workers have done (Beverton and others, 1959), because only fish in perfect condition were released and these were all caught by either traps or hand lines. On being caught and handled, many fish went into a tetanus with the mouth tightly closed, the operculae distended and all the fins erect; such fish were not used in the marking experiments as they often failed to return to normal when left in well-aerated aquaria. The effect of low air temperature on the fish was not known and, since it was considered likely that fish would be frozen by sub-zero air temperatures with resultant tissue damage, tagging operations were only carried out on warm days during the summer.

The determination of population size by Petersen's method requires for the basic model that the population be discrete as, for example, in a lake. For a marine population, however, the case is rarely as clear. Zone 1 has the shore at one end whilst the deepest zone has as its lower limit the lower bathymetric limit for *N. neglecta* in the area. To the north-west and south-east the limit is only an arbitrary line so that fish tagged in the experimental area, if they are part of a general coastwise movement, will be "lost" to the population and consequently lead to a gross overestimate of the population size. However, since about 10 per cent marked fish were recaptured, it is unlikely that this happened.

A movement up or down the fishing area has already been disproved and the results of tagging tend to confirm this as shown in Fig. 7. The arrows link the month and zone of release to the month and zone of recapture, indicating there is no obvious trend with time.

The population within the experimental area may therefore be considered constant and its size suitably evaluated by Petersen's method.

All fish that were tagged were measured before release in order to evaluate growth parameters for comparison with results from otolith readings. However, the results are insufficiently accurate because of lack of numbers and because most of the fish were large and therefore

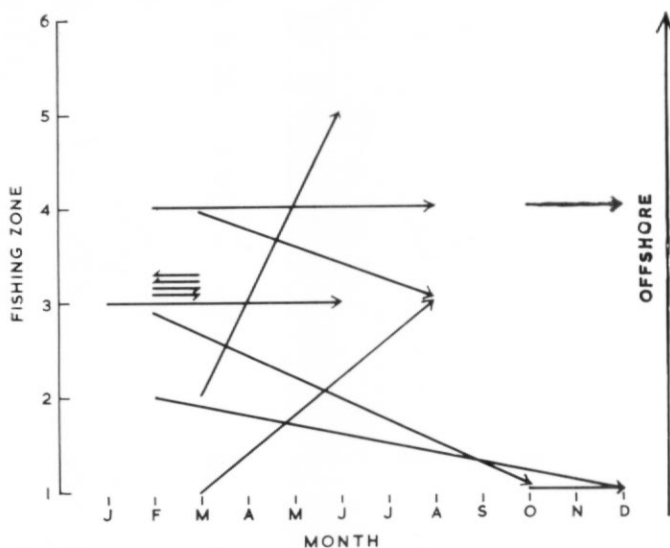


Fig. 7. Tagging movements. The arrows join the month and zone of first capture to the month and zone of recapture.

growing slowly. Determination of K , the coefficient of catabolism (Bertalanffy, 1938), by the method of Gulland and Holt (1959) therefore produced inconclusive results.

However, the mean growth increment per year for all fish recaptured is 1.17 cm. and the mean standard length of these fish at the start of the experiment was 35.1 cm. These results are in very close agreement with those obtained from otoliths where the calculated increment in size in 1 year of a fish 35.1 cm. standard length is 1.19 cm.

AGE DETERMINATION

Previous workers on Antarctic fish have used various methods for age determination and have obtained satisfactory results. Olsen (1954, 1955), one of the first investigators in the field, used otoliths for his work on *Notothenia rossii* and *Champscephalus gunnari* at South Georgia, although he, like Hureau (1964) failed to state the precise method employed. Wohlschlag (1962), on the other hand, relied on scale annuli as being indicative of age in *Trematomus bernacchii*. He was very careful to distinguish between the age of a fish and the number of annuli on its scales. Both otoliths and scales were collected throughout the period of the study. Scales were mounted on plain glass slides and otoliths were dried between the fingers and stored either in dry tubes or Sellotaped on to stiff card.

As the otoliths were not flat enough to examine directly, they were split in half through the nucleus, charred in a micro-bunsen flame and then examined under the low power of a microscope. The charring, as Christensen (1964) who developed the technique has shown, is first apparent at the start of the opaque zones and then proceeds towards the periphery. Although the degree of charring is quite critical, the worker can readily judge the amount required by the colour and smell of the split otolith. Fig. 8 shows an otolith prepared in this way showing quite clearly the charred opaque zones. The opaque zones are laid down in the spring and early summer, and the hyaline zones are formed in the early winter.

For small fish, since the otoliths were small, age determination was carried out on scales. These were found to be accurate for ages 1 to 4 years but after this the annuli were indistinct.

The results of age against size have therefore been determined from scale readings in the case of the smaller fish and from otoliths for the larger ones; it will be seen that they form a fairly smooth curve indicating that the two methods are comparable.

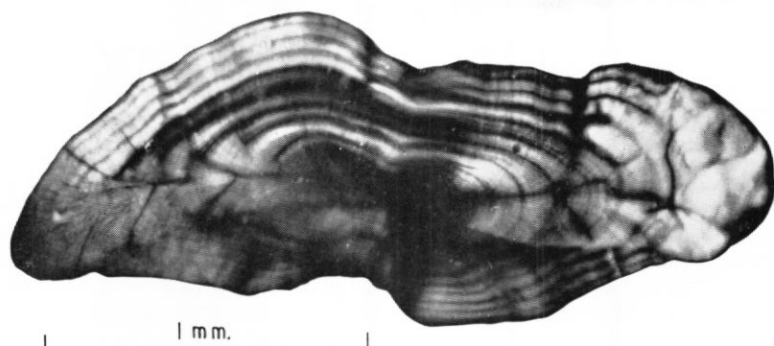


Fig. 8. Sagitta otolith of a 9-year-old *Notothenia neglecta*, split through the nucleus and charred to show the annual growth rings.

AGE AT RECRUITMENT

Norman (1938), in his monograph on Antarctic coast fishes, noted a great difference between very small and larger specimens of *N. coriiceps* (*N. neglecta*), and he suggested that the very young stages were probably pelagic in habit. With the fishing methods available it was impossible to confirm this directly, although it was possible to obtain some idea of the time scale in relation to the various stages by consideration of the fish caught on the bottom. During some of the summer months it was possible to catch fish by hand at extreme low water of spring tides. The fish caught in this way were generally 1 or 2 years old and in most cases they were very dark slate grey in colour characteristic of the demersal phase, although a few were silvery with a dark patch on each of their pectoral fins, Norman's (1938) pelagic phase. Therefore, it seems clear that the fish become demersal between the ages of 1 and 2 years. Later calculations, concerned with the biomass and production of the population during its demersal phase, will therefore be made on results of fish 2 years old and more.

POPULATION DYNAMICS

The results of age and size of the fish may be used to estimate the biomass and the annual production of the population. The mathematical models found most useful for the determination of these quantities have been those developed by Beverton and Holt (1957). These were originally constructed to represent exploited populations. For this work, however, calculations are simplified by the absence of a mortality due to commercial fishing. Since the population is unexploited, the quantitative ecologist is interested in the dynamics of the population throughout its demersal phase. In this case the period represented is from when the fish are 2 years old until they die. Unfortunately the fishing methods employed failed to catch all age groups in the proportions in which they occurred in the population. The implications of this and the method employed in dealing with the problem are discussed later.

Values for size of animals frequently require transformation from weight to length and vice versa, and for this an empirical relationship is required whose constants have a biological meaning. The length to weight relationship for many animals may generally be adequately fitted by a line of the form

$$w = bl^k,$$

where w is weight, l is length, and b and k are constants. This equation has the special case where $k = 3$, in which growth is isometric and the specific gravity remains constant. Although in nature these conditions are very rarely satisfied completely, if the above assumptions are made, the deviations caused are not great.

For *Notothenia neglecta* at Signy Island the constant k was found to be 2.994, a value near enough to 3 for the purposes of later calculations. The special form of the equation $w = b \times l^3$ has been used to relate weight to length, giving the following results:

$$\begin{array}{ll} \text{females} & w = 0.0290 \text{ length}^3, \\ \text{males} & w = 0.0279 \text{ length}^3. \end{array}$$

GROWTH

Many equations that have been derived to describe growth in animals frequently contain constants having no biological meaning. An exception is the equation derived by Bertalanffy (1938) and used frequently in fisheries biology (e.g. Beverton and Holt, 1957). This is:

$$l_t = L_\infty \{1 - e^{-K(t-t_0)}\}.$$

The constant, L_∞ , may be determined by using the method of Ford (1933) and Walford (1946) by plotting l_t against l_{t+1} . Where this crosses the line $l_t = l_{t+1}$ gives an estimate of L_∞ (the point beyond which there is zero annual increment in size). The two constants, K and t_0 , may be obtained by plotting $\log_e (L_\infty - l_t)$ against t , the slope of the line gives an estimate of K and where the line has an ordinate of $\log_e L_\infty$ gives an estimate of t_0 . For the purpose of later calculations the equation must be transformed to represent weight at age:

$$W_t^{\frac{1}{3}} = W_\infty^{\frac{1}{3}} \{1 - e^{-K(t-t_0)}\}.$$

In constructing a growth curve for each sex the mean weight of all fish aged t has been considered as w_t . The results are shown in Fig. 9.

Results of size at age for other species of Antarctic fish are very few; even so, comparison of the growth parameters of the different species for which results are published is very interesting. An important parameter of the Bertalanffy equation is the constant K which describes the rate at which the fish attains its maximum size. In Table II four species of Antarctic fish with respective values of K (calculated from published results) are divided into two groups by their feeding habits.

The marked difference in the two sets of independent results obtained for *Trematomus bernacchii* are almost certainly associated with the age-determination methods employed. Wohlschlag (1961) relied on scale annuli to indicate age but, although this method is fairly reliable for young fish, he admitted that the number of scale annuli almost certainly under-

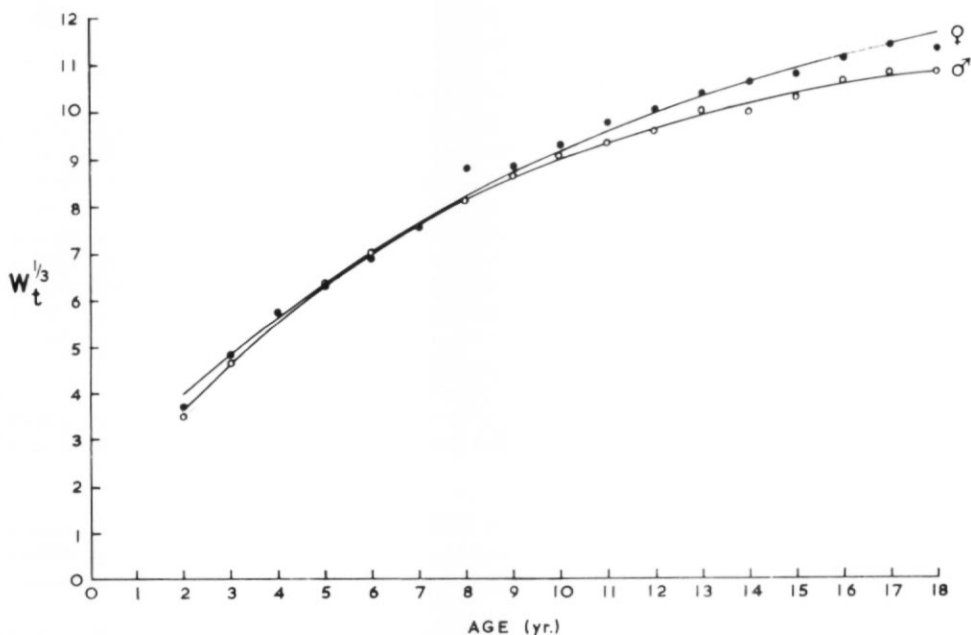


Fig. 9. The cube root of the mean weight of all *Notothenia neglecta* of each age ($W_t^{\frac{1}{3}}$) plotted against age, with fitted Bertalanffy curves having the following constants:

	K	t_0	W_∞
Females	0.091	-1.7	2,744
Males	0.129	-0.8	1,728

TABLE II. VALUES OF BERTALANFFY'S COEFFICIENT OF CATABOLISM (K) AND THE PRINCIPAL FOOD OF VARIOUS SPECIES OF ANTARCTIC FISH

Species	Food	K		Calculated from published results of:
<i>Notothenia rossii</i> $t = 1-5$ yr. $t > 5$ yr.	Benthos	0.15		Olsen, 1954
	Krill	0.29		Olsen, 1954
<i>Champscephalus gunnari</i>	Krill	0.33		Olsen, 1955
<i>Trematomus bernacchii</i>	Benthos	♀ 0.22	♂ 0.36	Wohlschlag, 1962
	Benthos	0.11	0.14	Hureau, 1964
<i>Notothenia neglecta</i>	Benthos	0.09	0.12	This paper

estimates the fish's age. For *Notothenia neglecta* and *Notothenia rossii* at Signy Island, I have encountered great difficulty in obtaining realistic scale readings after about age 3 years. This, however, in no way invalidates the use of the data for comparing sex-related effects in *T. bernacchii* (the aim of Wohlschlag's investigations). In common with other investigators, Hureau (1964) has used otoliths for his study and his results are therefore valid for inter-specific comparisons.

The K values for the benthos feeders are all about 0.1, if the different values for the sexes

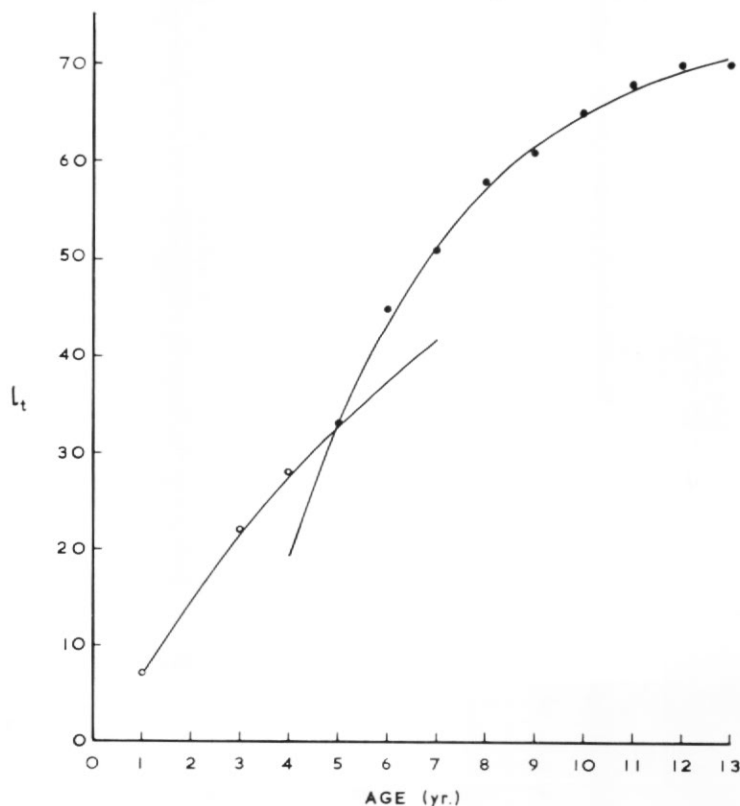


Fig. 10. Length (l_t) plotted against age for *Notothenia rossii* from South Georgia (results from Olsen, 1954) with the fitted Bertalanffy curves.

are amalgamated, and in all, the total range is only from about 0.08 to 0.15. The two results for fish which are known to be pelagic krill feeders are both about 0.3 and are thus indicative of a much faster growth rate. The results are made even more interesting because of a change in growth pattern in *Notothenia rossii*. Olsen (1954) deduced that, for the first 6 years of life, it inhabits the South Georgian fjords and feeds mainly on benthic organisms and when older it lives pelagically, feeding on krill. The effect of this is to produce a much enhanced growth rate so that L_{∞} is approached much more rapidly. A curve of age against length is therefore well fitted by two separate forms of the Bertalanffy equation (Fig. 10). Furthermore, it is interesting to note that the values of L_{∞} for both equations are about the same, as shown in the Ford-Walford plot (Fig. 11), as might be expected since the results are for one species throughout.

The fact that K for *Notothenia rossii* is capable of such great modification is of immense interest in the Antarctic ecosystem and particularly with regard to that part of the system associated with krill.

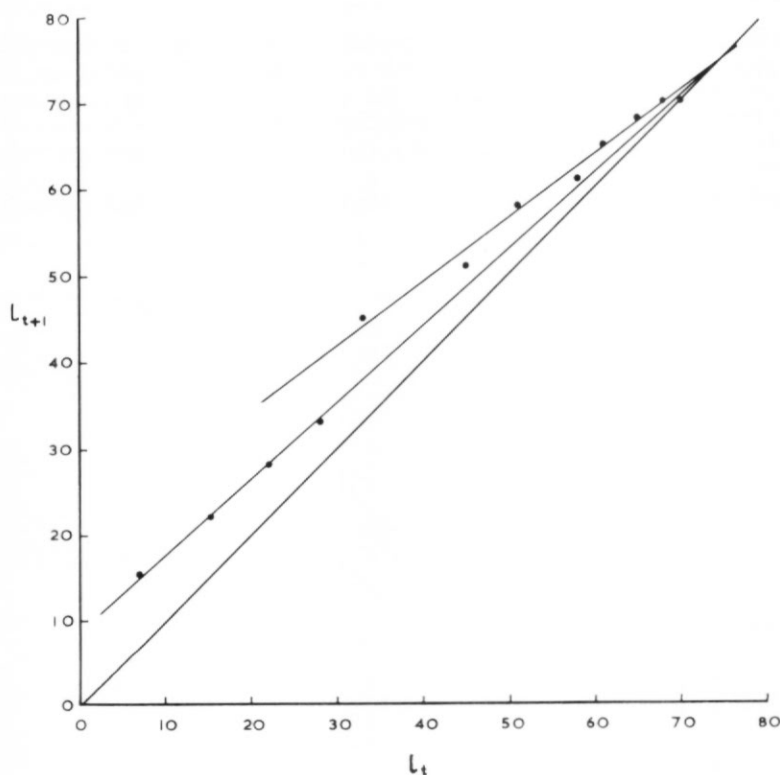


Fig. 11. Ford-Walford plot for *Notothenia rossii* using the results of Olsen (1954).

TOTAL MORTALITY

The total mortality is readily calculated when the relative abundances of particular year classes are known, e.g. N_0 , N_1 , etc., for then the fraction surviving is given by $\frac{N_1}{N_0} = S$ and the total mortality coefficient, Z , is given by:

$$e^{-Zt} = S = \frac{N_1}{N_0} \quad \text{or} \quad Zt = \log_e \frac{N_0}{N_1}$$

Z may be estimated by plotting \log_e (year class abundance) and determining the slope of the

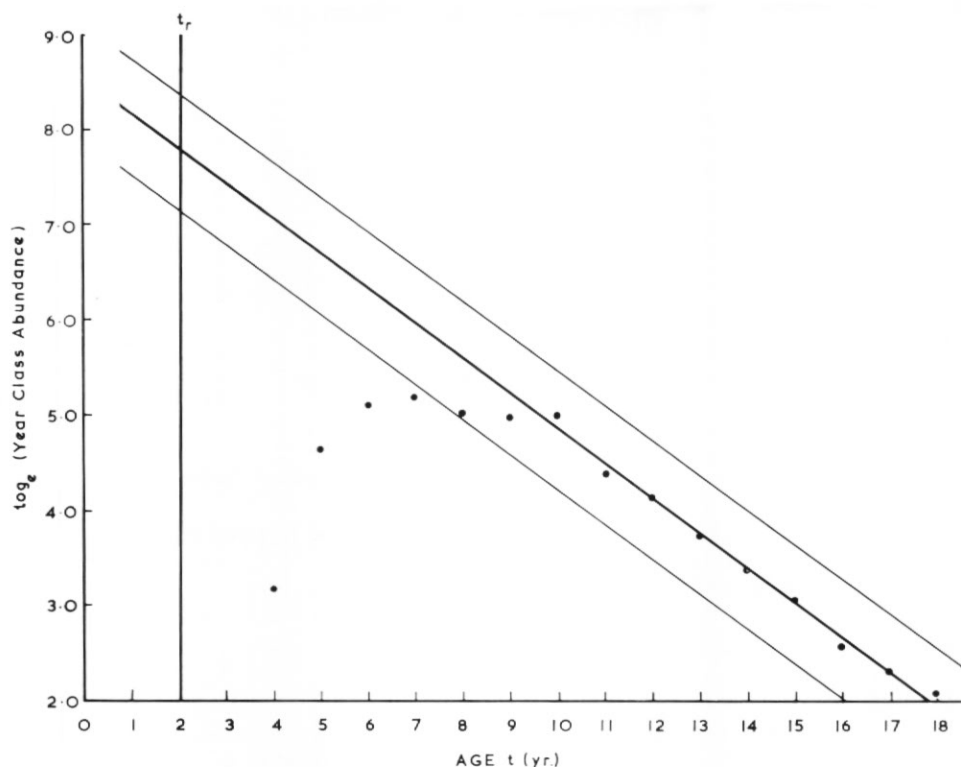


Fig. 12. \log_e (year class abundance) increased by the ratio of marked fish to marked fish recaptured plotted against t . The value of R has been estimated from the point of intersection of the regression line and the perpendicular at t_r and the dispersion of R from the intercepts of the lines of 1.96 standard deviations about the regression line.

line. It will be seen from Fig. 12 that after about age 9 years the results are well fitted by a straight line indicating a steady mortality rate. The standard deviation of the values of \log_e (age group frequency) about the regression line has been calculated from the formula

$$S^2 = \frac{1}{n-2} \left\{ \sum (y-\bar{y})^2 - \frac{(\sum (x-\bar{x})(y-\bar{y}))^2}{\sum (x-\bar{x})^2} \right\}.$$

The life of the fish may be considered in several stages (Fig. 13):

- i. Larval stages.
- ii. Post-larval pelagic phase.
- iii. Demersal phase.

It is well known that mortality is generally very high for larval stages of fish. The present study is, however, only concerned with *Notothenia neglecta* in the post-recruit phase, i.e. after it has become demersal. Fig. 12, the graph of \log_e (age group frequency) against age of fish shows that from about 9 years the points are well fitted by a straight line. The implications of this are two-fold. First, they indicate that natural mortality is constant with age. Secondly, since the results were obtained over only 2 years and most of the points fall on the line or very close to it, a steady rate of recruitment as well as mortality in preceding years is indicated.

In the construction of most population models a steady rate of recruitment has to be assumed, although it is appreciated that some years will be better than others for larval

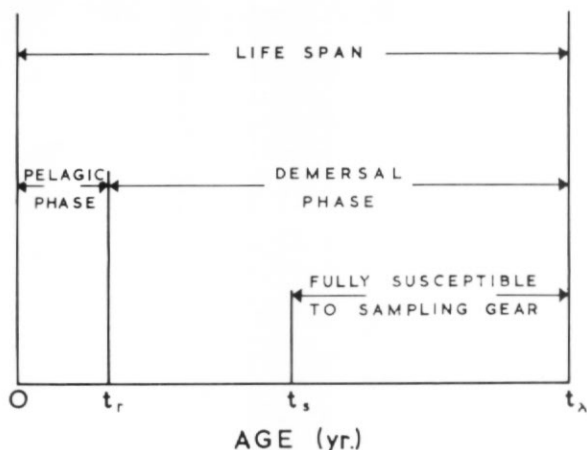


Fig. 13. A diagrammatic representation of the life span of the fish.

survival to the recruit stage. A steady mortality may also be inferred from the results but whether this is at the same rate requires further consideration.

The causes of natural mortality in a fish population include:

- i. Predation.
- ii. Parasitism and disease.
- iii. Food shortage.
- iv. Senility.

Although quantitative results are essential before any correction may be applied to the mortality coefficient, subjective observations can give an indication of whether there is any size specific mortality. Predation on Antarctic fish occurs on all size groups and therefore in all age groups. In the size range 30–500 g. fish are readily taken by the blue-eyed shag (*Phalacrocorax atriceps*) large flocks of which are frequently seen fishing in the experimental area. Fish of a size greater than about 300 g. are taken by seals. During the summer months there are moderate concentrations of the southern elephant seal (*Mirounga leonina*) which may be feeding at this time and also smaller numbers of the leopard seal (*Hydrurga leptonyx*). Throughout the year there are varying concentrations of Weddell seals (*Leptonychotes weddelli*) which reach a peak during the months of August, September and October. Another major predator of the smaller size groups is fish of the same species and it has been observed that large *Notothenia neglecta* will swallow small fish weighing up to 10 per cent of its own weight. Although the causes of predation vary with the age of the fish, the resultant mortality is not likely to vary significantly.

From examination of several hundred *Notothenia neglecta* from Signy Island, it is clear that the species harbours very heavy infestations of several parasites. Nematodes of the genera *Anisakis* and *Contracaecum* and various Acanthocephala and trematode species are found in the liver and coelom of larger fish. The percentage of fish of each 2 cm. size group infected with the parasite are shown in Fig. 14, from which it is clear the effects of the parasites will only be manifested in the larger sizes. A mortality effect is therefore likely to be related to age and therefore only effective on the oldest age groups. The effects of disease are totally unknown in the wild state and in the laboratory no deaths occurred which were not attributable to some other cause.

Senility, like disease as a cause of mortality, is very difficult to demonstrate and it is generally held that the proportion of animals dying as a result of ageing alone is virtually negligible. However, certain physiological processes may tend to be lethal to a greater extent with increasing age, e.g. spawning.

The mortality coefficients calculated from year-class abundances vary quite markedly. This is only to be expected as the results are from only 2 years' samples and are therefore not

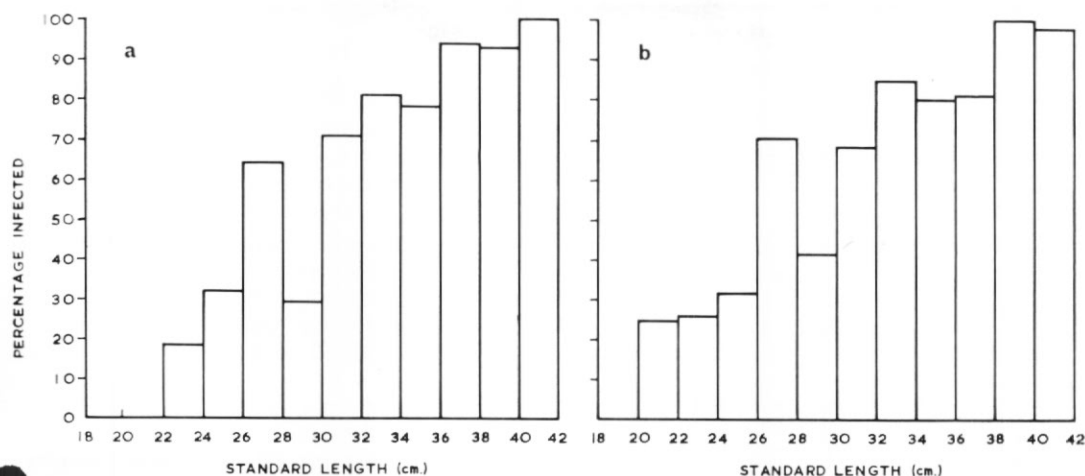


Fig. 14. The percentage of all *Notothenia neglecta* caught (grouped into 2 cm. length groups) that were infected with Nematoda (a) and other visceral parasites (b).

spread over a long enough period for fluctuations in recruitment to be cancelled out. The year-class mortalities were plotted against age and the following linear regression was calculated by the method of least squares:

$$Z = 0.364 - 0.023(t - 14.5).$$

The slope is not significantly different from zero. The mortality coefficient will therefore be considered constant with age for the period for which the results are calculated. Beverton and Holt (1957) have published results indicating an essentially linear relationship between natural mortality coefficient and age for several species and it will be assumed that this is true also for *N. neglecta*. Since the variation has been found not to be significantly different from zero for the older age groups, the coefficient will be considered constant throughout. No significant sex specific difference in mortality was detected.

Assuming a constant mortality for all age groups, variations in the size of each age group may be considered as being due to variations in recruitment. It is to be expected that the level of recruitment R will vary from year to year and it will thus have a mean equal to \bar{R} and a variance σ^2 . The size of each successive year class will be the result of a steady and constant mortality on preceding values of R and, since R is normally distributed over a period of years, so also will the values of each year-class abundance for each year. Therefore, the central limit theorem may be applied to the standard deviation of the results of \log_e (frequency of age group) for the sampling period. Although the value of R will have variance σ^2 for 1 year, the variance of the year class strength for n year's samples will be σ^2/n .

Thus variance R from regression = $0.202/2$ and standard deviation $R = \sqrt{0.101} = 0.319$.

The 95 per cent limits (equal to 1.96 standard deviations about the regression line) have been drawn in on Fig. 12; these indicate the probable range of variation likely in the size of any one year class.

RECRUITMENT AND POPULATION SIZE

The results of the year-class abundances used in the calculation of a natural mortality coefficient may also be used to determine the relative sizes of each year class prior to its being fully vulnerable to the fishing gear. If each of the year-class abundances calculated from the regression line in Fig. 12 is increased by the proportion of marked fish to marked fish recaptured, it will give an estimate of the total year-class strength. This basic method, attributed to Petersen and first described by Dahl (1918, 1919) (Le Cren, 1965), generally requires some slight modification to take account of characteristics of the particular population and its

sampling problems. The simple model described above, estimated year-class size = total of that year class caught \times $\left(\frac{\text{total number of fish marked}}{\text{total of marked fish recaptured}}\right)$, is only valid when the following conditions are satisfied:

- i. Tagged fish are very rapidly randomly distributed in the population.
- ii. There is no migration into or out of the experimental area.
- iii. There is no mortality of tagged fish during the course of the experiment.
- iv. There is no mortality of the tagged fish due to tagging.

It is virtually impossible to specify when the tagged population will be randomly distributed and therefore the only concession that may be made is to allow a reasonable period of time for it to come about and, furthermore, since there is no fishing going on in adjacent areas, the effects of migration will be undetected. However, in view of the very quiescent nature of the fish, it is unlikely that movements into or out of the fishing zone will have significant effect on a tagged population.

The tagged fish population will be susceptible to a mortality at the same rate as the untagged population and also there may be a separate tagging mortality (mortality due to the fish being tagged). The latter factor is unknown and will have to be assumed to be zero but the former has already been estimated in an earlier section using the formula $N_t = N_0 e^{-zt}$.

The tagging programme was fitted in as an integral part of the 2 year population study. The tagged population size will thus vary with time, because there will be sporadic increases due to the introduction of more marked individuals and steady reductions due to mortality. Because a tagging mortality of zero had to be assumed, it was essential that only fish in perfect condition be used and therefore only trap-caught or lightly lip-hooked fish were used. Furthermore, it was not known what the effect of a low air temperature and, or, contact with snow and ice would be on the fish and so tagging operations were only carried out on warm days during the months of January and February. The tagged population was therefore made up of fish tagged in the current year which, since they had only been in the tagged population a short time would have been subject to a small mortality, and fish tagged in previous years which would have been subject to significant mortality. The estimated tagged population size has been considered in two parts: fish tagged in the current year and fish of previous years. This is shown in Table III.

TABLE III. THE TAGGED POPULATION SIZE IN SUCCEEDING YEARS

	1965	1966	1967
Fish tagged in current year (<i>A</i>)	130	94	50
Estimated tagged population size excluding current year (<i>B</i>) (Previous year's population size), e^{-z}	0	89.9	127.2
Tagged population size (<i>A</i>) + (<i>B</i>)	130	183.9	177.2

The average number of tagged fish over the period is therefore $(130 + 183.9 + 177.2)/3 = 163.7$. During the period of the investigation 16 tagged fish were recaptured and this represents $16/163.7$ of the fish population susceptible to capture. The value of R may be obtained by extrapolating back to t_r , the line used in estimating the mortality coefficient and uprating the value by $163.7/16$. The age, t_r , which is the time at which the fish entered the demersal population has been found to be about 2 years. The mean value of recruitment is therefore $\log_e R = 7.77$ and $R = 24,230$.

Each value of year-class abundance has the same standard deviation about the regression line as calculated in the section on mortality and, since the values of year-class abundance for a year class are likely to be normally distributed, 95 per cent limits for R are $\log_e R \pm 1.96$ standard deviations. The range of values R is likely to take is therefore from 12,970 to 45,270. The results of weight at age and age frequency in the fish population may be used together

to determine the population biomass. Assuming the population is in a steady-state during the demersal life span, we first consider one year class t . The biomass of that year class will be $N_t W_t$.

The population biomass may be considered as the integral from t_r to t_λ (the maximum age of the fish) of $N_t W_t$ with respect to t .

$$\text{i.e. } \bar{P}_w = \int_{t_r}^{t_\lambda} N_t W_t \cdot dt.$$

The value of N_t may be presented in the form

$$N_t = N_0 e^{-Zt}$$

with the slight modification that since the lowest level on the time scale is t_r , the equation must be in form

$$N_t = R \cdot e^{-Z(t-t_r)}.$$

The Bertalanffy equation

$$W_t = W_\infty \{1 - e^{-K(t-t_0)}\}^3$$

may be used to represent weight at age and for convenience in the latter integration is rewritten as

$$W_t = W_\infty \sum_{n=0}^3 \Omega_n e^{-nK(t-t_0)}. \quad \begin{array}{l} \Omega_0 = +1 \\ \Omega_1 = -3 \\ \Omega_2 = +3 \\ \Omega_3 = -1 \end{array}$$

The population biomass then becomes

$$\begin{aligned} \bar{P}_w &= \int_{t_r}^{t_\lambda} N_t W_t \cdot dt \\ &= \int_{t_r}^{t_\lambda} R e^{-Z(t-t_r)} W_\infty \sum_{n=0}^3 \Omega_n e^{-nK(t-t_0)} \cdot dt. \end{aligned}$$

Grouping terms containing t ,

$$\bar{P}_w = R e^{Zt_r} W_\infty \sum_{n=0}^3 \Omega_n e^{nKt_0} \int_{t_r}^{t_\lambda} e^{-(Z+nK)t} \cdot dt,$$

and integrating

$$\bar{P}_w = R W_\infty \sum_{n=0}^3 \frac{\Omega_n e^{-nK(t_r-t_0)}}{Z+nK} \{1 - e^{-(Z+nK)(t_\lambda+t_r)}\}.$$

This equation may be used to determine the population biomass since all of the constants have been determined in the sections on growth and mortality. The calculation is best carried out in steps similar to those set out by Beverton and Holt (1957) for yield from a fishery and the necessary calculations have been set out in Table IV.

The total biomass within the experimental area will be the sum of the results for the two sexes—17,450,000 g.—and will vary from 9,346,000 to 32,630,000 g. This biomass is distributed over an area of 907,500 m.² and so density of biomass is 17,450,000/907,500 = 19.29 g./m.² and varies from 10.38 to 36.26 g. It must be remembered that the two extreme values calculated represent a range caused by variation in the level of recruitment. The values would almost certainly be closer to the mean if results had been taken over a large number of years, thus reducing the variance of year-class abundances about the line of log₁₀ abundance against age. The range does not indicate variations in biomass over the experimental area at one time which is determined very much by substrate and availability of weed cover, factors not incorporated into this population model.

TABLE IV. BIOMASS CALCULATIONS FOR *Notothenia neglecta*

Parameters:	Female	Male
\bar{R}	12,355	11,875
$\bar{R} \pm 1.96 \text{ S.D.}$	6,620; 23,100	6,360; 22,230
W_∞	2,744 g.	1,728 g.
t_0	-1.7 yr.	-0.8 yr.
t_r	2.0 yr.	2.0 yr.
t_λ	18.0 yr.	18.0 yr.
K	0.091	0.129
Z	0.36	0.36
$(t_\lambda - t_r) = \bar{\lambda}$	16	16
$(t_r - t_0)$	3.7 yr.	2.8 yr.

Sex	n	$Z + nK$ (A)	$1 - e^{-(Z+nK)\lambda}$ (B)	$\bar{\Omega}_n e^{-nK(t_r - t_0)}$ (C)	$\frac{(B) \times (C)}{(A)}$ (D)	$\Sigma(D)$
Female	0	0.360	0.9968	+1.0000	+2.769	0.267
	1	0.451	0.9993	-2.140	-4.742	
	2	0.542	0.9999	+1.526	+2.815	
	3	0.631	1.0000	-0.363	-0.575	
Male	0	0.360	0.9968	+1.0000	+2.769	0.409
	1	0.478	0.9995	-2.069	-4.188	
	2	0.596	1.0000	+1.415	+2.253	
	3	0.714	1.0000	-0.324	-0.425	

$$\bar{P}_w \varnothing = 0.267 \times 2,744 \times 12,355 = 9,055,000 \text{ g.}$$

$$\bar{P}_w \sigma = 0.409 \times 1,728 \times 11,875 = 8,395,000 \text{ g.}$$

$$\bar{P}_w \pm 1.96 \text{ S.D.} \varnothing = 4,841,000 \text{ and } 16,920,000 \text{ g.}$$

$$\bar{P}_w \pm 1.96 \text{ S.D.} \sigma = 4,495,000 \text{ and } 15,710,000 \text{ g.}$$

ANNUAL PRODUCTION

The annual production (A.P.), as defined by Beverton and Holt (1957), is the total growth increment of the population each year and, since the population is assumed to be in a steady-state, this may also be equated with the amount of organic matter that has progressed further in the food chain. The annual production therefore represents the turnover of organic matter in one season and this factor when related to the biomass gives a rate of increase of weight of the population per unit weight per year. This in turn adds a dynamic dimension to the simple food chain.

Beverton and Holt considered first the rate of growth of an individual fish at age t as $(dw/dt)_t$, and then considered the rate of growth of a year class summed over its post-recruit life. Thus

$$\text{A.P.} = \int_{t_r}^{t_\lambda} \left(\frac{dw}{dt} \right)_t N_t \cdot dt.$$

Using the differential form of the Bertalanffy equation, Beverton and Holt (1957) deduced

$$\text{A.P.} = 3K(W_\infty \bar{P}_w - \bar{P}_w).$$

This equation may not be solved directly since \bar{P}_w refers to the total numerical population size \bar{P}_N , whereas W_∞ does not. Rewriting the equation in terms of \bar{W} , the mean weight of all fish in the post-recruit phase:

$$\text{A.P.} = 3K(W_\infty \bar{W} - \bar{W}) \bar{P}_N \quad \begin{array}{l} \bar{W}_\varnothing = 264.5, \bar{P}_{N\varnothing} = 34,212, \\ \bar{W}_\sigma = 256.2, \bar{P}_{N\sigma} = 32,976. \end{array}$$

Solving the equation for both sexes gives the following results:

$$\text{♀ A.P.} = 2,927,000 \text{ g.}$$

$$\text{♂ A.P.} = 3,004,000 \text{ g.}$$

The total annual production of the population in the experimental area is therefore 5,931,000 g.; 6.59 g./m.² or 0.340 g./g.

ENERGY BUDGET

Values of biomass and annual production, although they are important quantities in the ecosystem, give only a very limited impression of the interrelationship between the fish and different trophic levels. A better understanding of the position of fish in the ecosystem may be obtained by considering the energy relationships of different trophic levels, as suggested by Ivlev (1945). One of the first determinations of this type was undertaken by Mann (1965), who worked on a population of fish in the River Thames, and an essentially similar approach will be used here.

The following approximations are, however, necessary for the calculations:

- i. The energy of egestion and excretion is 20 per cent of the energy intake.
- ii. The calorific value of fish flesh is 1 kcal./g. wet weight.

Both of these have been justified by Winberg (1956) and will be assumed to hold for the fish under consideration, so that the total energy budget may be written in the form:

Energy of food ingested = 1.25 (energy of metabolism + energy of growth).

Considering each term in the equation, the energy of food ingested may be calculated when the amount of food taken in and its calorific content are known. However, this was impossible with the time and apparatus available and so only subjective observations have been made which may be accurate to within an order of magnitude.

The "resting metabolic rates" for both sexes have been determined and these may be transformed to "energy of resting metabolism". The factor varies according to the material being respired but for a mixed diet R.Q. may be taken as 0.8 (personal communication from K. H. Mann).

Thus for female *N. neglecta*: Energy of resting metabolism = $13.8W_t^{0.787}$ kcal./yr., and for male *N. neglecta*: Energy of resting metabolism = $18.09W_t^{0.768}$ kcal./yr. (Data from Ralph and Everson (1968) transformed, assuming R.Q. = 0.8 and therefore 1 l. O₂ = 4.801 kcal. (Southwood, 1966).)

The relationship between "energy of resting metabolism" and "energy of metabolism" is difficult to define as it obviously varies with the "activity" of the fish. Mann (1965), using data from Pentelov (1939), showed that for trout the energy of resting metabolism was about half the energy of metabolism, whilst for pike (data from Johnson (1960)) resting energy was about equal to total energy. The difference is due largely to the behaviour of the two species. The pike is a relatively inactive species and only moves very occasionally to feed, whereas trout spends much of its time swimming. Observations on *N. neglecta* indicate a system very similar to that of the pike; in aquaria the fish show very rare bursts of activity and diving observations indicate that the fish lie still in thick weed for very long periods. The energy of resting metabolism will therefore be equated with the energy of metabolism.

Assuming that 1 g. wet weight of fish is equivalent to 1 kcal., the energy of growth may be calculated from Beverton and Holt's annual-production equations used earlier.

In addition, some energy is used in the production of ova and sperm. Results of analyses of gonads taken just prior to the breeding season are shown in Table V and from these results, assuming that the conversion value for fat is 9.5 kcal./g. and carbohydrate and protein 4.2 kcal./g. (Mann, 1965), the calorific value of *N. neglecta* ova = 1.343 kcal./g. and sperm = 0.977 kcal./g. Spawning occurs in late May when ova equivalent to 12.9 per cent, and sperm equivalent to 7.0 per cent of the body weight are released:

$$\left(\frac{100 \text{ gonad weight (May)}}{\text{total weight}} - \frac{100 \text{ gonad weight (June)}}{\text{total weight}} = 12.9 (\text{♀}), 7.0 (\text{♂}) \right).$$

These figures have been used in the calculation of the energy of gonad production.

The results for the total energy budget of each sex are set out in Tables VI and VII and summarized in Table VIII.

TABLE V. ANALYSIS OF *Notothenia neglecta* GONADS

	Dry matter (Percentage wet weight)	Lipid (Percentage wet weight)	Protein and carbohydrate (Percentage wet weight; by subtraction)	Calorific value (kcal./g. wet weight)
Ripe ovary	24.1	4.39	19.71	1.245
Spent ovary	18.0	2.18	15.82	0.872
Ripe testis	19.8	2.63	17.17	0.971
Spent testis	19.2	2.52	16.68	0.940

The calorific value of ova released = 1.343 kcal./g.
The calorific value of sperm released = 0.977 kcal./g.

TABLE VI. ENERGY BUDGET FOR MALE *Notothenia neglecta*

$\bar{R} = 11,875$ $W_{\infty} = 1,728$ g. $K = 0.129$ $t_0 = -0.8$ yr. $Z = 0.360$.
Resting energy = $18.09 (W_i)^{0.768}$ kcal./yr.
Sexual maturity occurs at $t = 9$ yr.
Weight of sperm released = 7 per cent total weight.
1 g. fish = 1 kcal.

t at start of year	Average weight (g.)	Average number	Energy of resting metabolism (kcal. $\times 10^{-3}$)	Growth	Energy of growth (kcal.)	Energy of reproduction (kcal.)
2	74.3	10,033	5,030	52.3	526,000	
3	143.8	7,037	5,420	69.5	488,000	
4	226	4,910	5,560	82	403,000	
5	318	3,425	4,940	92	314,500	
6	415	2,390	4,250	97	232,000	
7	513	1,667	3,500	98	163,000	
8	612	1,114	2,610	99	110,300	
9	705	813	2,210	93	75,600	39,600
10	794	566	1,655	89	50,400	31,000
11	879	395	1,092	85	33,600	24,200
12	960	265	923	81	21,500	17,500
13	1,034	179	660	74	13,250	11,830
14	1,101	121	473	67	8,120	8,490
15	1,161	85	346	60	5,100	6,770
16	1,217	60	254	56	3,360	5,810
17	1,269	42	196	52	2,190	3,660

TABLE VII. ENERGY BUDGET FOR FEMALE *Notothenia neglecta*

$\bar{R} = 12,355$ $W_{\infty} = 2,744$ g. $K = 0.091$ $t_0 = -1.7$ yr. $Z = 0.360$.
 Resting energy = $13.8 (W_t)^{0.787}$ kcal./yr.
 Sexual maturity occurs at $t = 9$ yr.
 Weight of ova released = 12.9 per cent total weight.
 1 g. fish = 1 kcal.

<i>t</i> at start of year	Average weight (g.)	Average number	Energy of resting metabolism (kcal. $\times 10^{-3}$)	Growth	Energy of growth (kcal.)	Energy of reproduction (kcal.)
2	90	10,489	4,780	42	441,000	
3	149	7,309	5,220	65	475,000	
4	221	5,106	5,000	80	400,000	
5	311	3,562	4,460	91	324,000	
6	401	2,435	3,730	98	237,500	
7	502	1,734	3,230	103	178,600	
8	607	1,202	2,570	108	129,800	
9	716	843	2,050	110	92,700	104,600
10	827	589	1,600	111	64,800	84,230
11	939	411	1,235	112	46,000	67,010
12	1,048	296	968	109	32,300	53,740
13	1,150	200	710	102	20,400	39,880
14	1,245	140	527	95	13,000	30,160
15	1,337	98	390	92	9,020	22,670
16	1,435	68	287	98	6,670	16,950
17	1,525	47.4	208	90	4,270	12,550

TABLE VIII. ENERGY BUDGET FOR *Notothenia neglecta* (kcal./m.²)

	Biomass	Year's total energy requirements	Production	Germ cell production	Egestion and excretion	Respiration
Female	10.06	55.02	2.76	0.476	11.00	40.78
Male	9.33	53.42	2.72	0.164	10.68	39.85

DISCUSSION

Although in the past many papers have been written on the ecology of Antarctic benthos, very few quantitative statements have been made. Using information ranging from systematic calculation to gross extrapolation, Holdgate (1967) produced a food-chain diagram incorporating estimates of biomass for most of the stages. These quantities were based on results from widely differing geographical areas and on the assumption that each specific locality is an "average" one for the Antarctic.

The present study is an attempt to provide the first exhaustive account of the ecology of

an Antarctic fish population which can be taken as a basis for integration into other future ecosystem studies. Unfortunately, figures for biomass and production of benthos in the experimental area have not been fully evaluated so that these values must be estimated from results from other regions.

Working from the Russian Antarctic research stations Mirny and Molodegnaya, Propp (1970) has divided the shallow inshore benthos into four bathymetric zones:

- i. Depth 2–10 m. with biomass of 20–25 g./m.².
- ii. Depth 6–25 m. with biomass of 450 g./m.².
- iii. Depth 25–30 m. with biomass of 1,000 g./m.².
- iv. Depth 30–50 m. with biomass of up to 3,000 g./m.².

All of these determinations are based on hand collections from rock surfaces whilst diving, and none are from sand or mud substrates similar to those which cover appreciable areas of Borge Bay. Furthermore, the communities described are not those forming the main part of the fishes' diet. The results may, however, be used with caution to indicate the probable biomass of other communities.

Observations made whilst diving at Signy Island show that the dominant forms in mud and sand are Mollusca: *Laternula elliptica* and *Yoldia aequioldia*, both burrowing bivalves. M. G. White (personal communication) has counted about 100 *Laternula* per m.² each of which would weigh about 50 g., and *Yoldia* caught in core samplers (Everson and White, 1969) have a density of about 600–1,000 individuals per m.² each weighing about 2 g. In addition, there are high densities of Amphipoda: *Cheiromedon femoratus* and *Tryphosa kergueleni*, and Isopoda: *Serolis* sp., and also burrowing polychaetes, thus tentatively indicating that the biomass is in excess of 2,000 g./m.².

Examination of freshly caught fish shows that the weight of food to fill a *Notothenia neglecta* stomach is about 5 per cent of the fish total weight. The digestion rate is not known but it appears that a stomach full of food is cleared in about one-third to half a week, so that the weight of food ingested per year is between $2 \times 52 \times \frac{5}{100} \times 19.4 = 101$ g./m.² and 151 g./m.².

The calculated food intake from the energy budget, assuming that 1 g. food is equivalent to 0.85 kcal., is 93.5 g./m.² which is very close to the lower suggested digestion rate. To maintain a balance in the ecosystem, this food intake rate would require an annual production rate of at least 60 per cent of the biomass on rock and 10 per cent of that in sand, both of which are reasonable.

The range of values suggested for the biomass of fish is probably much wider than is ever found naturally because the results were obtained over a period of only 2 years and vary due to fluctuations in recruitment. This effect would be minimized if sampling were carried out throughout the fish's life span. The mean fish biomass in the experimental area is average for an unexploited population, although there are very few suitable estimates available for comparison. Laevastu (1961) gave values of biomass of between 8 and 40 g./m.² for most economic exploited fisheries and later on stated that the average fish biomass of the North Sea is about 4 g./m.². More important in this context, however, is the value of annual production as it adds a dynamic quantity to the very mobile balanced equation describing the population. Values for annual production of various fish populations have been given by Odum (1959, p. 43–87) and once again the most appropriate value for comparison is the North Sea (1.68 g./m.²), which, assuming a biomass of 4 g./m.² may be considered as 0.42 g./g., is higher than for *N. neglecta* at Signy Island (A.P. = 0.34 g./g.).

These results may now be used to re-assess the values of Holdgate's (1967) general Antarctic food chain as part of the specific food chain immediately concerning the benthos of Borge Bay, Signy Island (Fig. 15).

The complexity of the system at the level of marine benthos emphasizes the difficulties of a quantitative food chain and the need for caution when analysing results of this type. A mean figure for the benthos would be very difficult to calculate as the extent of rocky and sandy areas remains unknown.

The figure for annual production of *N. neglecta* of one-third biomass is very low when compared with results for other species. Results for fresh-water fish quoted by Mann (1965) vary from 1.7 times the biomass for trout (Allen, 1951; Horton, 1961) at the upper end of the

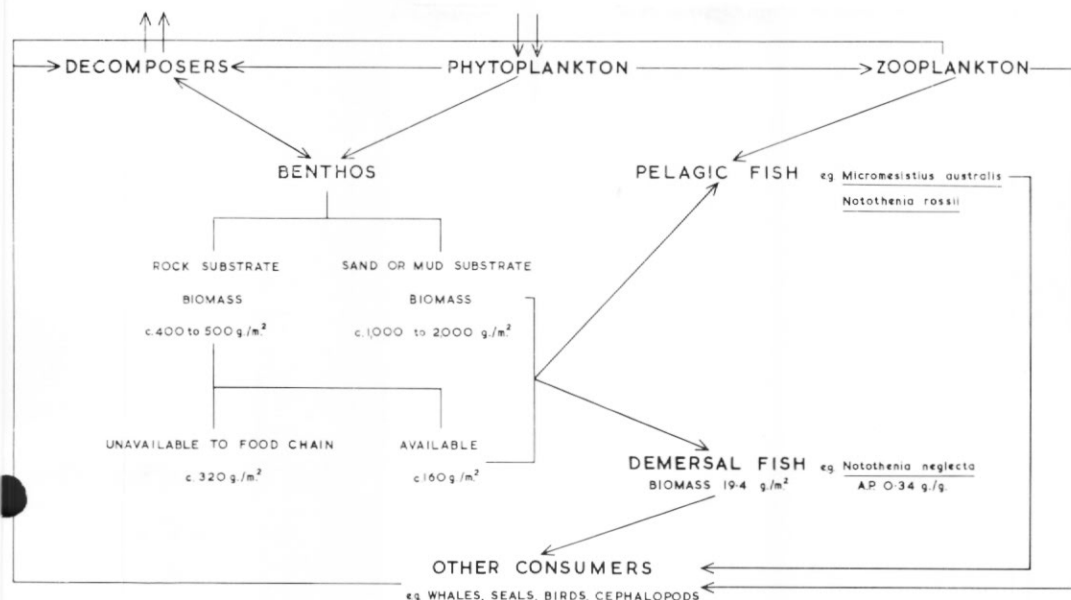


Fig. 15. Food-chain diagram for Borge Bay, Signy Island. (Modified after Holdgate (1967).)

scale through Mann's results, in which A.P. was about two-thirds biomass, to Gerking (1954), who found an A.P. of about half the biomass. Analogous results for marine fish are very few: plaice (*Pleuronectes platessa*) has an A.P. (*not yield*) equal to about half the biomass (calculated from results given by Beverton and Holt (1957)). The low results for *N. neglecta* may be due to the phenomenon of cold adaptation, discussed at great length by Wohlschlag (1960, 1964). A cold-adapted fish has an oxygen consumption rate appreciably higher than would be expected by extrapolation of Krogh's (1916) curve to polar temperatures and this increase is not necessarily reflected in the growth rate. The same argument applies to the analysis of ecological efficiencies (K_1 of Ivlev (1945)) of the two sexes in Table IX.

The mean results fall at the lower end of the range suggested by Slobodkin (1960) of from 5 to 15 per cent in aquatic environments, and also with increasing age successive values fall fairly steadily indicating that there is no marked ecological change in the species with age. The results of Olsen (1954) mentioned earlier are of interest. The increase in the Bertalanffy coefficient K is marked by a sudden increase in the ecological efficiency at the same point. Table IX also shows values of Slobodkin's ecological efficiency calculated from Olsen's results, transformed to weight by analogy with Signy Island fish ($w_i^k = 0.270 l_i$) and converted to energy values from the results of Ralph and Everson (1968). Since *N. rossii* is certainly more active than *N. neglecta*, for the calculations the energy of metabolism has been considered as twice the resting energy by analogy with trout (Mann, 1965).

The marked increase in the ecological efficiency in the sixth year occurs at the same time as the fish begin to utilize a new food source, krill. Similarly enhanced growth was noted by Mann (1965) for roach and also from Pentelov's (1939) results on trout, in the former case described from the natural feeding habits of the fish and in the latter case from controlled experiments. It therefore seems likely that *N. rossii* is capable of cropping krill much more efficiently than the benthos and conversely it would appear that food is energy limiting for a species utilizing only benthic organisms.

The implications of this are two-fold. First, that the ecological efficiency of *N. neglecta* may be increased by controlled fishing. This would allow an increased growth rate because of increased food per individual. Secondly, now that it has been established that the utilization of krill by *N. rossii* results in an increased ecological efficiency the question that arises is: how does the utilization of krill by other fish species affect their growth? Baleen whales, the

main utilizers of krill, have been greatly reduced in numbers by over-exploitation since the beginning of the century. It has been known for some time that pelagic fish, e.g. *Micromesistius australis* (Merrett, 1963), enter the Southern Ocean to feed and consequently their population dynamics become an investigation of great priority.

ACKNOWLEDGEMENTS

The field work necessary for this paper would have been impossible without the assistance of all personnel at the British Antarctic Survey station on Signy Island between December 1964 and March 1967. In this country, valuable assistance has been freely given by Messrs. B. W. Jones, M. J. Holden and T. Williams, Fisheries Laboratory, Lowestoft, and also by Dr. M. W. Holdgate, formerly of the British Antarctic Survey and now of the Nature Conservancy. Dr. K. H. Mann gave some helpful hints with regard to the energy budget, and Dr. R. C. Newell and my colleagues of the British Antarctic Survey Zoology Section read and criticized the manuscript. Finally, I should like to thank Mr. E. A. Smith for constructive criticism of my work.

MS. received 3 May 1969

REFERENCES

- ADIE, R. J. 1964. Geological history. (In PRIESTLEY, R. E., ADIE, R. J. and G. DE Q. ROBIN, ed. *Antarctic research*. London, Butterworth and Co. (Publishers) Ltd., 118–62.)
- ALLEN, K. R. 1951. The Horokiwi Stream. *Bull. mar. Dep. N.Z. Fish.*, No. 10, 1–238.
- BERTALANFFY, L. VON. 1938. A quantitative theory of organic growth (inquiries on growth laws II). *Hum. Biol.*, **10**, No. 2, 181–213.
- BEVERTON, R. J. H., and S. J. HOLT. 1957. On the dynamics of exploited fish populations. *Fishery Invest., Lond.*, Ser. 2, **19**, 1–533.
- , GULLAND, J. A., and A. R. MARGETTS. 1959. Whiting tagging; how the tag return rate is affected by the condition of fish when tagged. *J. Cons. perm. int. Explor. Mer*, **25**, No. 1, 53–57.
- CHRISTENSEN, M. J. 1964. Burning of otoliths, a technique for age determination of soles and other fishes. *J. Cons. perm. int. Explor. Mer*, **29**, No. 1, 73–81.
- DAHL, K. 1918. Studies of trout and trout waters in Norway. *Salm. Trout Mag.*, No. 17, 58–59.
- . 1919. Studies of trout and trout waters in Norway. *Salm. Trout Mag.*, No. 18, 16–33.
- EVERSON, I. 1968. Larval stages of certain Antarctic fishes. *British Antarctic Survey Bulletin*, No. 16, 65–70.
- . 1969. Inshore fishes from the South Orkney and South Shetland Islands, the Antarctic Peninsula and South Georgia. *British Antarctic Survey Bulletin*, No. 19, 89–96.
- , and M. G. WHITE. 1969. Antarctic marine biological research methods involving diving. *Rep. Underwat. Ass.*, 1969.
- FORD, E. 1933. An account of the herring investigations conducted at Plymouth during the years from 1924–1933. *J. mar. biol. Ass. U.K.*, **19**, No. 1, 305–84.
- GERKING, S. D. 1954. The food turnover of a bluegill population. *Ecology*, **35**, No. 4, 490–98.
- GULLAND, J. A. and S. J. HOLT. 1959. Estimation of growth parameters for data at unequal time intervals. *J. Cons. perm. int. Explor. Mer*, **25**, No. 1, 47–49.
- HOLDGATE, M. W. 1967. The Antarctic ecosystem. (In SMITH, J. E., organizer. A discussion on the terrestrial Antarctic ecosystem. *Phil. Trans. R. Soc.*, Ser. B, **252**, No. 777, 363–83.)
- HORTON, P. A. 1961. The bionomics of brown trout in a Dartmoor stream. *J. Anim. Ecol.*, **30**, No. 2, 311–38.
- UREAU, J. C. 1964. Contribution à la connaissance de *Trematomus bernacchii* Boulenger. (In CARRICK, R., HOLDGATE, M. and J. PRÉVOST, ed. *Biologie antarctique*. Paris, Hermann, 481–87.)
- IVLEV, V. S. 1945. Biologicheskaya produktivnost' vodoemov [The biological productivity of waters]. *Usp. sovrem. Biol.* [*Russ. Rev. Biol.*], **19**, No. 1, 98–120. [Translation by W. E. Ricker: *J. Fish. Res. Bd Can.*, **23**, 1966, No. 11, 1727–59.]
- JOHNSON, L. 1960. *Studies in the behaviour and nutrition of the pike (Esox lucius)*. Ph.D. thesis, University of Leeds, v, 181 pp.
- KROGH, A. 1916. *Respiratory exchange of animals and Man*. London, Longmans, Green & Co.
- LAEVASTU, T. E. 1961. Natural bases of fisheries in the Atlantic Ocean: their past and present characteristics and possibilities for future expansion. (In BORGSTROM, G. and A. J. HEIGHWAY, ed. *Atlantic Ocean fisheries*. London, Fishing News (Books) Ltd., 18–39.)
- LE CREN, E. D. 1965. A note on the history of mark–recapture population estimates. *J. Anim. Ecol.*, **34**, No. 2, 453–54.
- MANN, K. H. 1965. Energy transformations by a population of fish in the River Thames. *J. Anim. Ecol.*, **34**, No. 2, 253–75.
- MARR, J. W. S. 1935. The South Orkney Islands. 'Discovery' *Rep.*, **10**, 283–382.
- MERRETT, N. R. 1963. Pelagic gadoid fish in the Antarctic. *Norsk Hvalfangsttid.*, **52**, No. 9, 245–47.
- NORMAN, J. R. 1938. Coast fishes. Part III. The Antarctic zone. 'Discovery' *Rep.*, **18**, 1–104.
- ODUM, E. P., ed. 1959. *Fundamentals of ecology*. 2nd edition. Philadelphia, Saunders Co.

- OLSEN, S. 1954. South Georgian cod. *Norsk Hvalfangsttid.*, **43**, No. 7, 373-82.
- . 1955. A contribution to the systematics and biology of chaenichthyid fishes from South Georgia. *Nytt Mag. Zool.*, **3**, 79-93.
- PENTELOW, F. T. K. 1939. The relation between growth and food consumption in the brown trout (*Salmo trutta*). *J. exp. Biol.*, **16**, No. 4, 446-73.
- PERMITIN, Y. E. 1970. The consumption of krill by Antarctic fishes. (In HOLDGATE, M. W., ed. *Antarctic ecology*. London, Academic Press, 177-82.)
- PIRIE, J. H. H. 1908. Zoological log of the summer station "Omond House", Scotia Bay, South Orkneys. (In WILTON, D. W., PIRIE, J. H. H. and R. N. R. BROWN. *Zoological log. Rep. scient. Results Scott. natn. antarct. Exped.*, **4**, Pt. 1, 85-101.)
- PROPP, M. V. 1970. The study of bottom fauna at Haswell Islands by scuba diving. (In HOLDGATE, M. W., ed. *Antarctic ecology*. London, Academic Press, 239-41.)
- RALPH, R. and I. EVERSON. 1968. The respiratory metabolism of some Antarctic fish. *Comp. Biochem. Physiol.*, **27**, No. 1, 299-307.
- RAY, C. 1970. Population ecology of Antarctic seals. (In HOLDGATE, M. W., ed. *Antarctic ecology*. London, Academic Press, 398-414.)
- SLOBODKIN, L. B. 1960. Ecological energy relationships at the population level. *Am. Nat.*, **94**, No. 876, 213-36.
- SOUTHWOOD, T. R. E. 1966. *Ecological methods with particular reference to the study of insect populations*. London, Methuen & Co. Ltd.
- THURSTON, M. H. 1968. Notes on the life history of *Bovallia gigantea* (Pfeffer) (Crustacea, Amphipoda). *British Antarctic Survey Bulletin*, No. 16, 57-64.
- WALFORD, L. A. 1946. A new graphic method of describing the growth of animals. *Biol. Bull. mar. biol. Lab. Woods Hole*, **90**, No. 2, 141-47.
- WHITE, M. G. 1970. Aspects of the breeding biology of *Glyptonotus antarcticus* (Eights) (Crustacea, Isopoda) at Signy Island, South Orkney Islands. (In HOLDGATE, M. W., ed. *Antarctic ecology*. London, Academic Press, 279-85.)
- WINBERG, G. G. 1956. Intensivnost obmena i pishchevye potrebnosti ryb [Rate of metabolism and food requirements of fishes]. *Nauch. Trudy Belor. gos. Univ. V.I. Lenina, Minsk*, 1-253. [English translation: Fisheries Research Board of Canada, Translation Series, No. 194, 1960.]
- WOHLSCHLAG, D. E. 1960. Metabolism of an Antarctic fish and the phenomenon of cold adaptation. *Ecology*, **41**, No. 2, 287-92.
- . 1961. Growth of an Antarctic fish at freezing temperatures. *Copeia*, 1961, No. 1, 11-18.
- . 1962. Antarctic fish growth and metabolic differences related to sex. *Ecology*, **43**, No. 4, 589-97.
- . 1964. Respiratory metabolism and ecological characteristics of some fishes in McMurdo Sound, Antarctica. (In LEE, M. O., ed. *Biology of the Antarctic seas*. Washington, D. C., American Geophysical Union, 33-62.) [Antarctic Research Series, Vol. 1; National Academy of Sciences—National Research Council Publication, No. 1190.]