

Food abundance and territory size in juvenile coho salmon (*Oncorhynchus kisutch*)

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Feeding territory size and potential food abundance were measured simultaneously in a field population of juvenile (40–50 mm) coho salmon. Territory size was inversely related to the density of benthic food on the territory, as predicted from an energy-based model of territoriality. The relationship between the abundance of drift food and territory size was in the predicted direction, but was not significant. Territories were also smaller where intruder pressure was higher, but intrusion rate and food abundance were not directly correlated. Therefore, the effect of food abundance on territory size was not caused indirectly by attraction of nonterritorial fish to areas where food was abundant. In the laboratory, the distance from which a resident coho attacked an approaching model intruder increased asymptotically with hunger. The fish therefore appear to possess an appropriate behavioural mechanism (tactic) to adjust territory size to local food abundance.

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On a mesuré de façon simultanée l'abondance de la nourriture potentielle et la dimension du territoire d'alimentation chez une population de jeunes (40–50 mm) saumons argentés. Tel que prévu à l'aide d'un modèle de territorialité à base d'énergetique, on observe une relation inverse entre les dimensions du territoire et la densité de la nourriture benthique à l'intérieur du territoire. La relation entre l'abondance de la nourriture en dérive et les dimensions du territoire est telle que prévue, mais n'est pas significative. On observe aussi que les dimensions du territoire sont moindres lorsqu'il y a un plus grand nombre d'intrus, mais il n'y a pas de corrélation directe entre l'abondance de la nourriture et le taux d'intrusion. Par conséquent l'effet de l'abondance de la nourriture sur la dimension du territoire n'est pas causé indirectement par l'attraction des poissons non territoriaux dans des régions où la nourriture est abondante. En laboratoire, la distance de laquelle un saumon argenté "resident" attaque le modèle d'un intrus qui s'approche augmente avec la faim selon une asymptote. Ceci démontre que ces poissons semblent être en possession d'un mécanisme de comportement (une tactique) qui leur permet d'ajuster les dimensions de leur territoires selon l'abondance locale de la nourriture.

Coho salmon (*Oncorhynchus kisutch*) spend the first 2 years of their lives in streams, where they defend feeding territories. Typically the demand for space exceeds the holding capacity of the stream, and fish unable to hold territories are displaced downstream, and frequently out of the stream altogether (Chapman 1962). The fate of the displaced individuals is largely unknown, but limited evidence (Crone and Bond 1976; Mason 1976) suggests that fry leaving streams in their 1st year have an extremely low probability of returning as adults. For example, several thousand fry (first summer) leaving Carnation Creek, B.C., have been fin clipped; none have returned as adults (C. Scrivener, personal communication). Available evidence therefore suggests a direct relationship between the ability to hold a territory and fitness in this species.

Not all territories are equally advantageous, however. There is in general an optimal size for a feeding territory, one which maximizes the net rate of energy gain and thus growth rate (Dill 1978a). Maximization of growth rate has several potential advantages. Larger salmonids

are able to move into faster flowing midstream areas where food may be more abundant (Wańkowski and Thorpe 1979). Furthermore, although there appears to be a complicated interaction with time of migration (Bilton 1978), there is evidence that larger downstream migrant coho (smolts) have a higher probability of returning as adults (Olson 1978) and are larger as adults (Bilton 1978) than their smaller cohorts. Finally, adult size and fecundity are positively linearly related in coho salmon (e.g., Crone and Bond 1976). For these reasons growth rate maximization may be roughly equivalent to fitness maximization, and natural selection should operate to produce a mechanism allowing juvenile coho salmon to adjust territory size to the prevailing local optimum.

This optimum territory size will be a function of a number of variables, including food availability. As the density of available food increases, the optimal territory size is expected to decline in a hyperbolic manner for animals adopting a net energy maximization strategy (Dill 1978a; Hixon 1980). The purpose of the research presented here was twofold: (1) to test this prediction in a field population of coho salmon juveniles, and (2) if territory size varies with food abundance, to identify in

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the laboratory the behavioural mechanism (tactic) which would allow individual fish to make such an adjustment.

The effect of food abundance on territory size

Introduction

Field studies on a wide variety of species have indicated that territory or home range size is generally smaller when food abundance is higher (Gass 1979; Kodric-Brown and Brown 1978; Lance 1978; Myers *et al.* 1979; Miller and Watson 1978; Seastedt and MacLean 1979; numerous others cited by Dill 1978a). Although exceptions have been reported (e.g., Ebersole 1980; Salomonson and Balda 1977; Zach and Falls 1979) this relationship seems to be a general one. Curiously, despite a long standing (and economically important) controversy over whether their populations are food or space limited (e.g., Chapman 1966; Chapman and Bjornn 1969), few studies of this nature have been carried out on stream-dwelling salmonids. Slaney and Northcote (1974) found an inverse hyperbolic relationship between food abundance and territory size in a laboratory study of juvenile rainbow trout (*Salmo gairdneri*), but their work has been criticized by McNicol (1979) because fish density potentially confounds the results. McNicol himself (1979) found no clearcut relationship between food abundance and territory size in brook charr (*Salvelinus fontinalis*). Finally, Symons (1971) could demonstrate no effect in his laboratory study of Atlantic salmon (*Salmo salar*), but he altered food abundance only after the territories were established. This section presents the results of the first field study of the relationship between food abundance and territory size in salmonids. The approach is correlative rather than experimental.

Methods

The study was carried out in the Salmon River, in Langley, B.C., from July to October, 1979. This stream, described in Hartman (1965), is a major producer of coho salmon despite its small size. The coho population was particularly dense in 1979 (compared with the immediately previous and subsequent years) and the majority of underyearling coho were residing in glides (low velocity riffles). For this reason, several glide sites, with mixed clay and gravel bottoms, were selected as observation areas and had the following physical characteristics: depths varied from 5–28 cm ($\bar{x} = 18$ cm), water velocities from 0.02 to 0.33 m·s⁻¹ ($\bar{x} = 0.17$ m·s⁻¹), and temperatures from 11.5 to 17°C ($\bar{x} = 14.3$ °C). Within these relatively narrow ranges there were no apparent relationships between any of these parameters and territory size.

Territory size measurements were obtained for coho ranging between 40 and 50 mm total length. Each fish was observed between 0900 and 1500 h on sunny or cloudy-bright days, after establishing that the individual was holding a territory. Occasionally fish would move out of the immediate area and be lost to the observer, requiring data collection to be terminated.

Only data on fish which could be followed continuously for 10–20 min ($\bar{x} = 11.5$ min) are presented.

Territory maps were obtained by viewing the fish through an eyepiece mounted in a fixed position relative to an oblique sheet of clear plexiglass on a tripod. The tripod was placed on the stream bank (or in the stream itself) a few metres from the fish being observed, and in such a way that no shadows were cast on the territory. During the observation period the positions of all interactions with other fish and the maximum distances of all feeding forays from the fish's primary station were marked on the plexiglass plate (these two behaviours had similar distributions in space). The outside points were connected to form a convex polygon, which was then mapped back onto the stream bottom by placing stakes in the substrate in positions corresponding to the apices of the polygon as viewed through the eyepiece. Another stake topped with a 360° protractor was placed at the fish's primary station and the polar coordinates of all corner stakes recorded relative to this central one. A scale model of each territory was then reconstructed in the laboratory on graph paper, cut out, and weighed. Weight was then converted to territory area from the known weight per unit area of the graph paper. Thirty-one territories were measured in this way.

For the last 21 territories measured, the number of intruders crossing the territory perimeter in a 1- or 2-min period was also recorded, allowing calculation of intrusion rate per unit of territory area. Miscellaneous observations on territorial and feeding behaviour were also recorded, including locations of feeding motions (whether surface, midwater, or bottom).

There are three sources of potential food for coho salmon holding territories in glides, and an attempt was made to measure the abundance of each: terrestrial insects falling onto the water surface, midwater drift, and benthic organisms.

Surface prey were sampled using two 100-cm² boards coated with Tanglefoot and placed on stakes just above the water surface to the immediate left and right of each territory. These were left in place for periods of 50–100 min. Very few prey (mostly adult dipterans) were caught, and because this source was unpredictable and minor as a food supply it was not examined further.

Midwater drift organisms were sampled with 1-m long × 15-cm diameter net (240-μm mesh) placed adjacent to each territory for periods ranging from 45 to 90 min, bracketing the time when territory size was measured. It was not always possible to completely submerge this net, but since preliminary studies indicated that organisms were distributed approximately uniformly in the water column, captures were adjusted only for area sampled, i.e., they were not weighted by abundance at different depths. All organisms captured (excluding exuviae) were preserved in formalin and subsamples later counted, dried, and weighed. An oven malfunction resulted in the loss of samples for the first 15 territories; therefore, weight data were available only for the last 16. Potential food availability was expressed as milligrams dry weight per square metre of submerged net aperture per minute (i.e., as a rate). The percentage composition of the number of specimens in all subsamples is shown in Table 1.

Benthic organisms were sampled with a small Surber sampler: a 100-cm² frame with a net (240-μm mesh) on the

TABLE 1. Percent frequency distributions of organisms (by number) for midwater drift and benthic samples

Prey type	Drift, %	Benthos, %
Copepods (Copepoda)	22	12
Cladocerans (Cladocera)	21	2
Chironomids (Chironomidae)	19	65
Mayflies (Ephemeroptera)	11	3
Mites (Acarina)	10	4
Stoneflies (Plecoptera)	2	2
Beetles (Coleoptera)	2	0
Caddisflies (Trichoptera)	1	2
Worms (Nematoda, Annelida)	0	2
Others	11	9
Sample size		
Samples	31	31
Organisms	1359	3206

downstream end. Samples were collected at the territorial resident's primary station, by washing organisms off rocks and disturbing the bottom to a depth of ca. 5 cm. Laboratory analysis was the same as for drift samples (see above), except that the abundance of potential food was expressed as milligrams dry weight per square metre of territory (i.e., as standing stock). The numerical composition data (Table 1) show a high frequency of chironomids compared to the drift samples.

Results and discussion

The spatial structure of the coho population observed was not a regular territorial mosaic, but gave the overall impression of being very loosely organized. On occasion fish were seen to be replaced at a station by a new resident during an observation period; a similar situation ("rotating territory") has been described in trout (Newman 1956). In our case length of tenure cannot be specified, since the time of arrival of the original resident was unknown, and we cannot completely discount the possibility that the fish were disturbed by the observer. The fish frequently alternated between several stations in the territory, as in brook charr (McNicol 1979), and did not attack all potential intruders. The latter phenomenon (termed partial territoriality) has been described previously for salmonids by Newman (1956) and Jenkins (1969). Despite these complications, all measured territories were stable in size and position during the brief observation periods. They tended to be teardrop shaped, somewhat wider at the upstream end.

There was an apparent but nonsignificant negative relationship between territory area and rate of drift of potential prey by dry weight (Fig. 1) or by number. Because of the expected hyperbolic shape of this curve, regression analysis was carried out following log-log

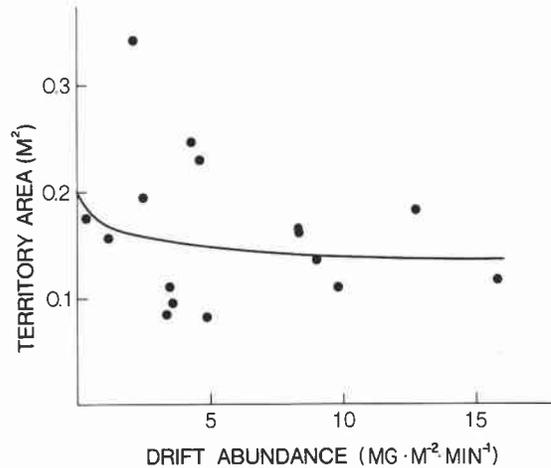


FIG. 1. The relationship between coho salmon territory area (square metres) and the abundance of potential midwater drift prey (milligrams dry weight per square metre per minute): $\text{area} = 0.17(\text{drift})^{-0.0845}$, $r = 0.21$.

transformation of the data ($r = -0.21$, $p > 0.10$). The correlation worsens if territory area is measured as front cross-sectional area, rather than as the area projected on the stream bed.

In contrast, there was a strong negative relationship (Fig. 2) between territory area and dry biomass density of potential benthic prey. For the log-log transformed data, $r = -0.65$ ($p < 0.01$). When the data for the last 21 territories are split into two groups by intruder density ($<$ or $>$ 30 intrusions $\cdot \text{m}^{-2} \cdot \text{min}^{-1}$) the effect becomes even clearer (Fig. 3). The log-log regression of territory area on benthic food abundance (Fig. 4) is significant for

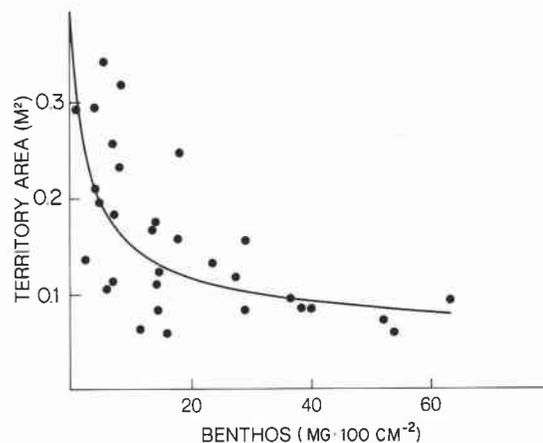


FIG. 2. The relationship between coho salmon territory area (square metres) and the abundance of potential benthic prey on the territory (milligrams dry weight per 100 cm^2): $\text{area} = 0.3345(\text{benthos})^{-0.3487}$, $r = -0.65$.

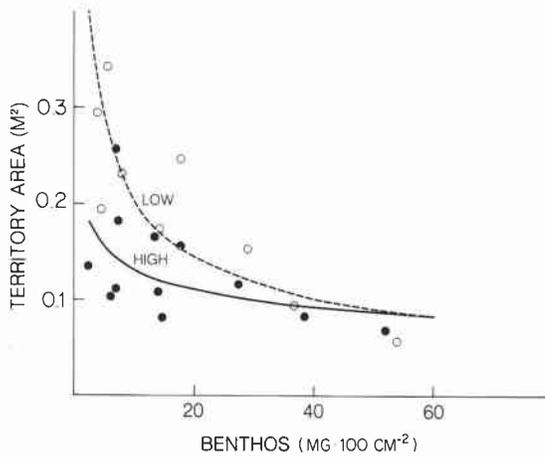


FIG. 3. The relationship between coho salmon territory area (square metres) and the abundance of potential benthic prey on the territory (milligrams dry weight per 100 cm²) for territories for which intruder pressure data were available. The data were split into two groups, depending on whether intruder pressure was high (>30·m⁻²·min⁻¹; filled circles) or low (<30·m⁻²·min⁻¹; open circles).

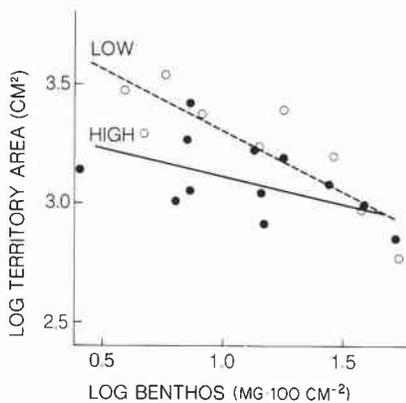


FIG. 4. The same data as in Fig. 3 plotted on a log-log scale. The fitted regression lines are the following. Low intruder pressure: $\log \text{ area} = 3.8057 - 0.4973 \log \text{ benthos}$, $r = -0.8445$; high intruder pressure: $\log \text{ area} = 3.3437 - 0.2288 \log \text{ benthos}$, $r = -0.5252$; all data: $\log \text{ area} = 3.5470 - 0.3498 \log \text{ benthos}$, $r = -0.6314$.

all data combined ($r = -0.63$, $p < 0.01$) and for the low intruder pressure data ($r = -0.84$, $p < 0.01$), and almost so for the high intruder pressure data ($r = -0.53$, $p < 0.10$).

The fact that territories were smaller when potential food abundance was high, even when intruder pressure was partially controlled for in the statistical analysis, suggests that this was a direct effect of food abundance rather than an indirect effect of large numbers of fish being attracted by abundant food (in contrast with the

sanderlings studied by Myers *et al.* 1979). This interpretation is further supported by the fact that intruder pressure did not increase with food abundance (Fig. 5). In fact, the relationship is a (nonsignificant) negative one, perhaps because there were fewer nonterritorial fish (potential intruders) where food was abundant owing to the establishment of a larger number of smaller territories. Thus, the present data support the predictions of Dill (1978a) and others that territory size should be smaller both when food is abundant and when intruder pressure is high. Numerous studies (summarized in the Introduction to this section) have found similar effects of food abundance, and several authors have observed inverse effects of intruder pressure on territory size: McNicol (1979) for brook charr and Myers *et al.* (1979), Vines (1979), Lederer (1977), Gill and Wolf (1975), and Wolf (1975) for various species of birds.

Finally, the data may be used to test the hypothesis, proposed by Gass *et al.* (1976) and others, that the abundance of potential food on the territory is constant regardless of territory size. If this were the case the relationship between food abundance and territory size would be perfectly hyperbolic, the log-log transform plots having slopes of -1.0 . The slopes for all data sets treated in this way differ significantly from -1.0 . For example, for all 31 data points the slope is -0.35 ($p \ll 0.01$); slopes for the data sets in Fig. 4 are given in the caption. In other words, at low food densities the fish hold smaller territories than expected from a hyperbolic relationship and thus have access to less food than do fish holding territories where food is more abundant. This is presumably because there is an upper limit to the size of an economically defensible territory.

It is somewhat curious that benthic food abundance is a better predictor of territory size than is the abundance

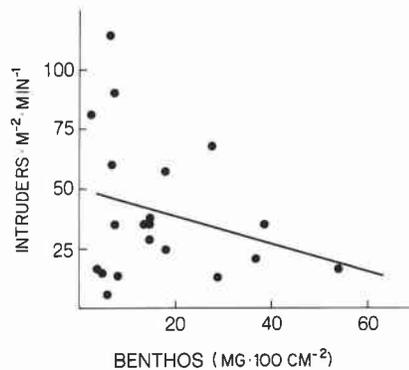


FIG. 5. The relationship between intruder pressure (number per square metre per minute) and the abundance of potential benthic prey on coho territories (milligrams dry weight per 100 cm²). A linear model maximizes the correlation coefficient which, however, is nonsignificant.

of drift, given that fish seem to feed mostly on the latter (78% of observed feeding motions). In part this may be a result of inadequate sampling. There is a great deal of small scale spatial and temporal variation in drift abundance, and our single measurement (for practical reasons) was taken just outside the territory. However, benthic organisms (predominantly chironomids) tend to be larger than those in the drift, and may make up a higher proportion of the fishes' energy intake than suggested by the data on feeding motions. Thus, during the daytime when drifting prey are relatively rare, territory size may be more closely related to the abundance of benthic prey. Glova (1978) has reported that stomachs of coho collected from glides and riffles contained primarily benthic prey (e.g., chironomid larvae).

This study provides the only field evidence that juvenile salmon may alter the size of their territories in response to changes in food abundance, despite much theorizing (e.g., Chapman 1966), and conflicting laboratory studies (Symons 1971; Slaney and Northcote 1974; McNicol 1979). Although based only on correlative evidence, the present result may be of considerable practical significance, suggesting as it does that artificial enhancement of food availability in rearing streams may lead to increased production of juvenile coho salmon, at least from glides. Such an experiment has been conducted by Mason (1976) with some success. He was able to increase summer carrying capacity, but gains were lost through overwinter mortality and (or) displacements to sea by winter freshets. Mason (1976) also reported that food enhancement resulted in reduced territory size, but provided no supportive data.

The effect of hunger on attack distance

Introduction

The preceding field data suggest that territory sizes of juvenile coho salmon vary inversely with potential food abundance, as predicted from theoretical models (e.g., Dill 1978a). The fish thus seem to behave optimally in a strategic sense, although it has not been demonstrated that individual fish adjust territory size. This section presents the results of an experiment to determine the behavioural mechanism (tactic) which the fish might use to make such an adjustment.

To do this, the salmon require some method of assessing food availability. As Charnov (1976) has suggested, an animal can use the degree of fullness of its gut (hunger) as an indicator of food availability. On average, the salmon will have less food in their stomachs (and thus be more hungry) when food is scarce.

Aggression has several components and may be measured in a variety of ways, but the measure most relevant to territory size is the reactive (attack) distance

towards territorial intruders; Thresher (1978) has termed this component of aggression "spatial commitment." The hypothesis tested here is that hungry coho have greater reactive distances to a standard intruder than do more well-fed individuals.

Methods

The experimental subjects were 44 juvenile coho, taken from the Salmon River in groups of four between May and August, 1979. Their average fork length was 39.4 mm, and they ranged in size from 38 to 41 mm.

Fish were held individually, and visually isolated from one another, in small (25 × 25 × 25 cm) aquaria with an airstone and a few pieces of gravel on the bottom. These aquaria were kept in a large water bath (Fig. 6) which held the temperature close to that in the stream at the time of collection (ca. 13–16°C). For testing, the aquarium containing the subject was floated to one end of the large tank and secured in place (see Fig. 6), and an opaque sliding door opened so that the fish could view the length of the test tank through a piece of plate glass.

The "intruder" was a color photograph of a 40-mm coho with erect fins, which had been cut out and laminated in plastic. This was moved along nylon strings towards the subject by an electric motor, starting at the opposite end of the water bath. The intruder was effectively invisible while moving against the white background, but was stopped at 5-cm intervals and made to assume a lateral display posture by pulling on a nylon line connected to the "flipper" apparatus shown in Fig. 6 (inset). The model intruder was held in this position for 2–3 s before being returned to the forward position and moved 5 cm closer. When the resident coho charged the front glass of its tank in response to a lateral display, movement and presentation of the model ceased, and the sliding door on the test aquarium was closed. The reaction of the fish was recorded on video tape and monitored simultaneously from a position outside black-out curtains which surrounded the entire experimental apparatus. Attack distance was defined as the distance between the fish and the model at the time the charge occurred (the sum of distances from fish to glass and model to glass).

Test fish were held for 4–6 days prior to testing, and fed five brine shrimp each day. The day before testing, the coho were given what we refer to as "scapegoat" treatment: a coho 5 mm smaller than the test coho was introduced to the latter's aquarium. This fish was quickly dominated by the resident, and then removed by the experimenter. This was an attempt to prime the aggressive response to the model by having the resident coho make an investment of time and energy in defending his feeding area.

On the test day the individual coho to be photographed was assigned randomly to one of four feeding levels: no food, 5 brine shrimp, 10 brine shrimp, and brine shrimp to satiation (range 13–19, \bar{x} = 14.5 shrimp totalling 6.8 mg dry weight). Thus, 5 and 10 shrimp comprise approximately 34 and 69%, respectively, of the average maximum gut capacity. The model intruder was presented immediately after feeding was completed. Not all fish reacted to the model (failure rate was

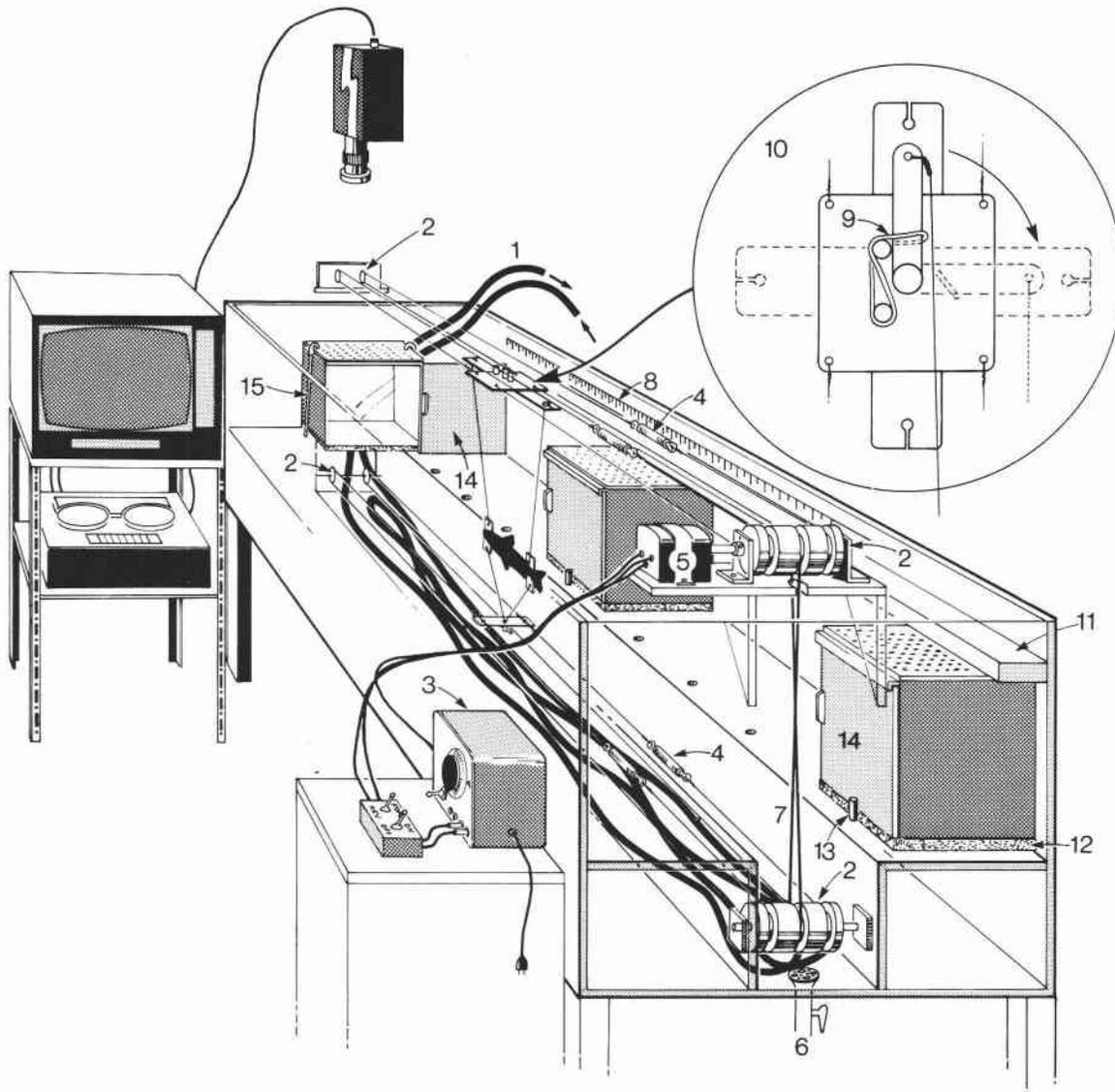


FIG. 6. The test tank for measuring coho reactive distance to model intruders. Legend: 1, hose for circulating cold water to maintain water bath temperature; 2, pulleys for lines holding the model; 3, variable transformer; 4, plexiglass turnbuckles to maintain constant tension on the four nylon lines; 5, electric motor; 6, drainpipe; 7, rubberized cord connecting top and bottom sets of pulleys; 8, metre stick; 9, elastic band to return model to frontal position; 10, flipper apparatus for presenting model in lateral display position; 11, ledge to hold down buoyant tanks; 12, styrofoam tank bottom; 13, peg to hold tank in position; 14, sliding doors; 15, elastic to hold test tank in position.

about 7%, and did not vary with hunger level), but the experiment was continued until 11 complete sets of data were obtained (four fish reacting per day, one at each hunger level).

Results and discussion

The more hungry the resident coho, the greater the distances from which they attacked model conspecific intruders their own size (Fig. 7). All pairwise comparisons of attack distance, except that between fish fed zero

and five shrimp (1.0 and 0.66 relative hungers, respectively), were significant ($p < 0.05$, t -test). Thus, attack distance apparently increases asymptotically with hunger. Since fish at low levels of food availability will on average be less satiated, this provides a mechanism by which the coho may adjust their territory area to food availability.

Threshold distances for aggressive behaviours (both display and attack) have been reported in a wide variety

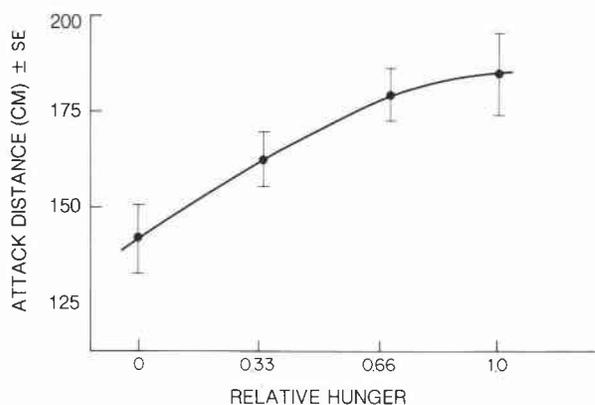


FIG. 7. The relationship between the hunger level of resident coho and the distance from which they attacked the model intruder (mean \pm SE). The line is fitted by eye.

of species, e.g., pumpkinseed sunfish (Colgan *et al.* 1981), damselfish (Thresher 1978; Moran and Sale 1977; Itzkowitz 1979), charr (McNicol 1979), anemone fish (Ross 1978), tree frogs (Fellers 1979), herring gulls (Grubb 1974), oystercatchers (Vines 1979), various marine crustacea (Hazlett 1978, 1979a, 1979b), and others (reviewed in Dill 1978b). Although several authors (e.g., Dill 1978b; McNicol 1979) have tested for the effect of hunger or food abundance on aggressive distance, the present study is the first to document such a relationship. However, there are good theoretical reasons (Huntingford 1976) to expect feeding behaviour and aggression to share a common motivational mechanism (i.e., hunger), and there is experimental evidence for this in some fishes, e.g., sunfish (Poulsen 1977). The picture is more confused in salmonids (see Dill 1978b) but some evidence is consistent with this motivational hypothesis (Symons 1968; Slaney and Northcote 1974). In view of this it is curious that effects of hunger on attack distance have not been more frequently observed. There are two likely reasons for this.

First, hunger must be controlled experimentally in a way which is relevant to the ecology of the species concerned. As suggested earlier in this paper, juvenile coho sometimes may hold only short tenure on their territories, and there is considerable temporal and spatial variability in food abundance. The animal clearly should monitor food availability via a short-term mechanism (i.e., one with a narrow temporal window), such as degree of fullness of the gut (hunger). Since a long-term monitoring mechanism would not be beneficial, it is perhaps not surprising that attack distances do not vary with past feeding history or daily ration size (Dill 1978b; McNicol 1979). Similar considerations probably apply to other species as well.

Second, territorial aggression is a multicomponent process. Thresher (1978) has elegantly demonstrated

that there are at least two components in damselfish: spatial commitment (which determines the size of the area defended) and attack readiness (which determines the vigor of defense). Thresher also showed that these two components (and there may be more) had partially independent motivational mechanisms. It is possible that hunger (however defined) may exert its effects on different components of the aggression process in different species. In coho salmon, past feeding history does affect attack velocity (Dill 1978b), a possible measure of attack readiness. Future studies will have to take into account more explicitly the multicomponent nature of aggression, and the likelihood of different time scales for operation of the motivational mechanisms.

It should be noted that the attack distances observed in the laboratory far exceed the radii of territories measured in the field (this paper). The discrepancy may be due to a variety of factors: the isolated holding conditions of the residents, the scapegoat treatment, the stark white background against which the model was presented, the low intrusion rate, or the fact that the fish were in still water (and thus not required to expend as much energy in an attack as they would in the field). Regardless of the reason, it is clear that the recorded attack distance is not a measure of territory size *per se*, but hopefully is an index of it. To the extent that this is true, we believe we have identified a behavioural mechanism (tactic) which would allow the fish to adjust their territory size to local food availability, as predicted by a net-energy maximizing strategy, and supported by the field correlation between territory size and potential food abundance.

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