

# Predation of 0-group flatfishes by 0-group cod: handling times and size-selection

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**ABSTRACT:** Behavioural aspects of capture and ingestion of 0-group dab *Limanda limanda* and plaice *Pleuronectes platessa* by 0-group cod *Gadus morhua* were examined in laboratory experiments. The ingestion time of plaice was longer than that of dab of the same length and gape limitation was observed at a lower prey:predator length ratio for plaice (0.39) than for dab (0.44). These observations can be explained by prey morphology because the relative body width of plaice is greater than that of dab. Selective predation on smaller size-classes of flatfishes observed in the field could not be accounted for by gape limitation. Pursuit, ingestion, and handling (pursuit + ingestion) times were positively related to flatfish size, and negatively related to cod size. Profitability of flatfishes (weight gained per unit handling time) declined monotonically with increasing prey size for the range of size ratios of cod and flatfishes used in the experiments. There was therefore qualitative agreement between profitability and the selection of smaller size-classes of flatfishes observed in the field. Capture efficiency and the number of times flatfishes were released during ingestion increased with increasing relative prey size. It is therefore suggested that negative size-selection by cod in the field could result from the probabilities of both capture and ingestion after capture, in addition to active behavioural selection.

**KEY WORDS:** *Gadus morhua* · *Limanda limanda* · *Pleuronectes platessa* · Size-selection · Feeding behaviour

## INTRODUCTION

There is a strong interest in size-dependent survival of early life stages of marine fishes in relation to recruitment (e.g. Cushing 1974, Peterson & Wroblewski 1984, McGurk 1986, Anderson 1988, Beyer 1989, Pepin 1991). This interest has prompted a number of recent laboratory and mesocosm studies of size-dependent piscivory by invertebrates and fishes (e.g. Folkvord & Hunter 1986, van der Veer & Bergman 1987, Litvak & Leggett 1992, Pepin et al. 1992, Rice et al. 1993, Witting & Able 1993, Bertram & Leggett 1994, Juanes & Conover 1994, Gibson et al. 1995). Some of the results have prompted a questioning of paradigms of size-dependent vulnerability to predation (Leggett & DeBlois 1994). Field studies illustrat-

ing size-selective predation are scarcer (for review of plaice *Pleuronectes platessa* see van der Veer et al. in press), and both negative and positive size-selection (predation on smaller and larger members of prey population respectively) have been demonstrated. However, a common feature of these field studies is that the larger members of the predator population consume the prey.

Juvenile cod *Gadus morhua* are piscivorous and found in large numbers in inshore areas used as nursery grounds by other gadoids, clupeids and flatfishes (Edwards & Steele 1968, Pihl 1982, Gibson et al. 1993, Gibson & Robb 1996). Ellis & Gibson (1995) illustrated that predation by cod on 0-group flatfish populations was negatively size-selective and was restricted to the larger individuals of the cod population (Fig. 1). The purpose of the laboratory experiments detailed here was to examine the processes of capture and ingestion of 0-group flatfishes by 0-group cod in relation to 3

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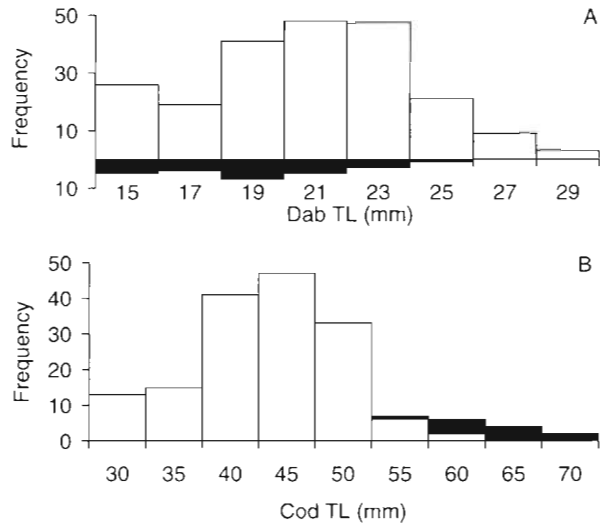


Fig. 1 (A) Length frequency distribution of dab *Limanda limanda* on Tralee Beach (Scotland) in mid-June 1992 (white bars) showing sizes of fish eaten by 0-group cod *Gadus morhua* (black bars below x-axis). (B) Length distribution of 0-group cod in mid-June 1992 showing sizes eating dab (black portions of bars). Data from Ellis & Gibson (1995)

alternative hypotheses potentially resulting in negative size-selection of prey: gape limitation, active predator choice based on handling times, and probability of prey capture.

## MATERIALS AND METHODS

0-group cod were captured between June and August 1992 from Tralee Beach on the west coast of Scotland, UK (see Gibson et al. 1993). 0-group dab *Limanda limanda* and plaice were also caught from Tralee Beach. Experiments were done in July and August, so the size range of fish used in experiments reflected size distributions in the field, cod 65 to 147 mm total length (TL), and flatfishes 23 to 47 mm TL. The range of prey:predator size ratios examined was 0.20 to 0.49.

Cod were acclimated singly to transparent Perspex arenas (60 × 33 cm, with water depth of 26 cm) with a constant flow at ambient temperature (14.5 ± 1.5°C). Illumination was from above and light intensities in mid-water were 0.26 to 0.44 × 10<sup>15</sup> quanta cm<sup>-2</sup> s<sup>-1</sup>. The cod were fed a single meal of live flatfishes or shrimp *Crangon crangon* daily in order to standardise hunger levels. The majority of a meal would be expected to have been evacuated from the stomach within 24 h at the ambient temperature (Tyler 1970, Jones 1974). The cod used in experiments had been fed flatfishes previously to provide experience. Ten

cod were used in 90 trials, and feeding activity was observed in 85% of trials. Experiments started when the dab or plaice of a single length were introduced together into the experimental arena by submerging a beaker beneath the surface of the water and allowing the flatfish to swim out. Experiments lasted for approximately 30 min, until all the flatfishes offered were eaten, or the cod showed no further interest in feeding.

Experiments were filmed in a lateral view and feeding behaviour was analysed from video recordings coded with a visible time code (to 0.04 s). The number of unsuccessful attacks prior to the successful capture and ingestion of each prey was recorded. Pursuit time was estimated from first orientation towards the prey to the time of capture. Ingestion time was estimated from the time the cod first captured the flatfish to when it was judged to have been conveyed to the stomach. A characteristic swallowing action and distension of the stomach region followed by flexing of the jaws was often evident and taken to signal the end of ingestion. The number of times the prey was released or escaped from the jaws between first capture and the end of ingestion was noted. Handling time has variably been considered to comprise subsets of times for recognition, pursuit, capture, ingestion and digestion (e.g. Werner 1974, Stephens & Krebs 1986, Kaiser et al. 1992). Recognition time was not discernible and assessment of digestion times was impractical, so handling time was taken as the sum of pursuit and ingestion times. Profitability of flatfishes was measured as the wet weight gained per unit handling time (mg s<sup>-1</sup>). Wet weights of flatfishes were estimated from relationships with TL derived for plaice and dab caught from Tralee Beach (Ellis 1994).

Predator and prey lengths were reduced to a single variable, the ratio of prey:predator length, to examine size effects on semi-continuous dependent variables (capture efficiency i.e. the reciprocal of number of attacks prior to ingestion of prey, the number of releases during handling, and the number of flatfishes eaten) by non-parametric Spearman rank correlation. The effects of independent variables (cod length, prey length, prey species, prey number) on continuous variables (pursuit time, ingestion time, handling time, profitability) were analysed using the Generalised Linear Model of ANOVA, after log<sub>e</sub> transformation of the dependent variable. Normality of errors was confirmed using Shapiro-Wilk tests. Only the pursuit, ingestion and handling times of the first 3 prey were used as the number of plaice eaten did not exceed 3. Temperature and interaction terms were included as factors in analyses, but were removed when shown to be non-significant (p > 0.05).

## RESULTS

## Pursuit

After recognition of prey, cod pursued flatfishes with a rapid acceleration and would often continue to pursue prey that escaped after the initial pursuit. Pursuit time was affected by cod size, flatfish size and prey number, but not flatfish species (Table 1). There was, however, a high degree of variation not explained by the analysis ( $R^2 = 0.13$ ). Pursuit time decreased with increasing cod size and increased with increasing prey size (Fig. 2A). Pursuit time increased as the number of prey eaten increased, illustrated by the least square means (means corrected for co-variables), which were 1.02, 1.40 and 1.99 s for the first, second and third prey eaten respectively. Cod length had the strongest effect on pursuit time.

## Capture

The capture efficiency for the first prey was analysed because predator hunger levels were equivalent and the number of observations and size ranges of prey were large. There was a negative correlation between capture efficiency and the prey:predator size ratio (Fig. 3A) for both dab ( $r_s = -0.666$ ,  $n = 29$ ,  $p < 0.001$ ) and plaice ( $r_s = -0.359$ ,  $n = 32$ ,  $p < 0.05$ ).

## Ingestion

It was not possible to distinguish the alignment of small flatfishes during capture and ingestion due to the speed of ingestion. Of the 77 occasions when the orientation was discernible, 77% were ingested tail first, and 23% head first. This reflects the orientation of capture, as most flatfishes were captured by the tail. The largest relative prey sizes were ingested tail first and horizontally. During ingestion of large prey, or prey caught in an oblique orientation, the grip on the prey would often be released due either to the struggling of prey or to the cod adjusting the orientation of the prey within the jaws. There was a positive correlation (Fig. 3B) between the number of times the first prey was clear of the jaws during ingestion and the prey:predator size ratio for dab ( $r_s = 0.638$ ,  $n = 29$ ,  $p < 0.001$ ) and both species combined ( $r_s = 0.553$ ,  $n = 61$ ,  $p = 0.001$ ). Ingestion times are indicative of the difficulty the cod had in ingesting the flatfish. At prey:predator length ratios of 0.49 and 0.48 for dab, and 0.42 and 0.40 for plaice, the flatfish were not ingested despite long handling times (Fig. 2B). The longest times preceding ingestion were for flatfish:cod length ratios of 0.44 for dab and 0.39 for plaice. Relatively smaller flatfishes (dab 0.35 and 0.43, plaice 0.30 to 0.38) were, however, handled without ingestion (Fig. 2B) when the cod released the prey and did not persist in attempting to ingest. Ingestion time was

Table 1. Results of generalised linear model analyses of variance. Note 16 flatfishes were pursued, but not ingested after capture. All interaction terms were initially included in the analyses, but were removed when found to be non-significant. The probability of the Shapiro-Wilk test for normality of errors is included

| Dependent variable                  | Source          | df  | Sum of squares | Mean square | F-value | p > F  | R <sup>2</sup> | Shapiro-Wilk p |
|-------------------------------------|-----------------|-----|----------------|-------------|---------|--------|----------------|----------------|
| log <sub>e</sub> pursuit time       | Cod length      | 1   | 9.1            | 9.1         | 10.3    | 0.0017 | 0.13           | 0.4491         |
|                                     | Flatfish length | 1   | 3.5            | 3.5         | 4.0     | 0.0482 |                |                |
|                                     | Prey number     | 2   | 5.5            | 2.7         | 3.1     | 0.0495 |                |                |
|                                     | Species         | 1   | 1.3            | 1.3         | 1.5     | 0.2211 |                |                |
|                                     | Error           | 118 | 104.0          | 0.9         |         |        |                |                |
| log <sub>e</sub> ingestion time     | Cod length      | 1   | 277.4          | 277.4       | 236.3   | 0.0001 | 0.71           | 0.7335         |
|                                     | Flatfish length | 1   | 178.8          | 178.8       | 152.4   | 0.0001 |                |                |
|                                     | Prey number     | 2   | 8.4            | 4.2         | 3.6     | 0.0316 |                |                |
|                                     | Species         | 1   | 5.0            | 5.0         | 4.2     | 0.0425 |                |                |
|                                     | Error           | 102 | 119.8          | 1.2         |         |        |                |                |
| log <sub>e</sub> handling time      | Cod length      | 1   | 209.7          | 209.7       | 225.1   | 0.0001 | 0.70           | 0.7491         |
|                                     | Flatfish length | 1   | 128.6          | 128.6       | 138.0   | 0.0001 |                |                |
|                                     | Prey number     | 2   | 5.8            | 2.9         | 3.1     | 0.0477 |                |                |
|                                     | Species         | 1   | 2.14           | 2.1         | 2.3     | 0.1325 |                |                |
|                                     | Error           | 102 | 95.1           | 0.9         |         |        |                |                |
| log <sub>e</sub> prey profitability | Cod length      | 1   | 207.7          | 207.7       | 221.7   | 0.0001 | 0.72           | 0.7897         |
|                                     | Flatfish length | 1   | 57.7           | 57.7        | 61.6    | 0.0001 |                |                |
|                                     | Prey number     | 2   | 5.6            | 2.8         | 3.0     | 0.0543 |                |                |
|                                     | Species         | 1   | 0.0            | 0.0         | 0.0     | 0.9541 |                |                |
|                                     | Error           | 102 | 95.5           | 0.9         |         |        |                |                |

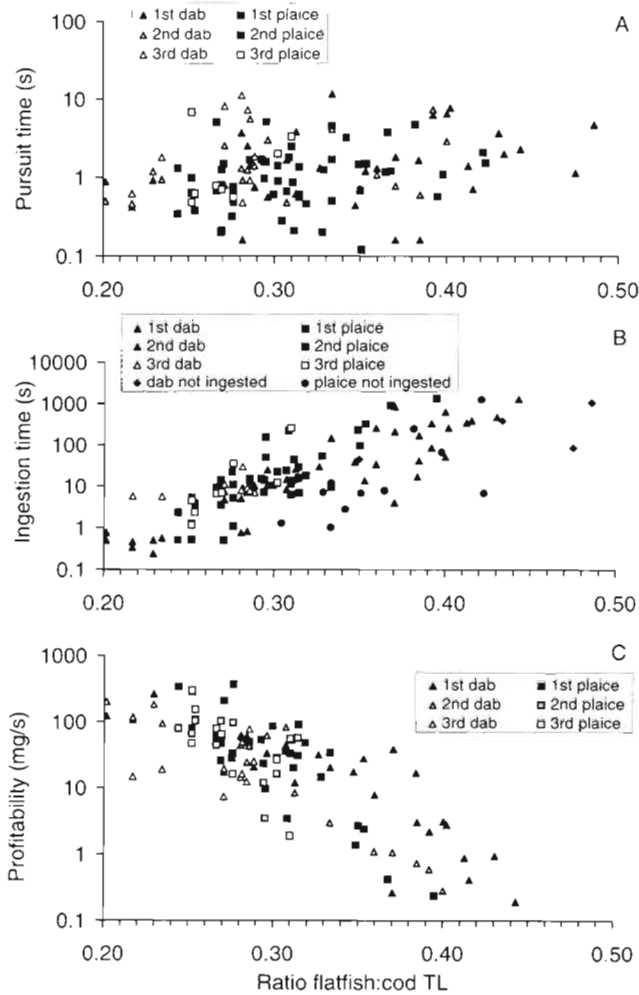


Fig. 2. Prey:predator size data for cod *Gadus morhua* feeding on flatfish (*Limanda limanda*, *Pleuronectes platessa*). (A) Pursuit time; (B) ingestion time; (C) prey profitability. Data shown are for first, second and third prey attacked and ingested, and in (B) also for first prey caught but not ingested. The data are presented as a prey:predator length ratio for ease of illustration

affected by cod size, flatfish size, prey number and prey species with cod size and flatfish size having the strongest effects (Table 1). Ingestion time decreased with increasing cod size and increased with increasing prey size (Fig. 2B). Ingestion time increased as the number of prey eaten increased (least square means 11.2, 15.7 and 26.2 s for the first, second and third prey eaten respectively). The ingestion time of plaice was longer than that of dab (least square means 13.2 and 21.0 s for dab and plaice respectively).

At low flatfish:cod size ratios the cod ate all the flatfishes offered and continued to show signs of foraging behaviour. In trials when the cod were satiated, there was a negative correlation (Fig. 3C) between the num-

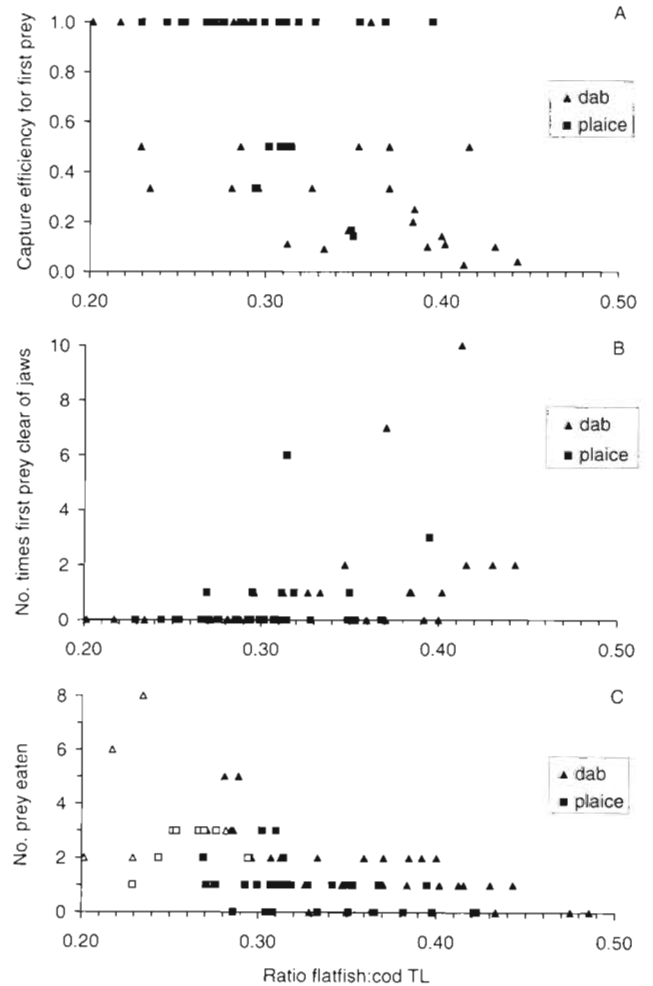


Fig. 3. Prey:predator size data for cod *Gadus morhua* feeding on flatfish (*Limanda limanda*, *Pleuronectes platessa*). (A) Capture efficiency, data for first prey; (B) number of times the prey was ejected or escaped from jaws before ingestion, data for first prey; (C) number of flatfishes eaten, open symbols indicating trials when cod ate all prey offered but were not satiated

ber of flatfishes eaten and the prey:predator size ratio for both dab ( $r_s = -0.653$ ,  $n = 28$ ,  $p < 0.001$ ) and plaice ( $r_s = -0.477$ ,  $n = 34$ ,  $p < 0.005$ ). More prey were therefore eaten at low prey:predator size ratios.

### Handling time and prey profitability

Handling time was taken as the sum of pursuit and ingestion time. Cod size, flatfish size, and prey number affected handling times, although flatfish prey species did not (Table 1). Again cod size and flatfish size had the strongest effects on handling time. Handling time decreased with increasing cod size and increased with

increasing prey size. Handling time increased as the number of prey eaten increased (least square means 15.1, 20.3 and 30.3 s for the first, second and third prey eaten respectively).

Prey profitability apparently decreased monotonically with increasing prey:predator size ratios within the range of size ratios examined. Predator size and prey size affected prey profitability, but prey number and species did not (Table 1). Profitability decreased with increasing flatfish size and increased with increasing predator size (Fig. 2C)

## DISCUSSION

If the first attempt at capture was unsuccessful, cod often chased prey; they can therefore be classed as pursuers rather than lungers (following definition of Hunter 1984). Cod capture prey by suction (Fuiman & Batty 1994), and flatfishes were usually ingested tail first, reflecting the fact that the majority were captured by the tail. Orientation of prey during ingestion, either head or tail first, has differed among studies of piscivory and has been suggested to be specific to particular combinations of predator and prey (Juanes & Conover 1994). Differences in orientation during ingestion have been explained by the location of the attack in relation to predator attack style and prey morphology. Pursuing predators (rather than lungers) tend to catch prey by the tail and ingest tail first (Popova 1978, cited in Juanes & Conover 1994). Moody et al. (1983) found that the same predator species attacked deep-bodied prey in the caudal region whereas round-bodied prey were attacked in mid-body.

### Prey ingestion

Cod only ingested flatfishes whole in all the laboratory experiments. They did not sever prey as some piscivores have been observed to do (Juanes & Conover 1994). Mouth gape is considered to set an upper size limit on the ingestion of whole prey (Hambricht 1991). As cod ingested flatfishes in the horizontal plane, horizontal mouth gape restricted maximum prey size (Hambricht 1991). Vertical gape is generally measured in predation studies, estimated after a subjective judgement as to when the mouth is fully open (e.g. Robb & Hislop 1980, Otterå & Folkvord 1993). Such estimates of gape will be of little use in prediction of maximum prey size (e.g. Werner 1974), as they do not account for the orientation of prey during ingestion, the extent of opening and distension of the jaws, and the ability to compress and distort prey (Hoyle & Keast

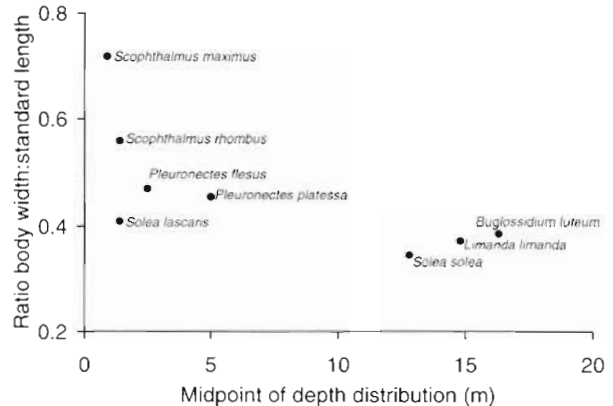


Fig. 4. Relationship between relative body width and depth distribution of 0-group flatfish. Mid-point of depth distribution taken from Riley et al. [1981], and ratio of body width to standard length estimated from illustrations in Wheeler (1969)

1987, 1988). These facts emphasise the utility of behavioural observations, assessing gape limitation by non-ingestion after extended periods of handling as in this study. The prey:predator length ratio for the largest prey eaten was greater for dab (0.44) than for plaice (0.39). Gape limitation therefore occurred at a lower prey:predator length ratio for plaice than for dab. This can be explained by the morphological difference between the 2 flatfish species because the relative body width (dorsal fin to anal fin) of plaice is greater than that of dab (Norman 1934). Cannibalism in populations of intensively reared cod, a roundfish, occurs at prey:predator length ratios of up to 0.67 (Otterå & Folkvord 1993) and further demonstrates the effect of body shape on vulnerability to predation.

In freshwater lakes a correspondence has been drawn between predation pressure from piscivorous fishes and the body shape of the small fish species present. Shallow-bodied species are abundant in piscivore-free lakes, whereas deep-bodied fish predominate where piscivores are present (Hambricht 1991). Nevertheless, an equivalent hypothesis cannot account for the observed depth distribution of different shaped flatfish species in the juvenile stage, in which they will be most vulnerable to predation. The relative body width of 0-group flatfishes decreases with increasing depth (Fig. 4;  $r_s = -0.802$ ,  $n = 8$ ,  $p < 0.05$ ) whereas piscine predation pressure is thought to increase with increasing depth (Burrows et al. 1994). However, body shape may not only affect vulnerability to ingestion by fishes but also by piscivorous birds (Hudson & Furness 1988). In addition body shape probably affects drag in turbulent conditions (Arnold & Weihs 1978) and agility necessary for capture of evasive prey (Holmes & Gibson 1983).

### Factors affecting pursuit and ingestion times

Both pursuit time and ingestion time increased as the number of flatfishes consumed increased, resulting in longer handling times as more prey were ingested. This may reflect the motivational state of the cod predator because handling times increase with satiation (e.g. Werner 1974). The effect of prey number on handling times was, however, far weaker than the effects of predator and prey size. Pursuit and ingestion times showed a negative relationship with cod size, presumably because attack speed will increase with increasing predator length, and gape will increase (Robb & Hislop 1980) facilitating ingestion of prey. Pursuit and ingestion times showed a negative relationship with flatfish prey size, presumably because larger flatfish show a faster escape response (Gibson & Johnston 1995) and prey body width increases with increasing prey size, making ingestion more difficult. The ingestion time of plaice was longer than that of dab of the same length. This is because the relative body width of plaice is greater than that of dab (Norman 1934) and prey morphology affects handling time (e.g. Hoyle & Keast 1987).

### Profitability of flatfishes

Profitability decreased with increasing flatfish size, over the range of predator and prey sizes used in the experiments. Such monotonically decreasing profitability curves have previously been noted and may be explained by a normal shaped curve truncated to the right of the peak, i.e. the optimum prey size (Hughes 1980). The profitability analysis suggested that the smallest flatfishes available will be the most profitable, and profitability of flatfishes increased with increasing cod size. These results are in qualitative agreement with the field observations that the largest 0-group cod fed on the smaller flatfishes (Fig. 1). Dekker (1983) recorded a mean dab:cod weight ratio of 0.00641 with a good fit ( $R^2 = 0.86$ ). This weight ratio corresponds to a mean length ratio of 0.19 (using length-weight relationships from Coull et al. 1989) and is lower than the length ratios used in the handling time experiments, and those observed in the field (Fig. 5).

### Prey size-selection by cod

There has been much debate over the last 20 yr as to whether the size-selection of prey by fishes is an active process due to predator choice, or a passive process due to size-related probabilities of encounter, capture and ingestion (e.g. Werner 1974, O'Brien et al. 1976,

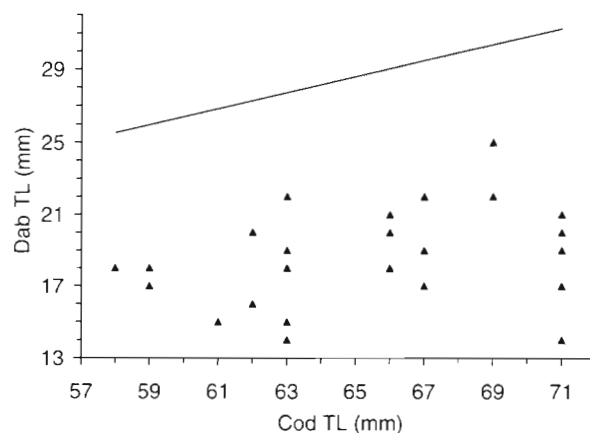


Fig. 5. Sizes of individual dab *Limanda limanda* eaten by cod *Gadus morhua* in the field. The upper size limit for gape limitation (a prey:predator size ratio of 0.44) is indicated by the continuous line. Data from Ellis & Gibson (1995)

Gardner 1981, Juanes 1994). Negative size-selection of dab could be generated actively by choice according to profitability, or passively due to either the greater difficulty of capturing larger prey, or gape limitation.

The sizes of dab eaten in the field were below the upper size limit set by gape limitation of the predator (Fig. 5). Also, although many cod <58 mm TL were caught, none had eaten dab, even though they were apparently not gape-limited. These results show that gape limitation was unlikely to account for the selection of the smaller size-classes of the dab prey population in this case. There was qualitative agreement between the profitability data and the field observations of the largest 0-group cod feeding on the smaller flatfishes. However, in our experiments capture efficiency decreased with increasing relative prey size. Also, the number of times the cod released its grip on the prey and the prey was clear of the cod's jaws increased with increasing prey size. The duration of both pursuit and ingestion increased with increasing prey size, giving larger prey a longer opportunity to escape during both pursuit and ingestion. These factors will decrease the probability of capture, and of ingestion after capture, of larger prey. These effects were noted in small, well lit, bare laboratory tanks. In the field, in low light intensities, where escape distance will not be so confined and a soft substratum exists for burying and crypsis, escape of prey during pursuit and ingestion may be more significant. Other recent studies of piscivory have illustrated the importance of escape of prey during pursuit (Juanes & Conover 1994) and after capture during ingestion (Gibson et al. 1995). In a recent review of prey selection by piscivorous fishes, Juanes (1994) concluded that negative size-selection was a common feature and was due to the escape of prey.

### Predator-prey size relationships and prey selection

Significant positive predator-prey size relationships have been demonstrated for cod feeding on fish (Daan 1973, Daan et al. 1990, Kikkert 1993, Hop et al. 1994, Ellis & Gibson 1995). However, caution must be exercised before assuming that such relationships are the result of 'preference' (e.g. Daan 1973, Ursin 1973, Hahm & Langton 1984) or an active prey selection process (see Juanes 1994). Although the mean size of fish eaten increases with cod size, so does the range of sizes (e.g. Daan et al. 1990), which can be large in relation to mean size (Hahm & Langton 1984). The dubious nature of size relationships was well illustrated by Wilson (1975), who showed for a range of predators that the upper limit of prey size increases with predator size without a concurrent increase in the lower size limit. Also, as the sizes of prey eaten will depend foremost on the size range available, significant positive correlations between predator and prey sizes may result from a concurrent increase in the size of both predator and prey due to growth (Ellis & Gibson 1995).

**Acknowledgements.** This work was carried out while T.E. was in receipt of a NERC CASE award (University of Liverpool/Dunstaffnage Marine Laboratory) studentship. The experiments were done under Home Office Project and Personal Licences issued in accordance with the Animals (Scientific Procedures) Act 1986. We thank Mike Burrows for comments on an early version of the manuscript, and the authors who permitted reference to the ICES manuscripts.

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This article was submitted to the editor

Manuscript first received: July 15, 1996

Revised version accepted: February 12, 1997