Impact of predation by juvenile *Clinus superciliosus* on phytal meiofauna: are fish important as predators?

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ABSTRACT: *Clinus superciliosus* (L.) is the dominant resident fish of the rocky intertidal around the Cape Peninsula, South Africa. Meiofauna is frequently recorded in the diet of immature individuals. Predation by juvenile fish on communities was examined in a series of laboratory experiments in which the meiofauna was provided with shelter in the form of several species of algae differing in their morphological complexity. Although algal complexity significantly influenced the success of predators, results suggest that the fish selected their prey on the basis of size. Typically, they took the largest meiofauna or juvenile macrofauna i.e. amphipods, isopods and polychaetes, and unless the fish were starved, smaller components such as copepods were ignored. Using these data and material from the literature it is concluded that permanent members of the meiofaunal community are unaffected by fish predation and that complex algae only become important as a refuge in tidal pools, where fish occur at high densities for relatively long periods of time. This represents the first attempt at estimating the overall impact of fish predation on rocky shore meiofauna.

INTRODUCTION

Meiofauna from both sandy and rocky substrata have been variously defined but are generally described as animals greater than 63 μm and less than 1 mm (Mare 1942, McIntyre 1969, Hulings & Gray 1971). This rather broad definition includes both juvenile macrofauna (temporary meiofauna) and permanent meiofauna (Warwick 1984).

In soft sediments meiofaunal communities often occur at high densities (McIntyre 1969, McLachlan 1983) and are thought to contribute substantially to secondary production in such systems (Koop & Griffiths 1982). While they are essential in fuelling the interstitial food webs (Gerlach 1978), their importance as a source of energy for higher trophic levels is unclear. Bottom-feeding larval and juvenile fish are, however, known to prey on meiofauna, especially benthic harpacticoid copepods (Hicks 1985). Coull & Bell (1979) have suggested that this effect may be significant only in muddy or detrital substrata. However, Hicks & Coull (1983) subsequently included sandy systems with epibenthic and phytal copepods, although they concluded that the impact of predation on meiofaunal assemblages remained unknown. McIntyre & Murison (1973) have suggested that predation on meiofauna as a whole is negligible, and, therefore, that they hold a trophic position at the end of their food chain. Invertebrate predators, such as polychaetes and decapods, are generally considered unimportant (Reise 1979 in Hicks & Coull 1983).

Rocky shore meiofauna can also occur at high densities (Hicks 1985) and are similarly thought to contribute significantly to secondary production (Gibbons & Griffiths 1986). Energy transfer to macrofauna has been postulated (Beckley & McLachlan 1980), although hard evidence is sparse. Harpacticoid copepods are frequently recorded in the gut contents of larval and juvenile fish (Gibson 1982) along with a smaller number of other meiofauna. From laboratory experiments, Coull & Wells (1983) argued that fish are important in structuring meiofaunal communities. On the other hand, from work on sublittoral algal beds, Choat & Kingett (1982) suggested that meiofaunal populations fluctuate largely independently of fish predation. Dethier (1980) has, nevertheless, demonstrated that fish predation determines the distribution pattern of the copepod *Tigriopus californicus* in tidal pools. Such pools, however, represent generally small and relatively discrete areas in the intertidal. The impact of
predation on meiofauna from algae on open rocks is unknown.

Many predators on rocky shores, unlike their counterparts on softer sediments, are obliged to forage for food items amongst algae. Algal complexity may influence the success of predators and thereby the composition of the meiofaunal communities. Several authors have examined the relationship between algal complexity, refugia from predators, and the diversity of different phytal animal groups. Coull & Wells (1983) did this for harpacticoid copepods, and Russo (1987) for amphipods, and found a correlation between fauna diversity and habitat structural complexity, but their data provide little evidence of the overall impact of predation on phytal meiofaunal communities.

Of the 21 resident fish species found in the tidal pools of the southwestern Cape, South Africa, the biology of the clionid *Clinus superciliosus* (L.) is best known (Veith 1979). It is the dominant species, accounting for 28% of the numerical total and 40% of biomass (Bennett & Griffiths 1984). Meiofauna (copepods and ostracods) form a regular part of the diet of this and other fish species (Bennett et al. 1983), especially of juveniles (Bennett pers. comm.). It has previously been considered a representative fish species (Bennett 1984) and as such was selected for these experiments.

An attempt is made in this article to determine the overall impact of fish predation on rocky shore meiofauna. The mediating role played by the structural complexity of algae is central to this, and experiments were designed that could be readily extrapolated to the field.

**METHODS**

Algae and meiofauna for all experiments were collected from the low intertidal at Granger and Three Anchor Bays (18° 24’ S, 33° 55’ W) on the west coast of the Cape Peninsula, South Africa. Clumps of algae *Gigartina radula* and *Corallina* sp. were removed with their associated fauna and transported to the laboratory in large plastic buckets. Fresh meiofauna were collected for each set of experiments.

**Laboratory.** To narcotise meiofauna, the algae were first immersed in isotonic magnesium chloride (73.2 g l⁻¹) for 10 min. Individual clumps were then shaken vigorously under running, filtered seawater onto a set of nested 1 mm and 62 μm sieves. Residue from the MgCl₂ treatment was then similarly sieved. Those animals retained by the 1 mm mesh were discarded as macrofauna (Gibbons & Griffiths 1986) while those remaining on the 62 μm sieve were rinsed into fresh filtered seawater, stirred into suspension and divided into 16 equal portions (rations) using a Folsom plankton splitter (Wickstead 1976).

For each experimental set, 4 of these rations were immediately preserved in buffered saline formalin (5%) to establish the efficiency and accuracy of the splitter (using χ²) and to identify the mean initial input ration (control). The null hypothesis for the χ² test was that the plankton splitter could separate the meiofauna into approximately equal portions. This was upheld (maximum χ² = 5.71; df = 16; p > 0.05) in the 4 repeated tests.

The 12 remaining live rations were distributed between 12 experimental aquaria (volume 1460 cm³). Each aquarium was fed by a constant flow of filtered seawater at 15°C. The outflow was covered by a mesh of 30 μm. Each experiment was in 2 parts: the first consisted of 3 treatments (no algae, Alga 1 and Alga 2), and the second of 2 treatments (no algae, Alga 3), with 4 replicates. In addition each experiment was repeated 4 times. To reduce the effects of allelo-chemicals as much as possible, all algae were members of the division Florideophyceae; viz, *Porphyra capensis* (hereafter *Porphyra*), an open, flat-fronded plant of medium size, *Gelidium pintoide* (hereafter *Gelidium*), a medium-sized, open plant with branching fronds, and *Corallina* sp. (hereafter *Corallina*), a short, closed plant with branching fronds, which forms dense turfs in the field. Algal surface areas were standardized using calibration curves relating surface area to weight. Each aquarium was filled with 50% fresh filtered seawater and 50% filtered water, which came from tanks holding the predator. This procedure was used since it had been noticed that meiofauna seek shelter more readily in the presence of fish. Leaving the flow off, one of the 12 meiofauna rations was added to each aquarium and allowed to settle and disperse for 2 h. Flow was then resumed and 2 *Clinus superciliosus* added to each tank. The fish were allowed to remain in the aquaria for 2 h, after which all algae and animals were treated again with MgCl₂, decanted onto a 62 μm sieve and preserved in buffered saline formalin (5%). All rations were then size-sorted through a 500, 280, 125 and 62 μm sieve series, prior to counting and identification of the major taxonomic groups. Meiofauna >62 μm but <125 μm were ignored because animals in this size class showed no changes in numbers relative to the control, irrespective of treatment.

Although Coull & Wells (1983) allowed their experiments to run for 24 h, their data could not be extrapolated to the field, as the foraging period was unrealistically long. Therefore, in the present experiments the period of exposure to predators was kept short, so encompassing the low overall density of fish per m², the high standing crop of algae per m² and the short available foraging time per tidal cycle.

Experiments were conducted using both ‘starved’ and ‘satiated’ fish. ‘Starved’ fish were kept without food for 6 h prior to the run (a length of time compar-
able to that in which they would be confined to tidal pools during emersion), while 'satiated' individuals were supplied with excess meiofauna for a prior 24 h. Thirty Clinus superciliosus, ranging in size from 26.6 to 29.7 mm (mean 28.4 mm, SD 0.8 mm) were collected from tidal pools in the same vicinity as the algae and meiofauna. All individuals were caught at low tide either by dip-netting or by anaesthetic (Benozcaine 111 g l^-1 / 26% ethanol). They were subsequently kept in large holding tanks for up to 3 wk prior to experimental runs, where they were handled daily in an effort to reduce shock during transfer to the experimental aquaria. Fresh algae with their associated fauna were fed to them daily.

One additional control was conducted to test for changes in meiofaunal numbers during the experimental period. Four replicate aquaria, without either algae or fish, were set up and allowed to run for a 4 h period. Differences in counts before and after were tested for significance using the $\chi^2$ test, where no change was considered the null hypothesis. This was upheld (maximum $\chi^2 = 4.82; df = 16; p > 0.05$) in each instance.

**Algal complexity.** Complexity was measured in a number of ways viz. (1) for a unit algal mass the (a) surface area; (b) volume; (c) surface area:volume ratio were calculated and (2) for a unit algal volume the (a) surface area and (b) volume:surface area ratio were calculated. The surface area was calculated using the method of Harrod & Hall (1962) as modified by Hicks (1977), where the change in mass of a surface-dried object (dried with acetone) dipped in commercial detergent (Teepol) and subsequently drip-dried is directly proportional to the surface area. Fronds of different weights from the 3 algal were treated thus and replicate measurements taken. For the weight differences, surface areas were calculated from the regression equation of Hicks (1977b): $A = 0.033363 + 0.002518W$, where $A$ is surface area and $W$ is the weight of the detergent film. The data were then regressed against the initial frond weights to provide calibration curves of surface area vs frond weight and the standardized surface areas were established from these. Surface areas for fronds of 1 g mass were also calculated. Volume was measured by water displacement in a graduated cylinder.

**Data analysis.** Predation rate is a function of prey density (Ware 1972, Stoner 1982). Coull & Wells (1983) considered that when the input rations for each experimental set are significantly different from each other, they represent covariables. Consequently their data were analysed by analysis of covariance (ANCOVA). Although the input rations for each set in the present experiment were also significantly different from each other (ANOVA, $p < 0.0001$), it was not strictly valid to analyse the data using ANCOVA, since only one experimental treatment (no algae) was repeated for each set and fish condition.

Plotting final against initial meiofaunal densities for the repeated treatment resulted in straight-line plots, with similar slopes that tended towards the origin. As this pattern was observed for both starved and satiated sets, the two were combined into a single data set. This was justified on the basis that the fish were foraging in a similar way in both sets; if they were not and the meiofauna were at densities below foraging optima these plots would have differed. To standardize the data by removing the effect of different input rations, data were expressed in terms of the difference between the initial (before predation control) and the final meiofauna density relative to the initial density, i.e.

$$\frac{\text{control density} - \text{final density}}{\text{control density}} \times 100.$$

When examining community responses, where it cannot be assumed that there are no interactions among component species, the appropriate parametric test is the multivariate analysis of variance (MANOVA, in this case 2-way Model 1 full factorial; Smith et al. 1962), and this technique was used to test for the community response to fish feeding condition and algal structure. Multivariate analyses are discussed by Marriot (1974), Morrison (1976) and Sokal & Rohlf (1981). The underlying assumptions of MANOVA include multinormality of error terms and homogeneity among group covariance matrices. Box's $M$ statistic has traditionally been used to test for homoscedasticity; however, since it is highly sensitive to slight heteroscedasticity that has no effect on the rate of Type I error, and is greatly sensitive to non-normality, the test is of little use (Mardia 1971, Olson 1974, Johnson & Field unpubl., Johnson pers. comm.). Unfortunately, no alternative is at present available. However, the problems of heteroscedasticity and non-normality can be minimised by reducing dimensionality (in this case the number of prey species) as much as possible; first by discarding rare species unlikely to contribute useful information, and then by principal component analysis (PCA). Thus, the number of variables was first reduced by excluding those species contributing less than or equal to 5% to any control (consistently insect larvae, tanaids, oligochaetes, juvenile anthozoans and newly settled echinoderms) and secondly, by conducting a PCA on the pooled-within-group covariance matrix (obtained by averaging the 10 within-group covariance matrices i.e. for each experimental treatment). Since the first 4 principal components accounted for 70% of the total dispersion, the MANOVA was conducted on these. As there was no consistent relationship among the means and standard deviations of each principal vector, the data were not transformed for MANOVA.
The Pillai's Bartlett trace was the statistic of choice since this is the most robust to departures from homoscedasticity and normality (Johnson & Field unpubl., Johnson pers. comm.).

In analysing the effect of fish condition and algal structure on individual taxa, univariate analyses of variance (ANOVA's, in this case 2-way Model 1 full factorial) were used. For these the Bonferroni adjustment was applied to the probability of Type I errors, otherwise alpha is 0.05.

All statistical analyses were conducted using SAS (Statistical Analysis Systems) software.

RESULTS

Algae

Standard complexity measures are given in Table 1 and regressions of surface area on frond weight and surface area on frond volume are presented in Tables 2 and 3 respectively. Although the ratio for Corallina here is much lower than previously reported (Hicks 1977b, Coull & Wells 1983), such discrepancies have been discussed by the latter authors.

Table 1. Surface area (SA) and volume (VOL) measurements of the 3 algae used in the experiments

<table>
<thead>
<tr>
<th>Alga</th>
<th>SA (cm² g⁻¹)</th>
<th>VOL (ml g⁻¹)</th>
<th>SA:VOL (g⁻¹)</th>
<th>SA (cm² ml⁻¹)</th>
<th>SA:VOL (ml⁻¹)</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Porphyra capensis</td>
<td>189.34</td>
<td>1.47</td>
<td>133.66</td>
<td>111.61</td>
<td>0.0099</td>
<td>25</td>
</tr>
<tr>
<td>Gelidium pristoides</td>
<td>207.25</td>
<td>1.23</td>
<td>168.66</td>
<td>104.34</td>
<td>0.0096</td>
<td>65</td>
</tr>
<tr>
<td>Corallina sp.</td>
<td>128.27</td>
<td>1.60</td>
<td>80.27</td>
<td>71.29</td>
<td>0.014</td>
<td>25</td>
</tr>
</tbody>
</table>

Table 2. Regression equations of frond surface area (A) on frond weight (W) for each of the algal species used in the experiments.

<table>
<thead>
<tr>
<th>Alga</th>
<th>Regression equation</th>
<th>r²</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Porphyra capensis</td>
<td>A = 236.1021 W - 46.7614</td>
<td>0.99</td>
<td>25</td>
</tr>
<tr>
<td>Gelidium pristoides</td>
<td>A = 240.0067 W - 32.7528</td>
<td>0.99</td>
<td>65</td>
</tr>
<tr>
<td>Corallina sp.</td>
<td>A = 144.105 W - 15.831</td>
<td>0.91</td>
<td>25</td>
</tr>
</tbody>
</table>

Table 3. Regression equations of frond surface area (A) on frond volume (V) for each of the algal species used in the experiments.

<table>
<thead>
<tr>
<th>Alga</th>
<th>Regression equation</th>
<th>r²</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Porphyra capensis</td>
<td>A = 213.9761 V - 102.3633</td>
<td>0.98</td>
<td>25</td>
</tr>
<tr>
<td>Gelidium pristoides</td>
<td>A = 240.9044 V - 100.5569</td>
<td>0.96</td>
<td>65</td>
</tr>
<tr>
<td>Corallina sp.</td>
<td>A = 158.127 V - 86.84</td>
<td>0.98</td>
<td>25</td>
</tr>
</tbody>
</table>

Controls; meiofauna

The structure of Corallina is such that it offers little space for large animals to move. Consequently, approximately 85% of all the input rations (bearing in mind that only animals greater than 125 μm have been counted) were comprised of animals between 125 μm and 280 μm (Fig. 1). Of these, long, thin harpacticoid copepods, the harpacticoid Porcellidium sp. (hereafter Porcellidium), nauplii and nematodes were invariably most abundant. Collectively, amphipods, isopods and polychaetes represented between 56 and 80% of those size fractions greater than 280 μm but only 25% of those between 125 and 280 μm.

The size class distributions for each of these major taxa are presented in Fig. 2.

The above results have in all cases been subjected to ANOVA; where non-significant scores (p < 0.05) were recorded among controls the data have been pooled.

Experiment

The 4 principal vectors generated by the PCA were responsible for 29, 21, 13 and 12% of the raw data
as a whole is influenced by algal structure, but not by whether the predator is starved or fed.

The results of ANOVA's on the designated taxa reinforce the results of the PCA (Table 5): significant interaction, algal and fish effects were noted for isopods and *Porcellidium*; significant algal and fish condition, but no interaction effects, were recorded for polychaetes, while significant algal effects only were noted for amphipods and long, thin harpacticoid copepods. Non-significant ANOVA statistics (p > 0.004) were recorded for all the other species groups.

The MANOVA of the first 4 principal vectors indicated a highly significant algal effect, while both the fish (condition) and interaction (fish x algae) effects were non-significant (Table 4). This suggests that the impact of fish predation on the meiofaunal community as a whole is influenced by algal structure, but not by whether the predator is starved or fed.

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Table 5. Effect of algal structure and fish condition on the predation impact by *Cinus superciliosus* on individual meiofauna taxa. ANOVA table; the Bonferroni adjustment must be applied to the probability of Type I errors thus alpha is 0.0042. Note only those groups showing significance at this level for either source have been included.

<table>
<thead>
<tr>
<th>Group</th>
<th>Source</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Polychaetes</td>
<td>Algae</td>
<td>12.60</td>
<td>0.0001</td>
</tr>
<tr>
<td></td>
<td>Fish</td>
<td>16.75</td>
<td>0.0003</td>
</tr>
<tr>
<td></td>
<td>Interaction</td>
<td>3.65</td>
<td>0.0154</td>
</tr>
<tr>
<td>Copepods</td>
<td>Algae</td>
<td>7.77</td>
<td>0.0002</td>
</tr>
<tr>
<td></td>
<td>Fish</td>
<td>3.34</td>
<td>0.0777</td>
</tr>
<tr>
<td></td>
<td>Interaction</td>
<td>2.33</td>
<td>0.0783</td>
</tr>
<tr>
<td>Porcellidium</td>
<td>Algae</td>
<td>8.35</td>
<td>0.0001</td>
</tr>
<tr>
<td></td>
<td>Fish</td>
<td>129.93</td>
<td>0.0001</td>
</tr>
<tr>
<td></td>
<td>Interaction</td>
<td>8.17</td>
<td>0.0001</td>
</tr>
<tr>
<td>Amphipods</td>
<td>Algae</td>
<td>127.08</td>
<td>0.0001</td>
</tr>
<tr>
<td></td>
<td>Fish</td>
<td>9.79</td>
<td>0.0039</td>
</tr>
<tr>
<td></td>
<td>Interaction</td>
<td>1.66</td>
<td>0.1856</td>
</tr>
<tr>
<td>Isopods</td>
<td>Algae</td>
<td>192.29</td>
<td>0.0001</td>
</tr>
<tr>
<td></td>
<td>Fish</td>
<td>45.11</td>
<td>0.0001</td>
</tr>
<tr>
<td></td>
<td>Interaction</td>
<td>13.85</td>
<td>0.0001</td>
</tr>
</tbody>
</table>

Fig. 1. Numerical composition of controls, broken down into size classes.

Fig. 2. Numerical distribution amongst size classes of each of the 'sensitive' species-groups. 'Sensitive' refers to those showing significant ANOVA scores (Table 5).

Table 4. Effect of algal structure and fish condition on the predation impact by *Cinus superciliosus* of phytal meiofauna communities: MANOVA of first 4 principal components. Note transformations were not applied to each principal component. Pillai's trace is the statistic of choice.

<table>
<thead>
<tr>
<th>Source</th>
<th>Value</th>
<th>F</th>
<th>df</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Algae</td>
<td>1.12</td>
<td>2.92</td>
<td>16</td>
<td>0.0004</td>
</tr>
<tr>
<td>Fish condition</td>
<td>0.07</td>
<td>0.47</td>
<td>4</td>
<td>0.7555</td>
</tr>
<tr>
<td>Interaction</td>
<td>0.60</td>
<td>1.33</td>
<td>16</td>
<td>0.1874</td>
</tr>
</tbody>
</table>
Fig. 3. Percentage predation on each size class for each of the 'sensitive' species-groups amongst the different experimental treatments.

Histograms of predation intensity (as percent) on each size class for each experimental treatment were constructed, and those showing similar patterns of predation were compared for significance using ANOVA. Where these were non-significant ($p > 0.05$) data have been pooled. The results are presented in Figs. 3 and 4.

Non-significant scores were recorded between starved and satiated Corallina treatments, irrespective of size class, for all species except Porcellidium.

**Polychaetes**

Predation on animals $>280 \mu m < 950 \mu m$ from most treatments (except Corallina) was high, irrespective of predator condition, however, removal of individuals $>125 \mu m < 280 \mu m$ was largely restricted to starved fish. Corallina offered the greatest degree of protection although this was lessened for the larger individuals.

**Amphipods**

With the exception of Corallina which provided good protection, differences between treatments were not significant irrespective of fish condition and size.

Fig. 4. Percentage predation on Porcellidium and other copepods amongst the different experimental treatments. Only individuals $>125 \mu m$ and $<280 \mu m$ are considered.
Isopods

*Corallina* provided greatest protection; otherwise differences between treatments, with the exception of individuals >500 μm < 950 μm, were insignificant irrespective of fish condition or size.

*Porcellidium*

Predation was not heavy, even when the fish were starved. There was no significant difference between *Corallina* and *Gelidium*. Although both afforded little or no protection to *Porcellidium* the impact of predation changed with fish condition. *Porphyra* provided a significantly greater amount of refuge than the other algae.

Other copepods

The impact of predation was minimal and appeared independent of both fish condition and the structure of most algae. *Corallina* provided individuals with greatest protection.

Discussion

**Algae**

The surface area:volume ratio (per unit algal mass) is commonly held to be the ‘best’ index of complexity (Coul & Wells 1983, Hicks 1985) as it incorporates 2 structural characteristics into a single term. By this measure *Corallina* has previously been identified as having a complex structure (Coul & Wells 1983, Hicks 1977b, 1985). However, of the species examined here, by this definition it is the least complex, yet it would be unreasonable to consider *Porphyra* as more complex (in terms of the number of habitats) than *Corallina*. Conversely, if one uses the volume:surface area ratio (per unit algal volume) as an index of complexity then *Corallina* becomes the most complex and *Porphyra* the least complex of the algae.

These different ratios relate to the physical morphology of individual algal fronds, and have little actual bearing on the overall complexity of the plant. In *Porphyra* the frond is a distromatic, foleaceous membrane, whereas in *Corallina* the thallus is multistromatic, branching and impregnated with calcite. The fronds of *Gelidium* are also multistromatic and branched, but are flattened and uncalcified. It is not the object of this paper to construct any new index, but clearly any new definition of overall algal complexity must incorporate not only details of frond structure but also the area occupied, height, density, flexibility and volume of the whole plant. Taking these factors into account the algae used here can be ranked in descending order of complexity, *Corallina* > *Gelidium* > *Porphyra*.

**Controls**

The meiofaunal community extracted from *Corallina* and *Gigartina* did not differ markedly from previous accounts (Sarma & Ganapati 1972, Beckley & McLachlan 1980, Gunnill 1982, 1983, Edgar 1983a, b, c). It could be argued that the meiofauna extracted from these algae were not adapted to living amongst the experimental species and might as a consequence have been more susceptible to predation. However, there are few alga-specific meiofauna (Hicks 1977a) and most are frequently recorded from several different plant species (Hicks 1977c, 1982). Moreover, while Coul & Wells (1983) noted selective predation on some species of copepods, at the level of the taxon meiofauna extracted from the alga *Champia novaezealandia* survived better amongst *Corallina* than *Champia*.

The results of the MANOVA support the findings of Nelson (1979, 1981), Crowder & Cooper (1982), Stoner (1982), Coull & Wells (1983) and Russo (1987), which indicated that algal complexity is important in determining the impact of predation. Complex algae, such as *Corallina*, reduce predator efficiency by providing a large number of refuges. However, as noted by Coull & Wells (1983), *Corallina* is rigid, so that although its increased complexity might allow for the provision of a greater number of refuges, its structure is such as to reduce predation in its own right. Coul & Wells (1983) observed the blenny *Helcogramma medium* to push aside the fronds of softer algae and to actively search for prey, but simply waited for meiofauna to move to the periphery of *Corallina* before capturing them. *Clinus superciliosus* is a fish of similar feeding habits and subsequent observations have revealed an identical behaviour pattern. It must, therefore, be concluded that the effects of rigidity and complexity on prey removal from *Corallina* cannot be separated. Despite the very large difference in structure of *Gelidium* and *Porphyra*, both gave poor protection to meiofauna and differences between them and the treatments with no algae were mostly insignificant. This supports the idea that physical complexity must attain some threshold level before it becomes an important component in structuring communities (Nelson 1979, Coul & Wells 1983). Hicks (1985) noted that there is an obvious interaction between body size and form of an organism and its adaptability to a particular algal growth form and, therefore, the amount of protection that it receives. For example, *Corallina* does not extend full
protection to all meiofauna: larger organisms, which must experience some problems in moving through the algal matrix hidden, fall prey to fish. *Porcellidium*, which is clearly not adapted to living on turf algae (being dorso-ventrally flattened) is more vulnerable on *Corallina* than it is on *Porphyra* (Hicks 1985, but see also Hicks 1982).

Paradoxically, the results of Marinelli & Coull (1987), who studied predation by juvenile spot *Leistomus xanthurus* on infauna amongst artificial *Diopatra* (Polychaeta) tubes, indicated that structures in complex habitats promoted mortality of certain taxa. These data suggested to them that either some interaction between predator and or prey existed with the refuge element such that certain prey became more vulnerable, or that the predators foraged more efficiently amongst structure. It was, however, very difficult for them to differentiate between predation per se and disturbance (by resuspension from the mud). Their results are not strictly applicable to the phytal meiofauna, however, as meiofauna from muddy sediments are not adapted to physical disturbance. Meiofauna amongst algae in the rocky intertidal, on the other hand, are subjected to often severe wave action and are consequently adapted to grip.

Whereas algal complexity did mediate the intensity of predation, the impact on the community as a whole was largely independent of fish condition. This suggests that the fish were taking the same prey items at a similar rate, irrespective of whether or not they were 'starved'. The ANOVA results supported this. Few species were taken by fish in any numbers, and these were consistently the temporary elements of the community, which made up the bulk of the larger size classes. The results suggest that the fish were foraging optimally, although the experiments were not designed to test for this. The greatest rewards per unit effort are obtained by taking the largest handleable prey items (MacArthur & Pianka 1966, Werner & Hall 1974, Krebs 1978, Krebs & McCleory 1984), assuming all members of the prey community are of a similar nutritional quality (Goss-Custard 1977). If these are dense then small, less profitable items are ignored. When the density decreases, as a result of depletion by fish (a situation exacerbated by refugia), so their profitability declines to below the optimum and the fish must switch to include more of the smaller, less profitable items in the diet (Elner 1987). It would appear that since small meiofauna were only significantly removed by 'starved' fish that drive may be important in determining this optimum. These results may, however, be an artifact of the experimental design, because the fish were not given the opportunity to move onto more profitable patches when the rewards dropped to below the optimum. i.e. the fish were forced to forage suboptimally. The inclusion of small items in the diet of predators has previously been discussed by Krebs (1978) and Hughes (1979).

Predator choice is not only determined by prey size, but also by prey motion (Pastorak 1980, Zaret 1980, Main 1985, Russo 1987) and pigmentation (Clements & Livingston 1984). Russo (1987) demonstrated that amphipod movement elicited strikes from the grey damselfish *Aburdtatus sordidus*, and certainly these and isopods were the most active in the experimental tanks.

Coull & Wells (1983) have argued on the basis of laboratory experiments that phytal meiofaunal populations are regulated by predators. However, if the evidence presented here is extrapolated to the rocky intertidal environment these same conclusions do not apply.

The overall density of resident fish on rocky shores around the Cape peninsula is low (Bennett & Griffiths 1984). Meiofauna are most frequently recorded in the guts of juveniles and the number of these is even lower (Bennett pers. comm.). Resident fish remain in tidal pools at low tide and with the exception of skulking species forage over the intertidal during immersion (Gibson 1982), returning with fidelity to home pools on subsequent emersion (Gibson 1982, Beeckley 1985). The time available for feeding each day is limited and is reduced further by the fact that fish are visual predators and forage only during the day (Gibson 1982). Fish from the sublittoral also forage in the intertidal during the periods of immersion, but the extent and magnitude of this movement is largely unknown. Rock pools provide seasonal refuges to the juveniles of many offshore and coastal reef fish species, although these are not entirely dependent on them and numbers tend to be low (Bennett 1986).

The standing crop of algae, and consequently meiofauna (Gibbons & Griffiths 1986), can be very high, so that the foraging area for individual fish is large and there is considerable opportunity to switch from one patch to another once conditions become suboptimal. Considering the above, and assuming that fish select their prey on the basis of size and motion (many epiphytal animals swim actively in the water column at high tide (Beckley 1980, Gunnill 1983)), it is concluded that the permanent meiofauna of intertidal algae are not influenced by direct predation from fish. Consequently, the complexity of algal structure and the provision of refugia is only likely to be of significance in tidal pool situations (as Dethier 1980), where fish are confined at high densities (Bennett & Griffiths 1984) and are unable to switch patches.

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LITERATURE CITED


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