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**Spatial and temporal variation in the settlement
of *Semibalanus balanoides* (L.) larvae
in East Fife, Scotland**



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Thesis submitted for the degree of Doctor of Philosophy
University of St Andrews

September 2003



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Acknowledgements

Firstly, many thanks to my supervisor Christopher Todd for all his assistance, guidance and support throughout this project. I would also like to thank Bob Wilson for his legendary rope skills, which were invaluable to the fieldwork experiments. Additionally thanks to the staff in the workshop at St Andrews University for the production of the settlement panels. Many thanks to John Hammond, Alan Wells, Jorge Fernandes and Ralph Bickerdike for “humour” in the office! Thanks to the staff at the Coastguard Station at Fife Ness who literally looked out for my safety on the shore; to Colin Hunter at the S.M.R.U.; George Hood at the Central Climate Unit at the Met Office; Helena Reinardy; Ian Johnson and all staff at the Gatty Marine Laboratories. This project was funded by a NERC postgraduate studentship, Grant N^o GT04 / 99 / MS / 272.

An additional many thanks to my internal supervisor Dr. Neil Hazon, for all of his help and instruction.

Finally many, many thanks go to my family and friends, without whose support this would not have been possible.

Abstract

Settlement and supply of cyprid larvae of the intertidal barnacle species *Semibalanus balanoides* was found to respond to a hierarchy of spatial and temporal cues. Within and between site experimental studies were conducted at three geographically spread locations around Fife in Scotland; Kinkell Braes in St Andrews, Kingsbarns, and Fife Ness on the East Neuk of Fife, Scotland. On a large scale settlement was primarily found to be wind-driven, with cyprid settlers increasing with onshore winds and decreasing with offshore winds, due to the passive movement of larvae. Large-scale movement of larvae was seen along the shore between sites, corresponding to prevailing wind direction, and increasing larval dispersal. On a meso-scale settlement was again wind-driven, with the degree of direct wave exposure influencing localised settlement patterns in sites only metres apart along the shore. On a micro-scale settlement, larval supply and capture were influenced by the presence of localised eddies around topographical features. However when compared over sites, larval traps performed consistently within a range of weather conditions; no reduction in efficiency occurred with a decrease in fixative retention to 63%. Cyprid supply and settlement was found to be correlated within and between sites with 73%, 70% and 35% of variation in settlement on grooved panels caused by variation in larval supply at St Andrews, Kingsbarns and Fife Ness respectively. The low, but not significantly different supply / settlement relationship at Fife Ness was caused by local hydrodynamic effects and was also seen in the adult distribution on the shore. Cleared quadrats on the rock surfaces were highly correlated to larval supply at each site with 72%, 34% and 56% of settlement variation caused by fluctuations in larval supply at St Andrews, Kingsbarns and Fife Ness respectively. This low correlation at Kingsbarns was due to unavoidable loss of data. Larval capture of the sublittoral barnacle *Balanus crenatus* occurred during the offshore transport of surface waters, which was thought to be correlated to an upwelling of lower waters and was negatively correlated to supply of *S. balanoides* cyprids.

Larvae settling upon upper (increased desiccation pressure) and lower intertidal sites (increased predation pressure) were found to have reduced larval fitness, as shown by a lack of rugotrophic and conspecific-mediated responses. Generally the presence of the conspecific extract increased larval densities, and was sufficient to promote settlement responses on otherwise unfavourable surfaces. An assessment of different settlement panels was made, and those with 48cm² of groove induced the greatest settlement, and also performed similarly across sites in a range of weather conditions. Lack of available settlement space caused larva-larva interactions and spacing out of cyprids on panels at high densities. Cyprid settlement responses within grooves were preferentially on the upper grooves within the panels, indicating an upward exploratory movement. On grooved panels with low to medium densities of settlers, the cyprids were located on the upper grooves whereas in higher settlement densities larvae spaced out approximately one body length apart. Additionally settlement was greater on upper grooves in the lower half of the panels indicating that larvae were concentrated within the water column and settled with rising tides over the panels. Comparison of the relationship of settlement on artificial grooved panels and cleared quadrats (per cm²) found that the natural rock surface was much preferred; cyprid settlement was 5%, 11% and 3% of that occurring on rock quadrats at the each site of St Andrews, Kingsbarns and Fife Ness respectively.

CHAPTER 1

INTRODUCTION



1. Introduction

1. 1. *Background*

1. 1. 1. *Larval dispersal mechanisms*

Sessile and mobile marine invertebrates recognise suitable substrata for settlement through the collection of information from their environment, which they derive from cues. The majority of marine invertebrates have planktotrophic larvae, which can remain in the water column for extended periods of time, such as barnacles, echinoderms, mussels, bivalves and certain encrusting bryozoans, e. g. *Electra pilosa*. These organisms have a free-swimming period of up to several weeks. Lecithotrophic species, e.g. ascidians, brood their larvae and these tend to metamorphose within minutes or hours after release from the adult. Therefore, dispersal potential varies widely among epibenthic species (Scheltema & Carlton, 1984, Keough & Chenoff, 1987, Strathmann, 1990, Harii *et al.*, 2002). This ‘decision’ of reproductive strategy has great effects upon the colonising ability of a species (Sutherland & Karlson, 1977, Seed & Hughes, 1992). Whilst in the water column, be it hours or weeks, the location of suitable settlement sites is highly important to their subsequent survival and therefore any information gleaned on the presence of food, future mates, potential predation pressure and any routine physical disturbances would be of great importance to the organism. Those larvae capable of identifying these elements would have an adaptive advantage. Although species with long range dispersal have the ability to settle in more distant geographic locations, this may result in poorer correlation between stimuli guiding choice and favourability of habitat thereby causing lower fitness at many sites within a species’ range (Strathmann *et al.*, 1981).

For sessile species with dispersing propagules the decision to settle, and the subsequent settlement pattern, is critical for survival because relocation following settlement is impossible. It is therefore important that the larvae should settle between the upper and lower limits, such as thermal and desiccation tolerances, at which the species is able to survive and be able to reproduce (Raimondi, 1988). The population size is regulated by the reproductive output of the adults and mortalities during each life history stage, which restrict the number of individuals reaching reproductive maturity (Minchinton & Scheibling, 1991). The distribution of the population will be determined by the density and spread of reproductive adults, the timing and magnitude of the reproductive output and the dispersal ability of the larvae (Roughgarden *et al.*, 1988, Gaines & Bertness, 1993). In open environments, such as those found in aquatic systems, the propagules may be dispersed within and between local populations, thereby ensuring flow in the gene pool and colonisation of new sites (Roughgarden *et al.*, 1988, Underwood & Fairweather, 1989). However, the long-distance dispersal of coastal species may be largely underestimated by neglecting to sample larvae adequately (Lefevre & Bourget, 1991).

Generally it is believed that these larvae can be considered as passive particles entrained by hydrodynamic factors (Grosberg, 1982), which are relatively unable to influence their distribution and shore abundance at a large spatial scale. However, these mechanisms of physical transport, e.g. wind and internal waves, may be good predictors for the spatial patterns of larvae and settlers seen upon the shore (Pineda, 1991, Bertness *et al.*, 1996). Additionally, ocean climatic phenomena such as El Niño may dramatically affect larval abundance and location (Connolly & Roughgarden, 1999, Bradbury & Snelgrove, 2001, Zeidberg & Hammer, 2002).

1. 1. 2. *Larval cues*

At a smaller spatial scale marine invertebrates are able to respond to a wide variety of cues from their environment including physical characteristics such as surface wettability, texture and colour (Gerhart *et al.*, 1992, Walters, 1992, James & Underwood, 1994, O'Connor & Richardson, 1994), light (Ryland, 1960, 1962, 1977, Svane & Dolmer, 1995), flow regime (Bushek, 1988, Dolmer & Svane, 1993, McKinney & McKinney, 1994) and orientation of substratum (Harris & Irons, 1982, Vandermeulen & DeWreede, 1982). Additionally biological cues also are important on a smaller scale. The presence of relevant food source (Hadfield, 1977, 1978b, Hadfield & Pennington, 1990, Lambert & Todd, 1994), conspecifics (Crisp & Meadows, 1963, Pearce & Scheibling, 1991, Toonen & Pawlik, 1995), primary algal host species (Ryland, 1962b, Kitamura *et al.*, 1993), predators (Johnson & Strathmann, 1989, Young, 1989, Hurlburt, 1993), dominant competitors (Young & Chia, 1987) and microbial surface films (Crisp & Ryland, 1960, Wiczorek & Todd, 1998b) have all been reported as critical.

The actual detection of the cues by larvae is less well known because for some invertebrates the morphological structures, physiological/biochemical processes and limits of detection have limited information as yet available (Linder, 1984, Clare & Nott, 1994). However there is evidence that the larval response to microbial cues is very sensitive where small-scale differences in composition, physiological condition and growth phase of the biofilm community may have a marked effect on settlement (Neumann, 1979, Anderson, 1995). There is also evidence that the presence of recruits from competing species can have an inhibitory effect on other species (Todd & Keough, 1994, Keough & Raimondi, 1995).

Settlement cues can either be adsorbed (Crisp & Meadows, 1962), like a surface cue, or water-borne (Lambert & Todd, 1994, Walters *et al.*, 1996) and cue molecules have variously been found to be peptides (Tamburri *et al.*, 1992, Zimmer-Faust & Tamburri, 1994), free fatty acids (Pawlik & Faulkner, 1986, Kitamura *et al.*, 1993) or to employ lectin-mediated induction (Maki & Mitchell, 1985).

Sessile and mobile marine invertebrates can be induced to settle (behavioural response) and metamorphose (morphological response) using chemical triggers such as potassium chloride and conspecific cues (Burke, 1983), which is useful for generating laboratory experiments. As mentioned before the mechanisms and signal transduction of cue reception and interpretation are largely unknown, although electrical impulses, neurotransmitters or hormones have a suggested involvement (Pawlik, 1992a).

1. 1. 2. 1. *Biofilms*

Biofilm components are also important cues in the settlement of a wide range of marine invertebrates (reviewed by (Wieczorek & Todd, 1998a)), as a complex fouling layer of bacteria, fungi, microalgae, protozoans, organic debris and inorganic particles is produced in such circumstances. These components are found to alter with habitat, such as substratum type and surface characteristics and can even be different in adjacent habitats (Fletcher & Marshall, 1982). Additionally some biofilms are actually inhibitory; Crisp & Ryland (1960) observed that filming and surface texture may or may not facilitate settlement, depending on the organism studied.

Seasonal changes in density, composition and physiological activity of epibenthic organisms may also be responsible for changing the settlement patterns of species that reproduce throughout long periods, as the presence of competitor species may be greater in some seasons than others (Underwood & Denley, 1984, Anderson, 1995).

1. 1. 3. *Delayed metamorphosis*

Larvae of many marine invertebrates become competent to metamorphose in response to specific chemical cues, so it is highly important that sessile marine invertebrates find a suitable site for permanent settlement to ensure survival. However the first surface the larvae contact may not be suitable, e.g. lacking specific chemical cues, and therefore some species have the ability to delay their metamorphosis until a suitable substratum is encountered (Pechenik, 1990, Walker, 1995). This rejection of sub-optimal sites has positive advantages, as the larvae would theoretically be able to encounter and examine more substrata, therefore having an increased chance of finding a suitable habitat (Meadows & Campbell, 1972). Moreover should larvae be swept offshore by strong winds, then there is a greater time period for the larvae to return to onshore settlement sites. Indeed, larvae of some species have been seen to postpone metamorphosis if they sense the presence of a dominant competitor (Young & Chia, 1981). However, the longer the larvae remain in the water column the greater the possibility of planktonic mortality and offshore current movement, therefore settlement may still occur in suboptimal habitats. Additionally barnacles have been observed settling in 'clean' sites without the presence of adults (Minchinton & Scheibling, 1991), suggesting that acceptance of suboptimal sites does occur.

This period of delay occurs in several phyla, and can vary with species from hours to days, and even weeks to months (Pechenik, 1990), but is not necessarily an adaptive advantage passed onto further generations (Hadfield, 1984). Furthermore, prolonging the larval period entails the depletion of energy reserves, therefore feeding planktotrophic larvae would seem to have the advantage over lecithotrophic larvae in these cases; this can lead to unsuccessful metamorphosis through all stages to adulthood, reduced growth rates and overall poor juvenile fitness (Wollacott *et al.*, 1989, Miller, 1993, Pechenik *et al.*, 1993). Studies indicate that the energy content of larvae at metamorphosis is of critical importance for the initial growth and discriminatory behaviour of juvenile barnacles (Thiyagarajan *et al.*, 2002b, Thiyagarajan *et al.*, 2003b).

Additionally this tendency for delaying metamorphosis may result in larvae becoming “desperate”, i.e. losing specificity for a conspecific cue, as the season progresses and larger numbers of larvae are delaying metamorphosis (Jarrett, 1997). Delaying metamorphosis may ultimately influence the larval recruitment success and adult fitness in the field by reducing the selectivity of the settling larvae (Olivier *et al.*, 2000). Larval morphological characteristics associated with delaying metamorphosis in the laboratory have been used to infer delayed metamorphosis in the field, although this approach only has potential for species exhibiting morphological characteristics associated exclusively with delaying metamorphosis (Pechenik, 1986). Studies of competent larval occurrence in water column samples determined that *Ptychodera flava* was able to delay metamorphosis for at least four months, with the larvae attaining competency in the three month period prior (Hadfield, 1978a).

Models of larval dispersal rarely incorporate larval behaviour, yet many potential settlers of marine invertebrates may navigate toward suitable settlement sites by responding to gradients of environmental stimuli. These larvae use a hierarchy of sensory cues to find suitable settlement sites (review Bourget, 1988). Barnacles are good model organisms for the study of open populations with space-limited recruitment, as they occur in many locations and are relatively easy to study (Hyder *et al.*, 2001). The barnacle larval response to a variety of cues has been much researched, from the classic work of Crisp and colleagues to current authors (Crisp, 1961, Larman & Gabbott, 1975, Moyse & Hui, 1981, Scheltema & Williams, 1982, Crisp & Bourget, 1985, Foster, 1987, Gabbott & Larman, 1987, Hui & Moyse, 1987, Bourget, 1988, Crisp, 1990, Rittschof *et al.*, 1992, Satchell & Farrell, 1993, Lambert & Todd, 1994, Wiczorek & Todd, 1998a, Qiu & Qian, 1999, Hentschel & Emlet, 2000, Anil *et al.*, 2001). For such benthic organisms with planktonic larvae recruitment has three components; water column larval supply, larval settlement patterns and survivorship to census (Bertness *et al.*, 1992). Barnacles are particularly good for such research as their larval stages are easily identified, collected and quantified (Wethey, 1984). Due to their wide dispersal, abundance, and seasonality *balanid* species such as *Semibalanus balanoides*, have often been used as target organisms for ecological studies of biological, physical and chemical relationships.

1. 2. *Semibalanus balanoides*

1. 2. 1. *Distribution*

Semibalanus balanoides (Linnaeus 1767) is a gregarious boreo-artic acorn barnacle species found on rocks and artificial substrata in the eulittoral zones of sheltered and exposed rocky shores (Phylum Arthropoda; Sub-phylum Crustacea; Class Cirripedia; Order Thoracica; Sub-order Balanomorpha; Family Balanidae; Sub-family Balaninae; Genus *Semibalanus*). It has been recorded in the north-east Atlantic from Spitzbergen to the north-west of Spain, on the Pacific coast of North America as far as British Columbia and on the Atlantic coast as far south as Cape Hatteras, but is absent from the Biscay coast of France. It is the dominant barnacle species in the eastern and northern regions of the British Isles, but can be rare or absent in the southern and western regions (Fig. 1); this species is also referred to as *Balanus balanoides* since 1950 (White, 2001).



Fig. 1 - Recorded distribution map of *Semibalanus balanoides* in Britain and Ireland. (White, 2001)

1. 2. 2 Species description

The adult of this species is easily distinguished by its membranous shell base, six calcareous grey-white shell plates, a distinctive diamond-shaped opercular aperture and only two radii caused by the fusion of rostrum and adjacent rostro-lateral plates. In comparison both *Elminius* and *Chthamalus* have a membranous shell base like *S. balanoides*, but can be distinguished as *Elminius* has four shell plates, and the rostrum of *Chthamalus* is a true rostrum with alae only (White, 2001). Additionally the shell shape may vary from the normal low truncate cone (on exposed shores), through steeper cones (on sheltered sites) to roughly cylindrical, and finally columnar club-shaped forms (in dense settlements), where the individuals are in close contact and can only grow upwards (Barnes & Powell, 1950).

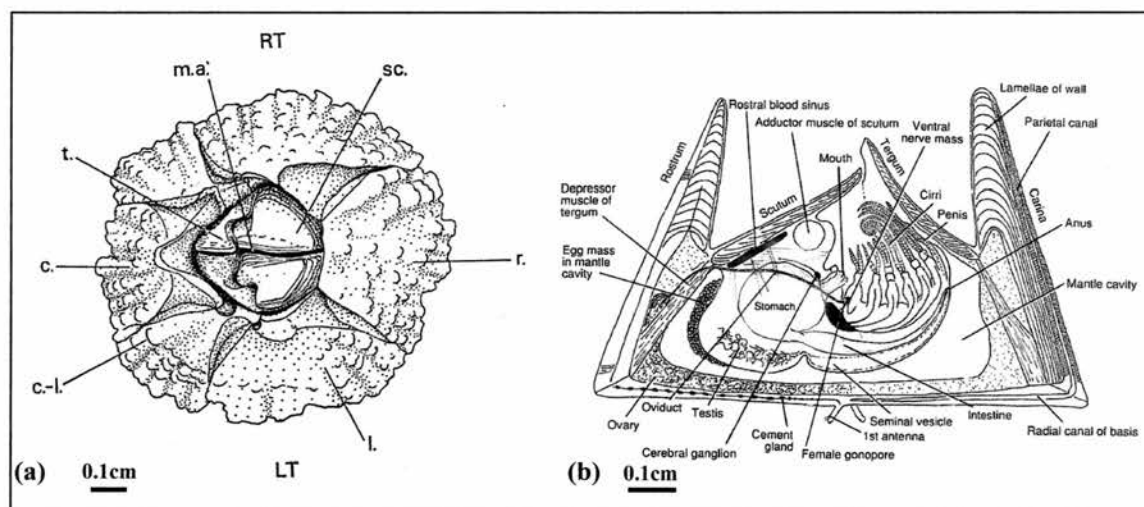


Fig. 2 – (a) External view of *Semibalanus balanoides* from above, taken from Stubbings, 1975 (c.: carina; c.-l: carino-lateral compartment; l.: lateral compartment; LT: left side; m.a.: mantle aperture; r.:rostrum; RT: right side; sc.: scutum; t.: tergum). (b) Vertical section through adult *Semibalanus balanoides*, taken from Ruppert and Barnes, 1994.

The adult may grow to 15mm in diameter, and can either actively or passively filter zooplankton, phytoplankton and detritus from the passing water using thoracic appendages called cirri, depending on current conditions (Rainbow, 1984). When a current is present the cirri are fully extended in the current flow (Crisp & Southward, 1961), but in the absence of water movement the barnacle rhythmically beats the cirri.

Feeding rate is important in determining the rate of barnacle growth; those lower down the shore are immersed for greater periods, therefore are able to feed for longer and subsequently have faster growth rates than those on the upper shore (Barnes & Powell, 1953). Growth rate also varies with current flow, orientation in current, food supply, wave exposure, surface contour and intra- or inter-specific competition (Crisp & Bourget, 1985).

1. 2. 3. *Reproduction*

Semibalanus balanoides is an obligate cross-fertilising hermaphrodite and may survive for some five or six years, depending on its position on the shore (Stubbings, 1975). In the U.K., copulation occurs from November to early December, with insemination by more than one male necessary to successfully fertilise all the eggs, ca. 400-10,000 in number (White, 2001). Fertilised embryos are incubated over the winter in two egg sacs within the mantle cavity, and nauplii larvae are released between February and April, in synchronisation with the spring algal bloom (Barnes, 1957). This timed release is enabled by the release of a hatching substance, which is secreted by adult barnacles following ingestion of phytoplankton (Crisp, 1956, Barnes, 1957, Gerhart *et al.*, 1990, Clare, 1995 review). Discharge of larvae in response to the spring bloom aids optimal growth for the planktonic nauplii, as food supplies are plentiful and sufficient time is available to develop and to ensure maximisation of growth in the summer months. During the next two months the nauplii mature in surface waters, passing through six moult stages before becoming the settlement stage, the cyprid larvae (Fig. 3). The first naupilus stage is non-feeding, depending on lipid and glycoprotein reserves until stage II, when it will commence feeding on phytoplankton such as diatoms until the cypris stage. Each moult increases

in size from ca. 350 μm at stage I to ca. 1150 μm at stage VI (Crisp, 1962). Temperature stress experiments have shown that all larval stages (naupilus and cyprid) are tolerant of temperatures up to 37-40°C, with stage VI displaying the maximum tolerance (Thiyagarajan *et al.*, 2000), thus exhibiting their resilience to harsh conditions.

In contrast to the naupilus larvae, the cyprid is lecithotrophic and therefore has a finite amount of energy with which to undertake swimming, temporal attachment whilst exploring surfaces, permanent fixation and metamorphosis (Lucas *et al.*, 1979). However cyprids do have a lower metabolic rate than the nauplii; the cyprid has an oxygen consumption rate of 0.6ml $\text{O}_2\text{h}^{-1}\text{g}^{-1}$ dry wt. at 10°C, whereas the previous naupilus stage consumes 1.9ml $\text{O}_2\text{h}^{-1}\text{g}^{-1}$ dry wt. (Lucas *et al.*, 1979). Therefore the cyprid can remain viable for settlement and metamorphosis for several weeks in the plankton (Lucas *et al.*, 1979).

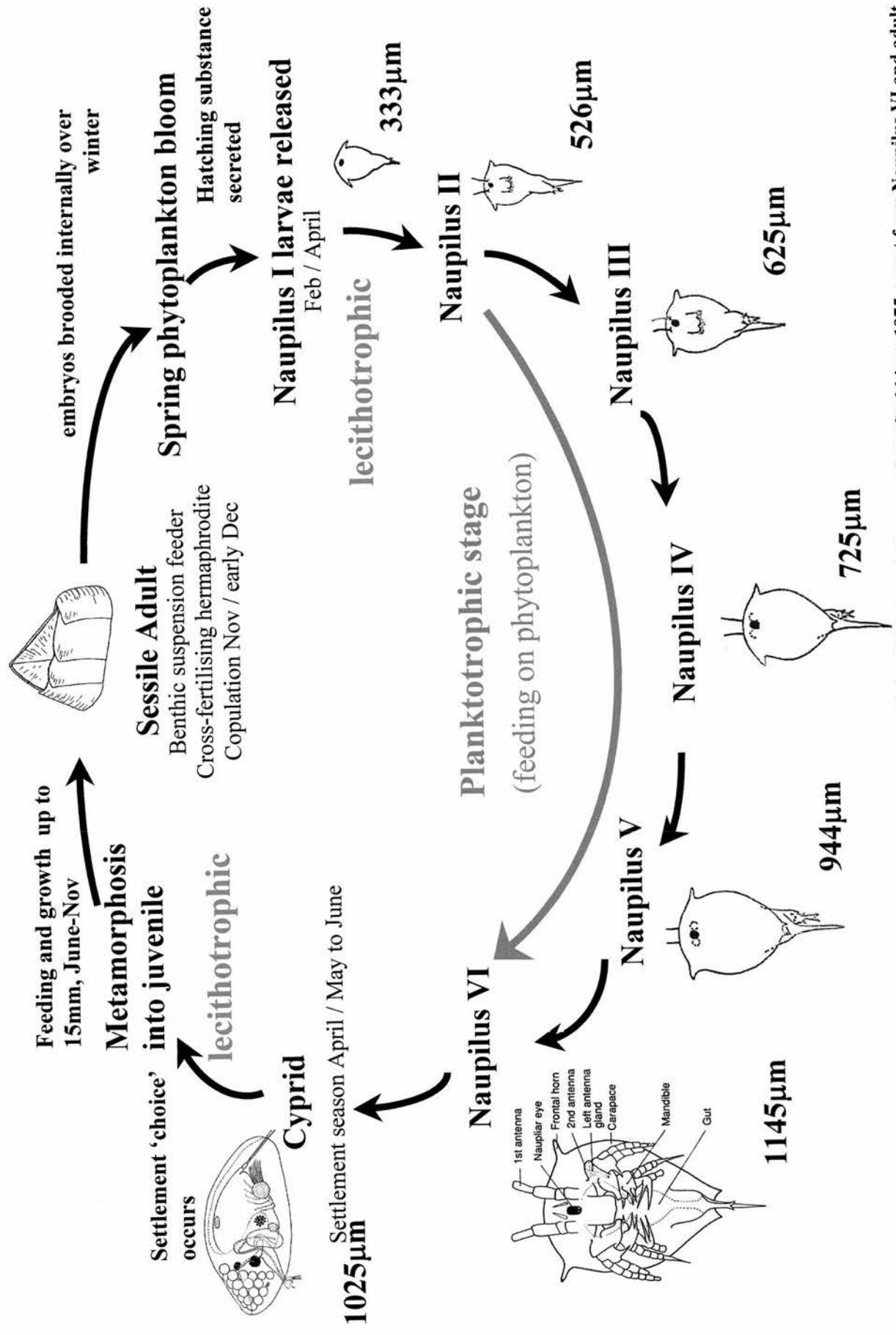


Fig. 3 – Life cycle of *Semibalanus balanoides*. Mean larval sizes taken from Crisp 1962, larval diagrams from Stubbings 1975, apart from Naupilius VI and adult, which were taken from Ruppert and Barnes 1994.

1. 2. 4. *Barnacle cyprid larvae*

It is at this cyprid stage that the larva acquires the competency to settle. The cyprid has a bivalved carapace, anterior antennules and posterior thoracic swimming appendages when extended out ventrally from the carapace (Walker *et al.*, 1987). As the cyprid is essentially pelagic, swimming and passive sinking in response to stimuli will position the cyprid at a level in the water column that will aid maximum survival, dispersal and chance of contacting surfaces (Walker, 1995). They can actively swim up to 95 body lengths. sec^{-1} (Yule, 1982), but require strong stimulation to maintain swimming; still water in the laboratory is found not to be conducive to movement (Crisp, 1955). The hydrodynamic body shape and the combined force of six pairs of thoracic appendages, in bursts of 10-40 limb beats, provide controlled lift with forward progression (Yule, 1982). Following a limb beat, the recovery stroke speed is one-third of that of the propulsive stroke, giving a jerky movement that is relatively inefficient compared to the gliding motion of copepods (Yule, 1982). When swimming ceases, and the cyprid is inactive, its negative buoyancy dictates it passively sinks at a rate of $\sim 26\text{cm}\cdot\text{min}^{-1}$; this rate is reduced significantly if thoracic appendages remain extended from the carapace, resulting in a spiral sinking path and rate of $\sim 19\text{cm}\cdot\text{min}^{-1}$ (Yule, 1982). Cyprids may be able to actively swim and prevent themselves being swept upshore in low wave action and low swell conditions (Young & Chia, 1987), but are unable to maintain their position in turbulent environments and are subject to hydrodynamic processes.

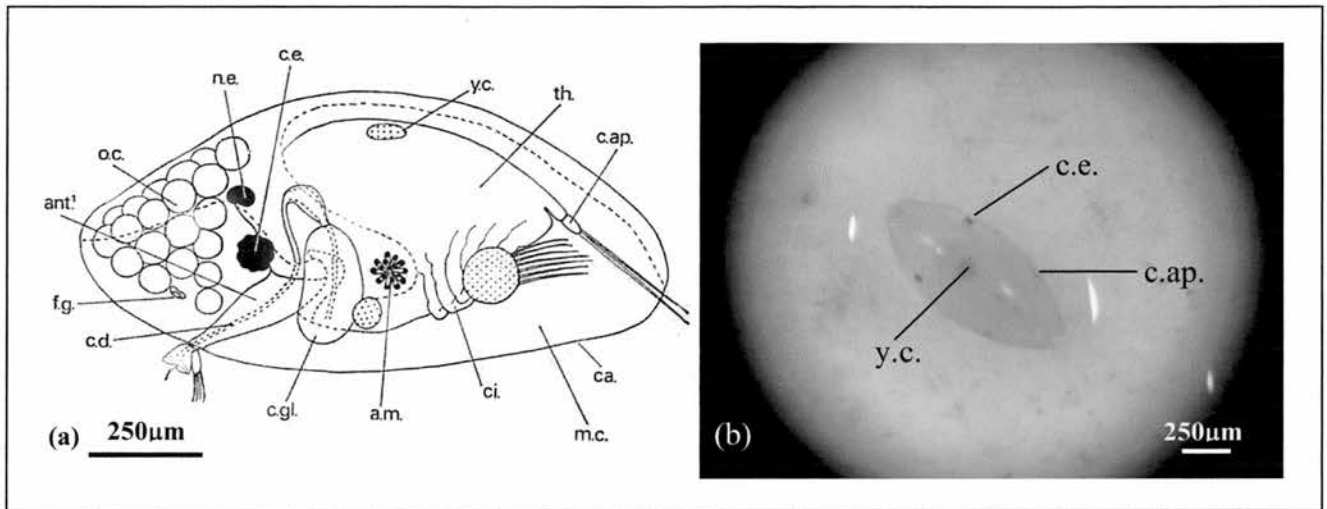


Fig. 4 – (a) Main features of a *Semibalanus balanoides* cypris larvae, visible in the living organism, from Stubbings, 1975. (b) Live *Semibalanus balanoides* cypris larvae, dorsal view © Jesús Pineda and Woods Hole Oceanographic Institute, subsequently annotated. (a.m.:adductor muscle of cypris shell; ant.: antennule; ca.: carapace; c.ap.: caudal appendage; c.e.: compound eye; c.gl.: cement gland; ci.: thoracic appendages; f.g.: opening of frontal gland; m.c.: mantle cavity; n.e.: naupilus eye; o.c.: oil cells; th.: thorax; y.c.: yolk cells)

Cyprids have obvious sense organs; eyes (naupilar eye and 2 compound eyes), frontal filaments (Walker, 1974), carapace setae (Walker & Lee, 1976), lattice organs (Jensen *et al.*, 1994) and antennular setae (Nott, 1969). The frontal filaments are thought to be involved in pressure perception (Walker, 1974), but the functions of the lattice organs and antennular setae remain speculative (Walker, 1995). They will use these organs to respond to a variety of stimuli such as gravity, light, pressure (depth), which can be used to maintain their position in the water column. However on contacting a surface, this must be assessed for its suitability for permanent fixation. When a competent cyprid encounters a surface it uses sensory organs called antennules to explore the surface (Fig. 5), maintaining substratum contact using a temporary adhesive secreted from numerous unicellular antennular glands (Walker, 1973, Walker & Yule, 1984, Yule & Walker, 1987). If the larvae are not suitably stimulated then they can detach and become pelagic again, but if they find the surface suitable then permanent fixation follows.

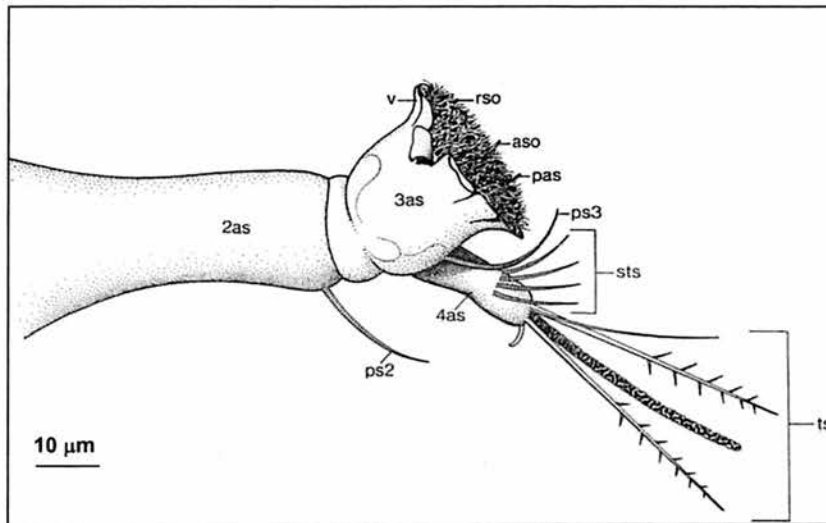


Fig. 5 – Schematic drawing of *Semibalanus balanoides* antennule, showing the principle features of the third and fourth segments. Taken from Moyse 1995 Fig. 1, redrawn from Nott and Foster 1969.

2as: second antennular segment; 3as: third antennular segment; 4as: fourth antennular segment; aso: axial sense organ; pas: postaxial sense organ; ps2: postaxial setae II; ps3: postaxial setae III; rso: radial sense organ; sts: subterminal setae of fourth segment; ts: terminal setae in fourth segment; v: velum.

The appearance of the attachment disc of the third antennular segment with its encircling skirt of cuticle, called the velum, gives the impression of a sucker and indeed in the past it has been referred to as an ‘antennulary sucker’ (Crisp, 1955). However suction has been disproved because the force required to remove the temporary attached cyprids from a slate surface is equivalent to 2-3 atmospheres, therefore precluding suction (Yule & Crisp, 1983). The attachment disc is covered in villi, which provide a large surface area for the optimum action of adhesive secretions in temporary attachment; studies indicate intertidal species have a greater villi density and therefore adhesive force to enable metamorphosis in higher wave action conditions than would be found sublittorally (Nott, 1969, Moyse, 1995). The differing strength of adhesion to surfaces with different physio-chemical properties is such that cyprids can assess the nature of surfaces, such as their roughness and critical surface tension (Yule & Walker, 1987). Increased temporary adhesion indicates a desire to settle in *Semibalanus balanoides* cyprids (Neal & Yule, 1992).

Temporary adhesion allows the exploration of surfaces as the antennular discs are alternately attached, detached and reattached in what is described as the cyprid ‘walk’ (Walker & Yule, 1984). In fact ‘footprints’ can be seen on the explored surfaces, because some of the proteinaceous adhesive covering the attachment disc is left behind at each ‘step’ (see Fig. 6).

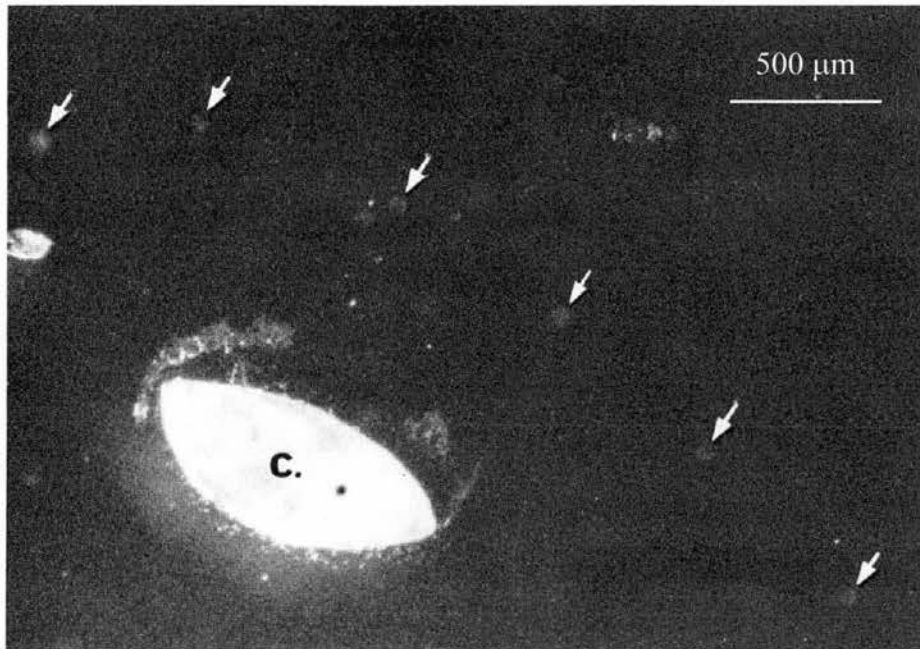


Fig. 6 – Micrograph showing a cyprid (c.) and the arrowed ‘footprints’ of such a larva making up a single track. Each ‘footprint’ is visualised as a droplet of water left behind on the surface of 3-HEPT glass (Fig. 1a from Walker and Yule, 1984).

Exploration takes place on three spatial scales. ‘Wide searching’ of areas <1m where antennular walking takes place with few changes in direction; if favourable stimuli are detected then the larval behaviour changes. This next stage involves ‘close searching’ of <5mm areas, where the cyprid pauses longer at each step, apparently testing the surface, and direction change frequently occurs. With continued positive stimulation then the behaviour pattern moves on to the third stage, ‘inspection’, in areas of <1mm where the cyprid steps to and fro in a confined area (Crisp, 1976, Crisp, 1984). Factors such as water flow, surface texture and topography, light intensity, biofilms and various stimulatory and

inhibitory chemical cues will influence whether this adhesion becomes permanent (Crisp, 1976, Bourget, 1988, Pawlik, 1992b).

At the end of this inspection stage the cyprid will orientate itself to surface contours, light and water flow and the final, and irreversible, attachment takes place (Crisp, 1976). Cyprid cement is released as a fluid from a pair of multicellular cement glands to embed the antennular attachment organs (Walker, 1973, Yule & Walker, 1987, Naldrett, 1992). This takes 1-3 hours to effectively bond to the surface and probably involves the polymerisation of the cement proteins. The chitinous bivalved shell is cast off and the body mass bends over to adopt a roughly horizontal position; this initially spherical metamorphosing animal becomes depressed and calcification occurs in the peripheral area to form a shell (Crisp & Stubbings, 1957, Stubbings, 1975). Once metamorphosis has proceeded to the juvenile form, then the individual can be considered recruited to that surface (Keough & Downes, 1982).

1. 2. 5. *Gregarious behaviour*

Many marine invertebrates with planktonic larval stages and sessile adults exhibit gregariousness when larval settlement occurs. In other words, the larvae settle and metamorphose in response to chemical or other cues produced by a member of their own species, otherwise called a conspecific cue (Knight-Jones & Stevenson, 1950, Knight-Jones, 1953, Crisp & Meadows, 1962, Crisp & Meadows, 1963, Meadows & Campbell, 1972, Larman & Gabbott, 1975, Crisp, 1976, Harvey *et al.*, 1976, Burke, 1986, Woodin, 1986, Dineen & Hines, 1992, Pawlik, 1992b, Dineen & Hines, 1994a, b). This gregarious behaviour is caused by the larvae recognising the presence of a conspecific cue, which conveys information that the site has favourable conditions for settlement, and hence

increased chances of survival. As barnacles are hermaphroditic sessile animals that require cross-fertilisation, settlement in close proximity to conspecifics is necessary for reproduction to occur (Meadows & Campbell, 1972).

1. 2. 5. 1. *Conspecific cue*

Gregarious settlement was first described in *Elminius modestus* (Knight-Jones & Stevenson, 1950) and laboratory experiments determined that the settlement pattern was due to cyprids recognising a protein in the cuticle of the adult shell (Knight-Jones, 1953). This led to further work on the involvement of soluble proteins from arthropod cuticles, called arthropodins (Crisp & Meadows, 1963), in the settlement of barnacle larvae (Crisp & Meadows, 1962, Crisp & Meadows, 1963). This 'settlement pheromone' was identified in *Semibalanus balanoides* and has an amino acid composition similar to actin (Gabbott & Larman, 1987). This protein pheromone cue is an active stimulant when adsorbed onto a surface, in the form of an aqueous protein extract taken from the adult barnacles (Crisp & Meadows, 1962, Crisp & Meadows, 1963, Ritschoff *et al.*, 1984, Gabbott & Larman, 1987) and differing concentrations may be detected by the cyprids within a diffusion boundary layer over the treated panels (Dodds, 1990). This settlement cue is so potent that its presence is able to induce larval recruitment into areas well above the normal distribution limits of the adult (Raimondi, 1988).

Arthropodin is thought to be recognised through the antennular sense organs (Fig. 5), although the method of detection is contested. Originally it was thought that an enzyme released from the antennules allowed the sense organs to detect particular amino acid sequences (Knight-Jones, 1953, Nott & Foster, 1969), and more recent work using synthetic peptides with *Balanus amphitrite* supports this theory (Tegtmeyer & Rittschof,

1988, Zimmer-Faust & Tamburri, 1994). Another theory relates to the chemical behaviour of arthropodin, which is related to the 'sticky' protein actin (Larman *et al.*, 1982), and therefore the cyprid may increase adhesion through stickiness (Yule & Crisp, 1983). Although temporary adhesion is greatly increased when arthropodin is adsorbed on a surface (Yule & Crisp, 1983, Yule & Walker, 1984), not all adsorbed proteins cause an adhesion increase, e.g. bovine serum albumin (Crisp, 1990, Dineen & Hines, 1992, 1994a). Additionally such physiological sensitivity would be required to differentiate stickiness, and therefore current theory is that recognition of the settlement factor is chemical rather than physical. Cyclic AMP may be involved in the pheromonal modulation of barnacle settlement (Clare *et al.*, 1995), and is known to be involved in the signal transduction pathways of olfaction in mammals (Anholt, 1991), abalone (Morse, 1990) and lobsters (Michel & Ache, 1992). The fourth antennular segment bears sensory setae which resemble putative olfactory receptors in crustaceans (Hallberg *et al.*, 1992); during cyprid searching behaviour this fourth segment is flicked through the water column, which is observed in decapods and found to stimulate the olfactory receptors (Clare & Nott, 1994).

In barnacles this conspecific cue may be from the adults, new metamorphs, older juveniles, other cyprids (squashed or alive) or even the footprints of other cyprids (Walker & Yule, 1984, Wethey, 1984, Chabot & Bourget, 1988, Raimondi, 1988, McGee & Targett, 1989, Raimondi, 1990, 1991, Clare *et al.*, 1994, Miron *et al.*, 1996, Jarrett, 1997, Hills *et al.*, 1998, Keough, 1998). The more attractive a surface is, the more footprints per unit area are acquired, which stimulates a gregarious response even in the absence of conspecific adults (Yule & Walker, 1984, 1985). Newly-settled *Chamaesipho tasmanica* individuals were not found to influence the later settlement of arriving cyprids, but as the

recruits aged their presence was associated with more abundant new settlers (Jeffery, 2002). The detected presence of conspecifics may 'fast-track' larvae through pre-settlement display behaviour and ensure rapid settlement (Hills *et al.*, 1998). However that is not to say that settlement does not occur without the presence of conspecifics, otherwise new sites would not be colonised (Mullineaux & Butman, 1991, Miron *et al.*, 1996).

1. 2. 6. *Biofilms and barnacle settlement*

Such conspecific chemical cues are highly important in influencing larval choice of substratum (Pawlik, 1992a, Zimmer-Faust & Tamburri, 1994) and have been much studied in many barnacle species (Crisp & Meadows, 1962, Larman *et al.*, 1982, Ritschoff *et al.*, 1984, Maki *et al.*, 1988, Dineen & Hines, 1994b, Hills *et al.*, 1998, Olivier *et al.*, 2000). Larval settlement is also affected by the presence, absence and composition of microbial surface films (Hudon *et al.*, 1983, Maki *et al.*, 1990, Neal & Yule, 1994, Wiczorek *et al.*, 1995, Wiczorek & Todd, 1998a, Jenkins *et al.*, 2000). Once a clean surface is placed in seawater, organic macromolecules and microbial organisms rapidly colonise the surface, developing a biofilm that changes the chemical, biological and physiological substratum properties and acting as a cue for many marine invertebrates (Keough, 1998). Through biofilm composition manipulation it has been found that some bacterial species stimulate barnacle settlement, whereas others inhibit the process (Maki *et al.*, 1988). However the isolation of particular bacterial species which are then grown as pure culture biofilms is unlikely to truly represent a natural biofilm, and therefore it is unlikely that the larvae will encounter such a situation.

After the initial biofilm has developed, other incumbents begin to colonise the surface and thus change the nature of the biofilm once again; these include fungi, microalgae,

protozoans, organic debris and inorganic particles. These components are found to alter with habitat, such as substratum type and surface characteristics (Fletcher & Marshall, 1982). This complex nature of biofilms means it is often hard to discover which element the larvae may be responding to, and the removal of one component may generate an artificial biofilm by altering the hierarchical relationship of organisms (Todd and Gurney-Smith, unpubl). Previous studies have shown a range of effects of biofilms on barnacle settlement; facilitatory (O'Connor & Richardson, 1996), inhibitory (Maki *et al.*, 1988, Maki *et al.*, 1992, Maki *et al.*, 1994) and even weak or no effect (O'Connor & Richardson, 1998). Additionally the nature of a biofilm may be changed depending on the underlying type of substratum (Maki *et al.*, 1992, Maki *et al.*, 2000), thereby changing its influence on larval settlement.

1. 3. Larval settlement

1. 3. 1. Substratum effects

The application or presence of adsorbed cues (arthropodin) and biofilms may modify the exchanges across a solid surface, such as altering its wettability and impeding oxidation (Taylor *et al.*, 1994). Most larvae prefer to settle on rough rather than smooth surfaces, and surface contour is also important in the location of cyprid settlement (Wethey, 1984). Studies on *Semibalanus balanoides* found that preferential settlement occurred in cracks and pits in the substratum (Crisp & Barnes, 1954), a behaviour known as rugotropism. A significant survival difference between 'concave' and 'convex' areas was seen in *Semibalanus balanoides*, therefore indicating that natural selection favours settlement in depressions (Connell, 1961, Wethey, 1984, Walters & Wethey, 1996). Additionally it was found that the presence of such pits alone was sufficient to promote recruitment, again indicating a selective advantage; cyprids encountering pits without conspecifics settled

rapidly, whereas treated pits induced chemical-mediated behaviour with subsequent settlement (Hills *et al.*, 1998). Once settled, these cyprids may disrupt water flow in their vicinity in a manner similar to that created by a pit and may positively influence settlement of other cyprids nearby through the resulting velocity gradient (Crisp, 1955). Hard substratum areas for settlement in the sublittoral zone may be rare (Hui & Moyses, 1987), so other settlement may need to be adaptive (Fig. 7).

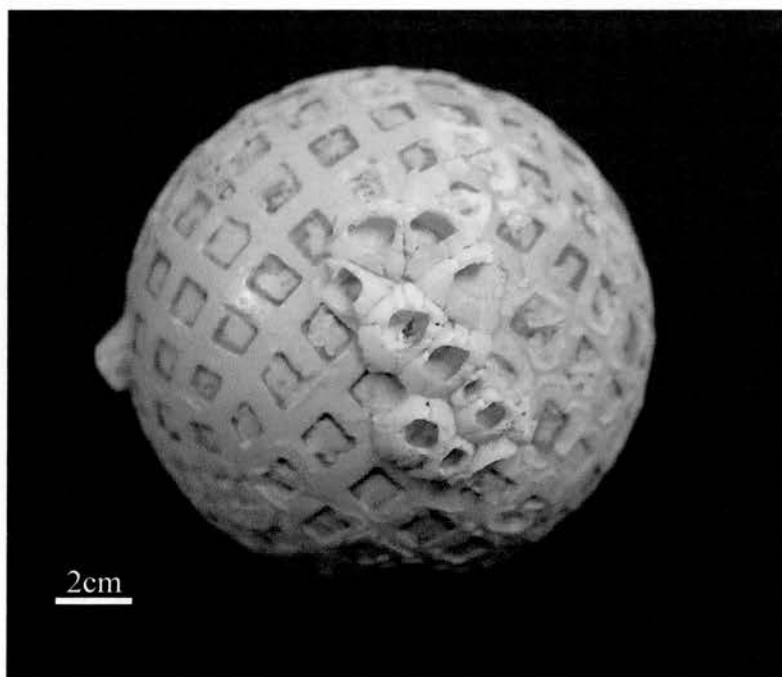


Fig. 7 – Golfball exhibiting adults of *Semibalanus balanoides*. Found by author on West Sands, St Andrews, Fife.

1.3.2. *Space availability*

This preferential settlement in cracks and pits, combined with the larval gregarious behaviour, leads to clumped juvenile/adult distributions (Knight-Jones, 1953, Crisp & Barnes, 1954, Crisp & Meadows, 1962, Crisp & Meadows, 1963, Larman & Gabbott, 1975). Furthermore the amount of substratum available for settlement will affect cyprid settlement behaviour; a reduction in unoccupied space will decrease the intensity of attachment, because intraspecific competition will cause avoidance of crowded sites (Bertness, 1989). The degree of exposure to adult conspecifics rather than the amount of

available space is thought to be most influential on the larval settlement pattern. Raimondi (1990) stated that in areas of equal size, but with differing shapes, more barnacles would settle in regions with longer perimeters of adult barnacles. In different sized patches the larvae would be expected to settle in greater densities in smaller patches (Bertness *et al.*, 1992, Pineda, 1994b, Pineda & Caswell, 1997) in response to conspecific adult cues on the area perimeters, as it is more likely that the larvae will encounter the settlement cue (Minchinton, 1997, Jeffery, 2000). Additionally hydrodynamic edge effects can cause larvae to settle around the edges of cleared patches (Raimondi, 1990). In studies of quadrats cleared of conspecific adults and uncleared controls, those cleared were colonised by more cyprids, with due to competition early post-settlement mortalities occurring on uncleared rather than cleared planks (Miron *et al.*, 1999).

Bertness *et al.* (1992) used cleared quadrats of 5 x 5cm (25cm²) to monitor larval settlement. However, as rock type is highly unlikely to be identical across the sites used in experiments, an artificial substrata is required to compare settlement in the different locales. Previously 8 x 13cm roughened black acrylic panels used in field experiments were found to be successful in recruiting settlers (Todd & Gurney-Smith, unpubl.), hence these panels were used as the basic design. Solutions of the settlement factor have not been found to promote settlement, therefore indicating that the cyprids must respond to a specific molecular configuration manifested by the protein only when physically or chemically bound to the surface (Crisp & Meadows, 1963). This recognition was termed to involve a 'truly contact chemical sense', and whilst water currents can force the passive larvae into contact with the substratum, cyprids will swim off readily from surfaces without extract (Crisp & Meadows, 1963). This is in contrast to extract-painted surfaces where cyprids rapidly cover the substratum (Crisp & Meadows, 1962) after displaying a

long and complicated pattern of behaviour (Knight-Jones & Crisp, 1953; Crisp, 1961). Additionally, experiments by Crisp & Meadows (1963) found that should larvae come into contact with a cue-treated surface, and then be introduced to a non-treated surface of the same material, no settlement occurred. Hence the stimulus to settle can be considered surface bound with little or no diffusion effects (Crisp & Meadows, 1963). Therefore would allow settlement panels to be placed in close proximity in the field, without the fear of lack of independence. Additionally this also would permit the deployment of greater numbers of replicates in environments of limited suitable rock substrata.

In such space-limited systems the settlement pattern may change from a random to uniform distribution, as individuals will enter the system and occupy space and affect subsequently arriving larvae (Connell, 1963, Wethey, 1984, Bertness *et al.*, 1992). Studies on the effect of newly settled *Chamaesipho tasmanica* individuals on later settlement found that only as the recruits aged was their presence associated with more abundant new settlers (Jeffery, 2002), as with *Elminius modestus* (Keough, 1998). Conversely in *S. balanoides* (Wethey, 1984, Kendall *et al.*, 1985, Minchinton & Scheibling, 1991) and *Chthamalus anisopoma* (Raimondi, 1990) new settlers were found to inhibit further settlement. *S. balanoides* cyprids settled closer to other larvae, but further away from metamorphs (Wethey, 1984) and settlement may then decline and be less suboptimal sites colonised as available space is reduced (Connell, 1961, Bertness *et al.*, 1992). Some studies report *S. balanoides* cyprids also show specific avoidance behaviour for shells of conspecifics (Hui & Moyse, 1987) although this behaviour is not universal (Miron *et al.*, 1996). Cyprids will space themselves out from each other at least one body length apart, and also from spat or adults, as such territoriality allows enough space for the post-metamorphic juveniles to grow during this vulnerable time in their life cycle (Hui &

Moyses, 1987). Studies have shown that density-dependent post-settlement mortalities do occur in *S. balanoides* cyprids, but the recruitment density reported differs – from only 1.3 individuals per cm² (Minchinton & Scheibling, 1991) to that exceeding ~25 individuals per cm² (Connell, 1985). Where density-dependent mortality does occur there is still a positive relationship between the number of individuals at successive life histories, except where density-independent mortalities occur due to intense predation (Minchinton & Scheibling, 1991), indicating that adult densities and the total settlement density are highly correlated.

1. 3. 3. Mortalities

Post-settlement mortalities are directly related to recruitment in the mid intertidal (Minchinton & Scheibling, 1991) with the first four months being the crucial stage in which most post-settlement mortalities occur, with low mortality in the period following (Gosselin & Qian, 1997). Dessication and predation are widespread and may be the most important causes of these early juvenile mortalities (Dungen, 1985, Hunt & Scheibling, 1997), with increasing tidal height corresponding to an increase in mortality (Bertness *et al.*, 1992, Miron *et al.*, 1999, Menge, 2000). Predation is an important factor in structuring intertidal communities (Connell, 1961) and *Semibalanus balanoides* predation by whelks and limpets was observed to change the pattern of settlement (Denley & Underwood, 1979, Hawkins, 1983, Minchinton & Scheibling, 1991, Hunt & Scheibling, 1997) although barnacles can avoid substrata previously occupied by *Nucella lamellosa* (Johnson & Strathmann, 1989). Predators such as whelks seek rock crevices for protection from wave exposure (Menge, 1978) and their own predation (Vadas *et al.*, 1994). Therefore when they leave the safety of the crevice for feeding, ‘haloes’ of bare space in the pattern of barnacle settlement are seen, and the probability of encountering a

barnacle increases with increasing distance from the crevice (Denley & Underwood, 1979, Johnson *et al.*, 1998). Some field experiments involve the removal of predators, to study species interactions or prevent mortalities, but this risks introducing artefacts through disturbance (Underwood, 1986, Wellenreuther & Connell, 2002).

1. 3. 4. Tidal height

Along with substratum type and space availability, *Semibalanus balanoides* cyprids are also able to distinguish differences in tidal height as shown by clear vertical stratification of recruitment (Bourget, 1988). Tidal height is considered to be a significant factor in determining these vertical patterns when larvae are abundant, i.e. at the beginning of the season, but not in periods of low larval abundance (Olivier *et al.*, 2000). On an exposed rocky shore, the vertical distribution of cyprids reflects the vertical distribution of settlers because greater numbers of cyprids and settlers occurred at low tidal levels (Minchinton & Scheibling, 1991). *Semibalanus balanoides* cyprids actively avoid the high shore in preference for the low shore, where there is an increased chance of post-settlement success as desiccation pressures will be less (Raimondi, 1988, Bertness *et al.*, 1992, Ross & Underwood, 1997). Desiccation relief through wave crash on the upper shore is highly unlikely, as studies show that wave splash only reduces exposure time by <2% (Lively & Raimondi, 1987). Settlement at lower tidal heights may confer greater growth rates, because longer periods of water cover will increase the amount of food passing the barnacles (Crisp, 1960, Bertness *et al.*, 1991). The artificial use of conspecific extracts can counter the barnacle avoidance of higher shores (Raimondi, 1988, Satumanatpan & Keough, 2001), but in nature consistently fewer larvae arrive and settle in higher levels and are therefore not present to act as inductive cues for future recruitment (Jeffery & Underwood, 2000, Jeffery, 2002).

Settlement in high zones may also be related to cyprid quality; triacylglycerol / cholesterol cyprid ratios decrease with increasing intertidal levels (Miron *et al.*, 1999) and the majority of high zone settlement occurs later in the season, indicating that older larvae are less discriminate (Bertness *et al.*, 1992; Minchinton & Scheibling, 1991). Older cyprids found attaching on otherwise less acceptable substrata may be accepting these surfaces to ensure survival, as energy reserves may be low (Crisp, 1988). However more recent studies have found that older *Balanus amphitrite* cyprids did not attach in higher numbers than younger cyprids (O'Connor & Richardson, 1994). Specificity for the adult cue was found to decline with age in the laboratory (Crisp & Meadows, 1963) and in the field (Olivier *et al.*, 2000), again suggesting changes in the selectivity of the settling larvae. Additionally a marked variation in cyprid carapace length occurs in a single species (Barnes, 1953), which reflects the quantity of energy stores (Walker, 1995).

1.3.5. Cyprid quality

As the cyprid is a lecithotrophic larvae with a finite amount of energy to carry out movement and metamorphosis, the attachment success of cyprids largely depends upon the amount of stored energy reserves (Lucas *et al.*, 1979, Satuito *et al.*, 1996, Thiyagarajan *et al.*, 2002b, 2003a). During naupliar development, triacylglycerols are accumulated from the algal food and stored in specialised lipid cells as endogenous energy reserves (Lucas *et al.*, 1979, Walker *et al.*, 1987) and the amount stored depends upon the algal food quantity and quality available to the nauplii (Qiu & Qian, 1997).

The ratio of triacylglycerols to cholesterol can be used as measure of physiological condition in planktonic, newly settled and newly metamorphosed spat (Miron *et al.*, 1999); in the laboratory metamorphic success and growth increases with increasing cyprid

organic content (Jarrett, 2003, Thiyagarajan *et al.*, 2003a). As the recruitment season progresses in the field, the organic content of *Semibalanus balanoides* cyprids declines (Miron *et al.*, 1999, Jarrett, 2003), and their discriminatory behaviour is therefore linked to such triacylglycerol ratios (Thiyagarajan *et al.*, 2002b). Thus the magnitude of attachment and metamorphosis is significantly influenced by cyprid energy reserves (Thiyagarajan *et al.*, 2002a). Additionally those cyprids with large energy reserves were found to be indifferent to the presence of cues and therefore may attach solitarily to form new colonies or gregariously in proximity to conspecifics (Thiyagarajan *et al.*, 2002b). Environmental effects can also influence the amount of stored energy; increased temperature leads to an increase in metabolic rates (Thiyagarajan *et al.*, 2003a). The larval quality can also vary among cohorts, and therefore propagule quality should be considered in relation to population and community structure studies (Jarrett & Pechenik, 1997, Jarrett, 2003).

1. 3. 6. Food availability and larval production

Factors operating over large scales, such as those controlling timing and intensity of phytoplankton blooms, are likely to determine the number of available larvae through their influence on larval food supply (Barnes, 1956). Research has found that there is a considerable variation in the onset, duration and density of settlement with year, with earlier commencing settlement seasons being correlated with earlier algal blooms (Hawkins & Hartnoll, 1982). Additionally the occurrence of 'failure' settlement years, where settlement is very poor due to low larval amounts, coincided with irregularities of the spring plankton bloom (Barnes, 1956, Hawkins & Hartnoll, 1982). Seawater temperature was also found to affect barnacle larvae development, as it increased the metabolic rate of the larvae, whereas at lower temperatures less energy is assimilated (Harms, 1984, Qiu & Qian, 1999, Anil *et al.*, 2001). Therefore this inter-annual variation

in the spring bloom regulates the size of the larval pool, determines the availability of cyprids at the shore and the subsequent recruitment observed (Minchinton & Scheibling, 1991, Jenkins *et al.*, 2000).

1.3.7. Larval supply and assessment

1.3.7.1. Larval supply

Numerous studies have found that the size of larval pool, otherwise known as larval supply, is positively correlated to settlement because it determines the number of larvae potentially able to settle (Connell, 1985, Gaines *et al.*, 1985, Minchinton & Scheibling, 1991, Bingham, 1992, Gaines & Bertness, 1992, Jeffery, 2000, Jeffery & Underwood, 2000). Indeed it has been considered the main factor structuring populations of intertidal and subtidal barnacles (Grosberg, 1982). However some reports show initially poor correlations of supply to settlement, but these were found to be a function of infrequent sampling (Gaines & Bertness, 1993) or short experimental periods (Olivier *et al.*, 2000), thereby highlighting the need carefully to document relationships between larval supply and settlement (Miron *et al.*, 1995).

Cyprids are often aggregated in the plankton (De Wolf, 1973, Gaines *et al.*, 1985, Roughgarden *et al.*, 1987, Roughgarden *et al.*, 1988) and hence larval supply may enhance gregarious settlement (Jeffery, 2000). Settlement spatial variation on a high intertidal zone was found to reflect the spatial distribution of cyprids in the water column, and larval density explained ~86% of the variation observed in weekly settlement rates (Gaines *et al.*, 1985). The cyprid uses environmental cues, such as light and pressure, to position itself within the water column to maximise survival, dispersal and contact with the adult habitat (Grosberg, 1982, Gaines *et al.*, 1985, Shanks, 1986, Lefevre & Bourget, 1991,

Walker, 1995, Ross, 2001, Frank & Widder, 2002). Additionally larval arrival at settlement sites may be correlated to the lunar cycle; larval supply increased at new and full moons, with few arriving during the intervening period (Jeffery & Underwood, 2000). Larval supply also increased with high tides occurring at night (Setran, 1992, Ross, 2001). This latter observation implies that the behaviour of the cyprids in the water column may itself determine the initial supply of cyprids (Ross, 2001), although this was observed in a low wave action environment.

A lack of cyprid stratification may be due to strong vertical mixing and high wave energy on exposed rocky shores and therefore local patchiness in plankton may result in inaccurate sampling results, as poor larval supply may not correspond to low settlement (Minchinton & Scheibling, 1991). Hydrodynamics may then be determining local settlement patterns as turbulent mixing by eddy diffusion can both disperse and aggregate larvae depending on conditions (De Wolf, 1973, Bertness *et al.*, 1996). Moreover, when cyprids are uniformly distributed in the water column next to a substratum, the observed variation in settler density among intertidal heights may be due to differing immersion times (Minchinton & Scheibling, 1991).

1.3.7.2. Larval quantification

1.3.7.2.1. Larval tows and pumps

Larval concentrations in the water column have previously been quantified using larval pumps (Minchinton & Scheibling, 1991, Bertness *et al.*, 1996, Satumanatpan & Keough, 2001) or plankton tows using conical nets (Gaines *et al.*, 1985, Ross, 2001). Plankton tows are generally conducted using a boat, but in low water level situations may have to be taken by hand (Ross, 2001). Measurements of flow rates through the plankton net for known time periods aids in the calculation of filtered water volumes. Additionally it is unlikely that plankton tows can occur frequently enough to properly assess temporal variations in larval concentrations, and may confine studies to a single site only (Gaines *et al.*, 1985, Gaines & Roughgarden, 1985, Shanks, 1986, Yund *et al.*, 1991). Pumps are generally considered to be more useful indicators of larval concentrations as samples can be taken next to chosen sites, a known volume can be filtered and samples can be taken in virtually all weather conditions (see Fig. 8, and Gaines *et al.*, 1985).

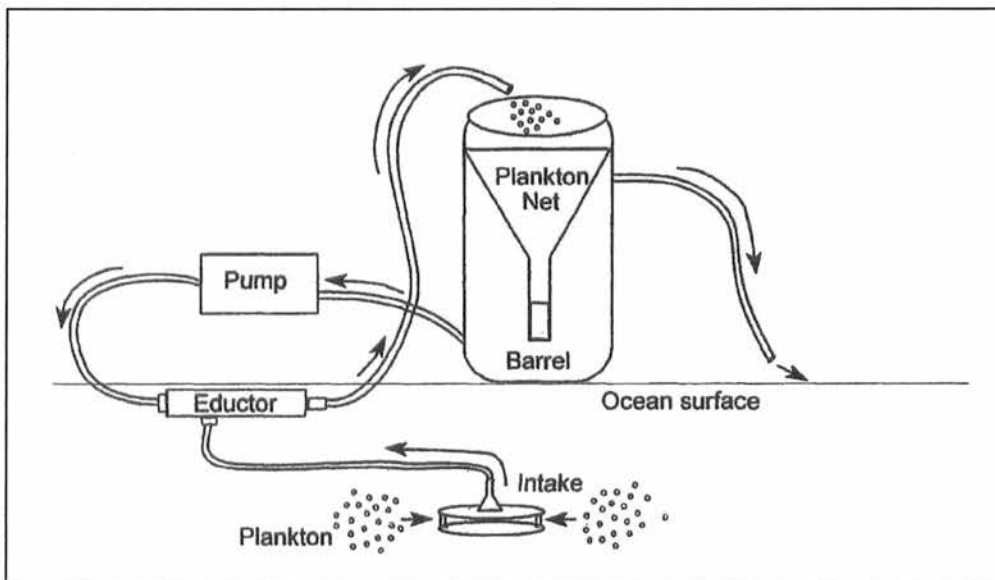


Fig. 8 – Schematic diagram of a plankton pump system used in Snelgrove *et al.* 1998, not to scale.

These sampling methods provide a brief glimpse of larval distribution at a given point, which can then be correlated to recruitment in the adult population. However these

traditional approaches may be poor estimates of larval abundance if temporal variation is high, as occurs in barnacles, and larval abundance is only one component of recruit delivery (Gaines & Bertness, 1993). Small-scale local hydrodynamic flow variances can alter microhabitat colonisation patterns (Crisp, 1955, Mullineaux & Butman, 1991), therefore sampling by nets and pumps is unlikely to provide a realistic view of larval supply at the settlement sites.

1. 3. 7. 2. 2. Larval traps

The rate of larval delivery to a settlement site can be measured using capture rates in larval traps, and these have been found to closely parallel the temporal dynamics of shoreline settlement over a wide range of oceanographic conditions (Yund *et al.*, 1991, Bertness *et al.*, 1992). Larval tubes are similar in design to sediment traps and provide a relative measure of horizontal flux passing the tubes; as passive collectors they offer the observer the opportunity of detecting variation in the larval arrival rate (Yund *et al.*, 1991, Gaines & Bertness, 1993). However, they must be sampled frequently (hourly / tidally / daily) over the season to provide a clear link to shoreline settlement (Gaines & Bertness, 1993). The dissolution of cylinders of dentist chalk (calcium sulphate) can be used as an evaluation of water flux (Yund *et al.*, 1991, Castilla & Varas, 1998) or simple sediment traps can be used as an alternative indicator of energy in water movement, through suspension of particulates in the water column.

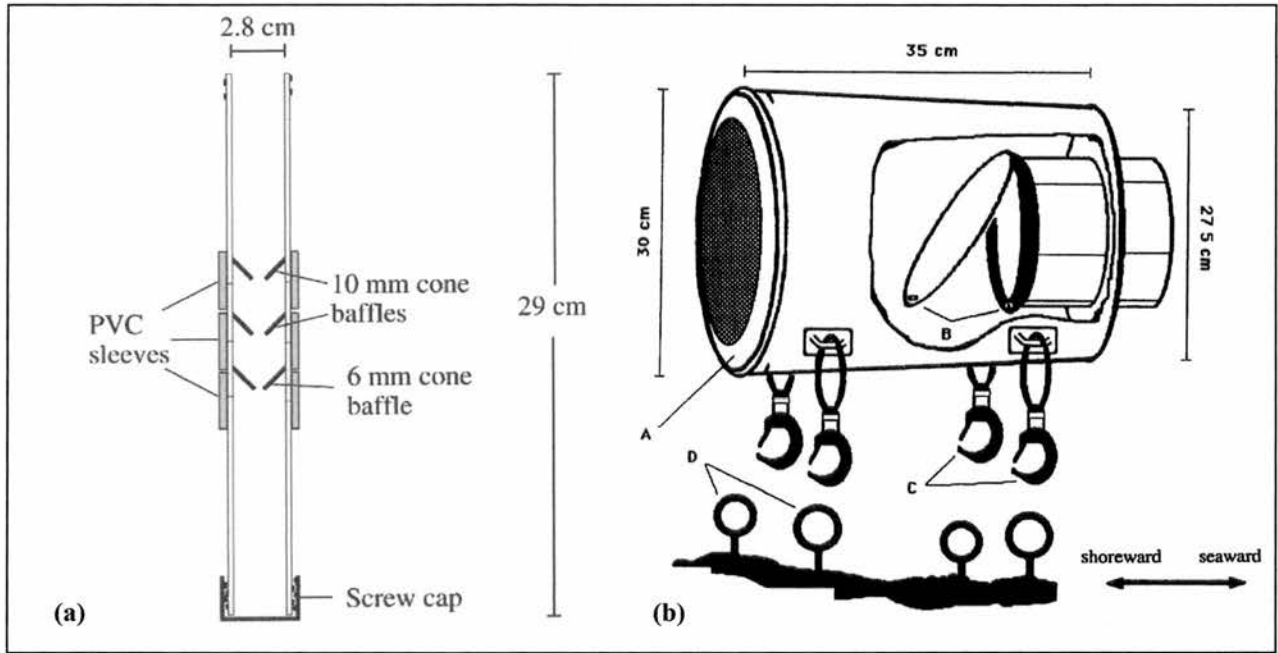


Fig. 9 – (a) Larval trap design, not to scale, taken from Todd 2003. (b) Intertidal plankton trap with cut-away showing PVC pipe and rubber flapper valve, taken from Setran 1992. A: removable plastic lid with Nitex mesh netting; B: opposing 5.0g magnets; C: brass spring-clips; D: stainless steel eye-bolts set in intertidal substrate.

Larval trap designs vary, e.g. Fig. 9a and 9b, with some incorporating meshes that may be prone to clogging (Fig. 9b, and Setran, 1992), or be of a complicated and bulky design (Castilla & Varas, 1998), which in itself may affect local hydrodynamic flows. For use in field experiments traps should be inexpensive, simple to build, light, easy to install and be effective when used in differing wave conditions, such as on sheltered or exposed rocky shores (see Fig. 9a, and Todd, 2003). Larvae passing over the trap mouth of such simple cylindrical tubes will fall or be transported into the tube, which is filled with fixative, and are retained in the ‘dead space’ at the trap bottom (Gaines & Bertness, 1993, Todd, 2003). The collection efficiency of these traps will depend upon the ratio of trap height to mouth diameter, Reynolds number and aspect ratio; higher flows (indicated by increased Reynolds numbers) will decrease efficiency, whereas an increase in aspect ratio over certain ranges will increase efficiency (Butman *et al.*, 1986). Thus traps will be undercollectors or overcollectors depending on the physical mechanisms causing the bias collections. However as most supply and settlement studies are comparative, data

provided by relative flux is considered sufficiently accurate (Yund *et al.*, 1991). Studies of the water movement through traps using dyes suggest that particles can be resuspended from the trap bottom, by eddies circulating through the entire trap (Butman, 1986), which could result in the removal of larvae and dilution of the fixative. Deep cylindrical tubes, such as in Fig. 9a, were found to be least susceptible to resuspension (Butman, 1986). Additionally any disturbance near the trap mouth, or through the trap, will increase the between-replicate variability (Butman, 1986). Baffling traps was originally proposed as a solution to decrease turbulence at the trap mouth in order to increase the collection efficiency (Gardner, 1980), but it was also found to decrease efficiency and produce high between-replicate variation (Butman, 1986). Trap-induced particle-particle interactions and trap-wall adhesion should also be considered when choosing larval and sediment traps (Butman *et al.*, 1986).

Larval supply and its transport by hydrodynamic factors to suitable substrata play a primary role in the pattern of barnacle settlement, with conspecifics, substrate and mortalities operating on a smaller scale (Bertness *et al.*, 1992).

1.3.8. Hydrodynamic influences

As mentioned previously, although cyprids have the ability to swim (Yule, 1982) and can maintain their position in the water column in low energy environments (Ross, 2001), they are relatively unable to control their dispersal and hence are passive particles subject to hydrodynamic factors (Eckman, 1983, Gaines *et al.*, 1985, Raimondi, 1988, 1990, Pineda, 1991, Raimondi, 1991, Bertness *et al.*, 1996, Jeffery & Underwood, 2000). At the large spatial scales that can be involved in the distribution of larvae, physical transport processes can aid in the prediction of settlement patterns, with nearshore flow rates

contributing to among-site variations (Minchinton & Scheibling, 1991, Gaines & Bertness, 1993, Pineda, 1994b) by dispersing and returning the larvae to the littoral zone (Pineda, 1994a). Consistent patterns of larval transport can be observed, for example due to flushing rates in bays which will affect the retention time of larvae (Gaines & Bertness, 1992).

1. 3. 8. 1. *Wind effects*

Additionally studies of daily larval supply and settlement of *Semibalanus balanoides* have been strongly correlated to local wind patterns within and among years (Bertness *et al.*, 1996), with more wave exposed shorelines receiving higher flows and larval influxes than less exposed shores (Gaines & Bertness, 1993). A number of previous studies have shown that sites can be ranked consistently by recruitment density over years (Victor, 1986, Raimondi, 1990, Sutherland, 1990, Carroll, 1996) and it has been proposed that such correlations were a result of differences in coastline orientation to prevailing winds (Kendall *et al.*, 1982, 1985). Furthermore this occurs within bays; (Bertness *et al.*, (1996), found that when prevailing winds came from the south, settlement was enhanced on the northern side of the bay, and vice versa. Hawkins and Hartnoll (1982) compared settlement on two differing sides of an island and determined a positive correlation with onshore winds. Additionally larval densities within the water column and settlement were strongly correlated with daily wind patterns, detailing the transport of larvae by these wind-driven currents (Bertness *et al.*, 1996).

1. 3. 8. 2. *Hydrodynamic processes*

Turbulent mixing, e.g. eddies, will further disperse or aggregate the larvae (De Wolf, 1973, Pearce *et al.*, 1998, Bradbury & Snelgrove, 2001), especially in surf-zone areas

(Denny & Shibata, 1989). Tidally-generated internal waves create circulating cells near the water surface and larvae can become concentrated in the slicks between the cells and carried onshore; the pattern of transport of these internal waves was found to relate to barnacle settlement rate (Shanks & Wright, 1987). Strong winds are able to generate upwelling which results in the transportation of surface water, a process known as Ekman transport, and therefore also the movement of larvae offshore (Roughgarden *et al.*, 1987, Roughgarden *et al.*, 1988). In fact nauplii and cyprids have been observed up to 100km offshore (Lefevre & Bourget, 1991), again emphasising the dispersal potential of such pelagic species. When these strong winds relax, as occurs periodically, the upwelling front moves onshore (Roughgarden *et al.*, 1988, Farrell *et al.*, 1991, Roughgarden *et al.*, 1991) although such relaxation events can be less frequent than offshore events in some locations to produce lower recruitment and weaker benthic interactions (Parrish *et al.*, 1981). Internal tidal bores also create upwelling in a direction perpendicular to the coastline, and can transport neustonic larvae shoreward (Pineda, 1991, 1994a, 1999). Oceanographic gyres occur over coastal banks and in ocean basins where their large-scale rotary currents, with little net displacement, can result in the retention of larvae (Gagné and O'Boyle 1984, as cited by Bradbury and Snelgrove, 2001). At gyre edges, convergent fronts may form near the ocean surface and its subsequent downward net movement causes larvae to be accumulated (Shanks, 1995). Periods of calm weather can be related to recruitment pulses of larvae (Farrell *et al.*, 1991).

Hydrodynamics can also affect cyprid settlement on a smaller scale. Protruding elements can alter shear stress, turbulence and advection thereby influencing the flow characteristics over the substratum (Crisp, 1955, Eckman, 1979, 1983, Wethey, 1986, Havenhand & Svane, 1991, Mullineaux & Butman, 1991). Therefore the adult distribution pattern will

affect the flow environments (Raimondi, 1990, Miron *et al.*, 1996), although reports differ as to whether cyprid settlement was influenced by such changes in advection (Raimondi, 1990, Miron *et al.*, 1996, Jeffery, 2002).

1. 4. *Spatio-temporal studies*

The distribution of the adult barnacle population can therefore be described as a temporal variation in large scale physical processes (sea temperature, plankton abundance, reproductive output, upwelling systems, local wind patterns, shoreline structure) transporting relatively 'inert' larvae to sites where smaller scale biological influences (local hydrodynamics, larval behaviour, conspecifics, substratum characteristics, tidal height, mortalities) determine the final settlement pattern. The analysis of spatial and temporal patterns in nature is essential to gain an understanding of the scales at which such important ecological processes are acting (Levin, 1992), and a hierarchical sampling programme is required to fully comprehend these scales of variation (Underwood, 1981, Minchinton & Scheibling, 1991, Hughes *et al.*, 2000, Jenkins *et al.*, 2000).

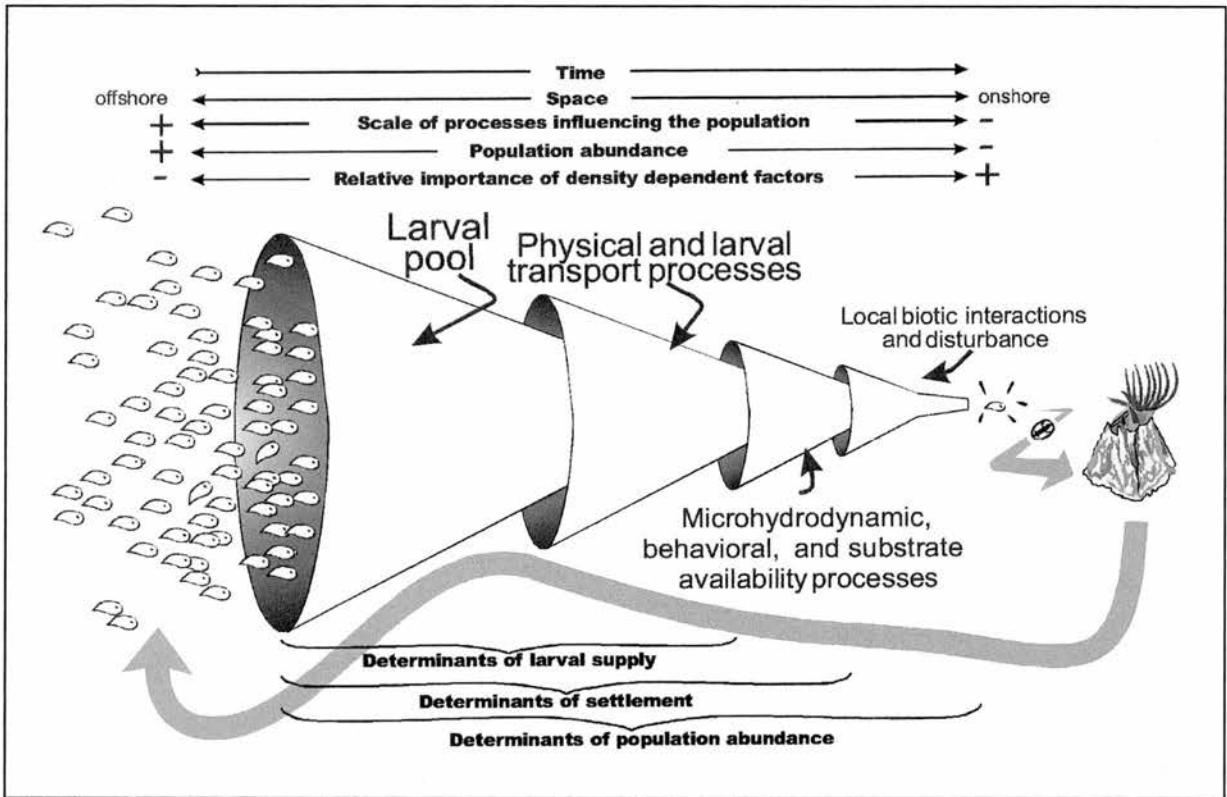


Fig. 10 – Representation of the proximate processes that influence settlement rate and population density. Taken from Pineda 2000, redrawn from Pineda 1994b.

Previous studies monitoring settlement over a season have considered that settled larvae can be termed recruits if they have survived the period up until observation (Keough & Downes, 1982, Bertness *et al.*, 1992). This assumes that no post-settlement mortality occurs, but frequent sampling ensures that such mortalities are negligible and so a reliable estimate of settlement may be made (Minchinton & Scheibling, 1993). *Semibalanus balanoides* cyprids take on average 1.5 days from settlement to metamorphosis (Connell, 1961), therefore a daily census of attached unmetamorphosed cyprids constitutes a reliable estimate of settlement (Connell, 1985, Raimondi, 1991, Pineda, 1994b), preferentially tidally if possible (Wetthey, 1984). When comparing settlement at differing sites, it is important to sample at the same frequency because any variations compound problems in interpreting results (Minchinton & Scheibling, 1993).

Cyprid counts on cleared quadrats on natural substrata provide a measure of daily recruitment, and on uncleared quadrats can aid assessment of post-settlement mortalities (Hawkins & Hartnoll, 1982, Minchinton & Scheibling, 1991, Bertness *et al.*, 1992, Jeffery, 2002). However if used for daily assessment this involves the removal of settlers and cleaning of the quadrat area to remove conspecific cues, which may provide a surface less attractive to settlers than the surrounding community (Minchinton & Scheibling, 1991). Additionally the removal of predators, to ensure that recruitment counts have the same bias throughout the season, can also lead to the production of an artificial environment (Underwood, 1986). For example, the lack of limpet grazing may reduce grazing or crushing of cyprids, but may also create unnatural biofilms. This problem of using natural substrata has led to the use of artificial plates or panels to record settlement recruitment (Jarrett, 1997). These have the advantage of providing a choice of a suitable settlement site, which can be removed from the field for enumeration and these counts can then be compared to counts on adjacent natural substrata. Moreover, it can aid in settlement comparisons between differing locations, because differences in natural rock type among sites could be an additional source of variation (Jenkins, 1997). Such artificial substrata can also aid in the comparison of yearly recruitment between sites and also with tidal height, where differing biofilms or presence / absence of conspecifics may lead to confusion in result interpretation (Raimondi, 1988, Minchinton & Scheibling, 1991).

1.5. Study aims

This study aims to investigate larval supply and settlement in *Semibalanus balanoides* over a period of three seasons. Wind patterns, conspecific cues, sea turbidity, tidal height, substratum type and shore topography effects will be examined to determine their influence on settlement patterns on various macro- and micro-geographical scales in different habitats. The specific factors to be examined in these aims can be clarified by the following null hypotheses:-

H₀ – settlement does not differ with tidal height.

H₀ – settlement is not influenced by the presence of conspecific extracts.

H₀ – substratum texture has no affect on larval settlement.

H₀ – there is no difference in the observed settlement on natural and artificial substrata.

H₀ – cyprids settle randomly across a panel.

H₀ – the orientation of a site upon a shore has no affect on settlement.

H₀ – settlement does not differ on a micro-scale (within one site), meso-scale (within one location) or macro-scale (between locations)

H₀ – local hydrodynamics do not affect larval supply and settlement.

H₀ – large-scale hydrodynamic processes do not affect larval supply and settlement.

H₀ – settlement does not alter with changes in the prevailing wind direction.

H₀ – there is no relationship between larval supply and settlement.

CHAPTER 2

MATERIALS AND METHODS



2. Materials and Methods

2. 1. *Settlement substrata*

2. 1. 1. *Settlement panels*

2. 1. 1. 1. *Basic panel design*

Sheets of black acrylic (0.6cm thick) were cut into 8.0 x 13.0 (w x h) settlement panels, with a surface area of 104.0cm² and a 0.6mm central-drilled hole to facilitate attachment in the field. The fixing hole was 3.7-4.3cm from the left / right edge and 6.2-6.6cm from the top / bottom edge. Various different panel types were used, based on this basic design, and were deployed in a portrait orientation.

2. 1. 1. 2. *Sanded and unsanded panels, with and without conspecific extract*

A number of these panels were kept unsanded and used to investigate the effect of smooth substratum on the settlement of *Semibalanus balanoides* cypris larvae; these were used only once because conspecific cues could not be confidently removed through washing (see Figs. 11a and 12a). Other black acrylic panels (again 8.0 x 13.0 x 0.6cm) were sanded using an orbital sander to provide a roughened surface, which is known to be preferred by cypris larvae (Crisp and Ryland 1960), and hereafter these settlement plates will be referred to as plane panels (Figs. 11b and 12b). The same orbital sander was used, using the same technique for a set time period to ensure equal roughening throughout the season. A crude aqueous extract of adult barnacles was prepared for use as an inductive settlement cue (see 2.2); this was used to investigate larval settlement responses to the presence or absence of a conspecific cue. Randomly chosen unsanded and sanded panels were painted with the extract and allowed to dry before deployment in the field, hereafter known as 'positive' panels or panels with

extract. Observed settlement was then compared to the same panel type that had not been painted, i.e. without extract.

2. 1. 1. 3. *Grooved panels*

2. 1. 1. 3. 1. *Horizontal and vertically grooved panels*

In later years of the study grooved panels were constructed, again of 8.0 x 13.0 x 0.6cm black acrylic. So-called 'horizontal' and 'vertical' grooved panels were plane, sanded panels that each had a 12cm² area of groove (0.5cm wide by 0.1cm deep) milled into the acrylic surface. Horizontal grooved panels comprised of three grooves across the panel surface; measured from the top of the panel the first groove lay from 2.5-3.0cm, the second 5.5-6.0cm and the third 9.5-10.0cm (Figs. 11c and 12c). Vertical panels were only milled with two grooves, to ensure the same area of groove was present on each panel (12cm²); each of these lay 2.5-3.0cm in from the left or right edge, and were 12cm long (Figs. 11d and 12d).

2. 1. 1. 3. 2. *Multiple grooved panels*

During the final study year, plane sanded panels were milled with multiple grooves in an effort to increase the numbers of settling larvae. Each panel consisted of 12 grooves (8.0cm w x 0.5cm h x 0.1cm d) located 0.0-0.5cm, 1.0-1.5cm, 2.0-2.5cm, 3.0-3.5cm, 4.0-4.5cm and 5.0-5.5cm from the top and bottom edge (Figs. 11e and 12e). This left a 2cm width area around the screw hole, which was necessary to maintain panel strength, and a groove area of 48cm².

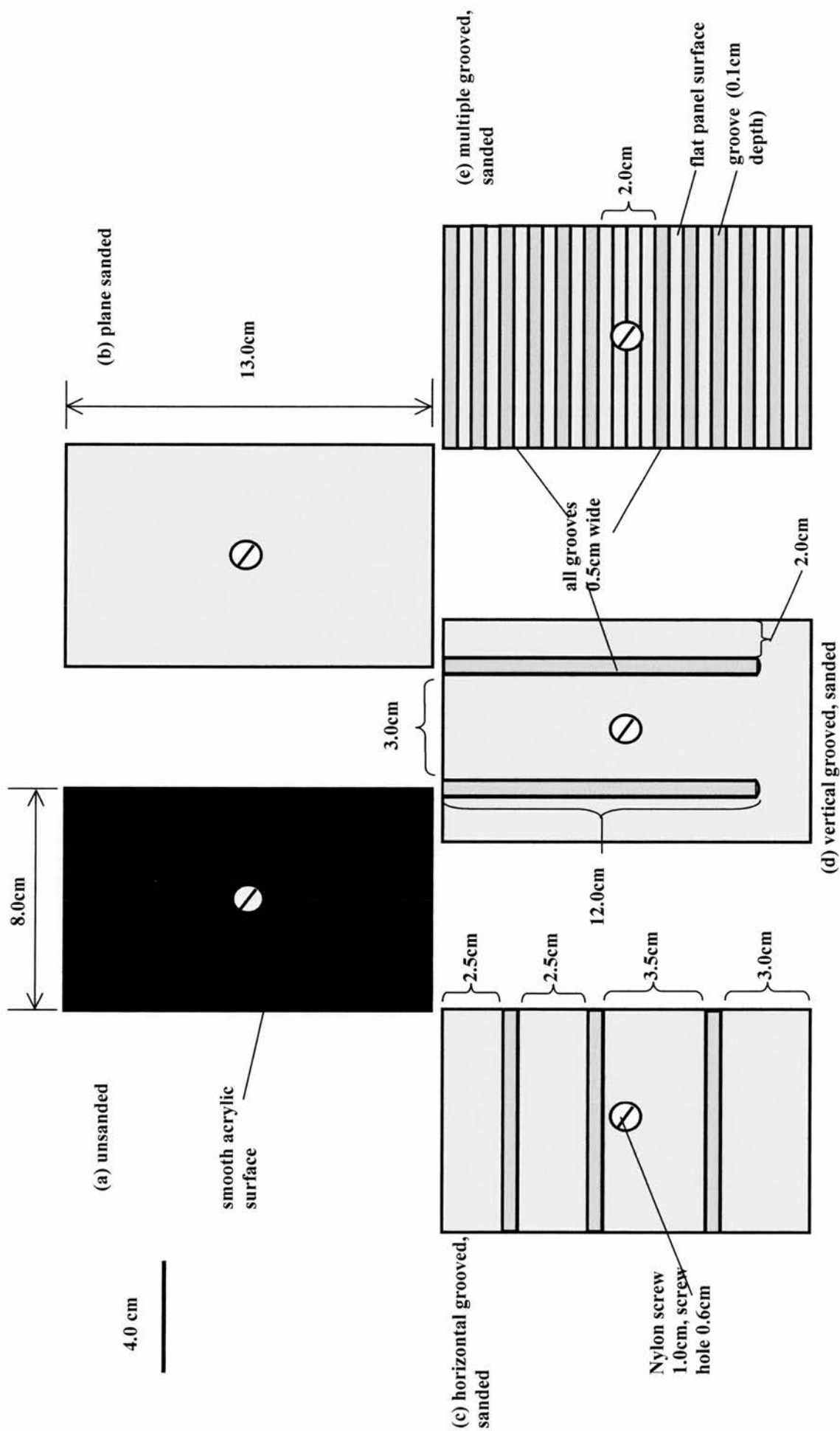


Fig. 11 – Diagrammatic representation of (a) unsanded, (b) sanded or plane, (c) horizontal groove, (d) vertical groove and (e) multiple grooved settlement panels.

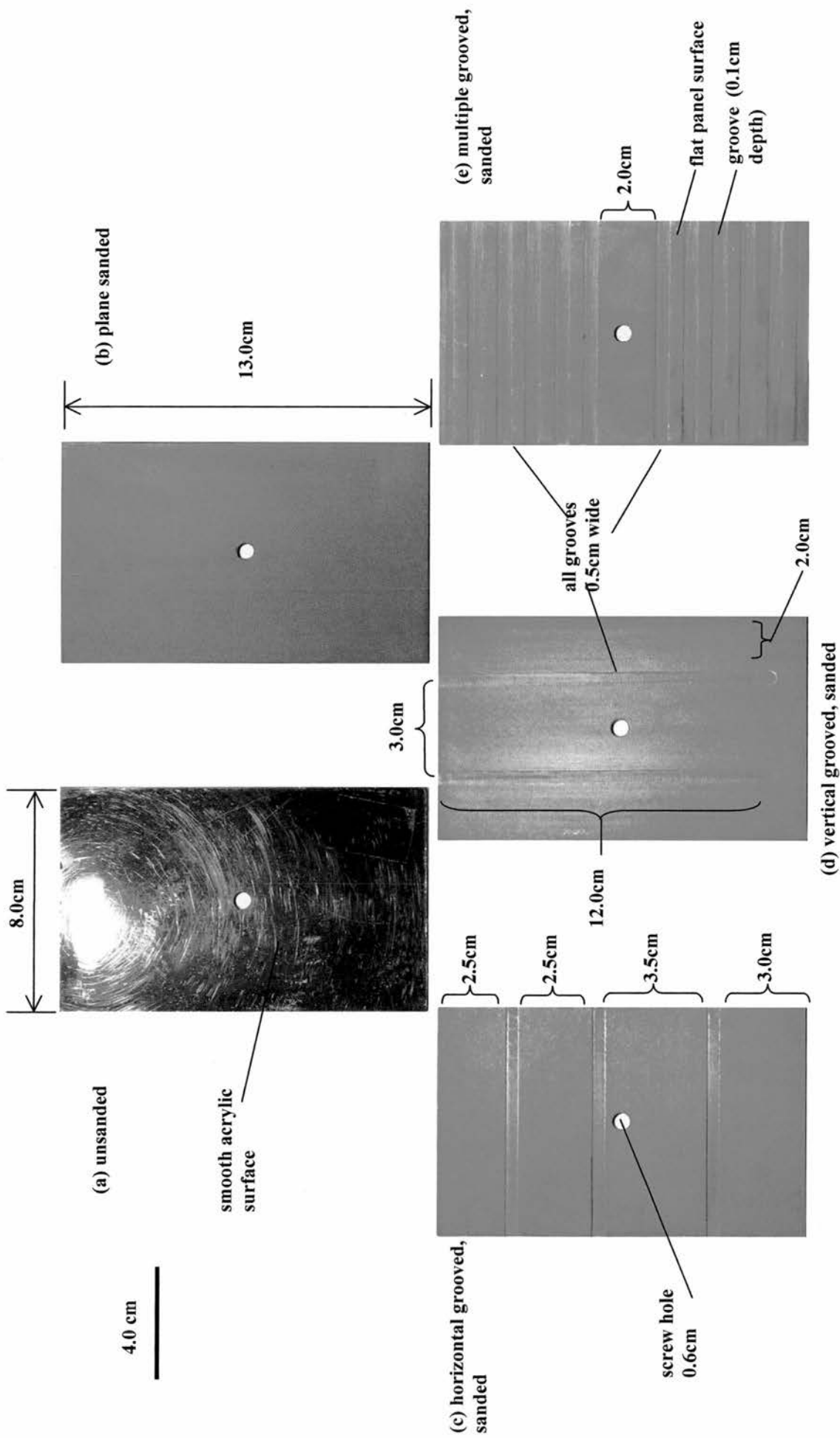


Fig. 12 – Actual photographs of (a) unsanded, (b) sanded or plane, (c) horizontal groove, (d) vertical groove and (e) multiple grooved settlement panels.

2. 1. 1. 4. *Panel preparation*

In total 200 plane sanded panels, eight plane unsanded panels, 16 horizontally grooved panels (used with extract), 16 vertically grooved panels (used with extract), and 104 multiple grooved panels (used with extract) were made for deployment in the field. The 200 plane panels were randomly subdivided as follows; 84 as a set used with conspecific extract, 84 as a set without any application of conspecific extract, and 16 as a set used for horizontal / vertical / plane panel comparisons with the remaining 16 kept as spares. After being randomly allocated to these groups, the sets were numbered on the back with PVC tape. Prior to use, plane and grooved panels were washed and scrubbed using stiff toothbrushes and hot freshwater, left to air dry, sanded using a rotary sander, washed again as before and left to air dry. During this process care was taken to ensure that none of the panel surface that was to be exposed to settlement in the field was touched in order to prevent any effect of finger grease, such as might cause inconsistent extract adsorption, and to maintain true replication.

Panels were then randomly allocated from these sets to random positions on clear acrylic mounting plates (71.0cm x 24.0cm x 0.6cm, see Fig. 13) by using randomly generated Minitab tables (v.12.1). To avoid random clumping of panel treatments, panels and their locations were re-randomised daily in each sampling season. Panels designated for use with the conspecific extract were then painted, as described in section 2. 2. Once dried, panels were attached to the mounting plates with 0.6cm (1.0cm head) nylon screws; panels were secured with a nylon wing nut on the reverse of the mounting plate (nylon screws length 2.0cm, head 1.0cm, Product N^o: 115-0421; nylon wingnuts 0.6cm bore diameter, Product N^o: 115-4689, both from Altec, <http://www.altecweb.com>). These mounting plates were then located to the field

where they were attached to 0.6cm depth clear acrylic backplates by 0.35cm width cable ties (HellermannTyton, Product N^o T30L, RS Components, <http://www.rswwww.com>) through 0.7cm corresponding holes in the mounting plate and backplate (see Fig. 13). Settlement panels were separated by 0.5cm on the mounting plates; suitable rock space that could accommodate panels in a vertical orientation was difficult to find, therefore panels were positioned close together. This also was important in considerations of replication and microhabitat larval responses, and this spacing was sufficient to ensure true replication, as mentioned in 1. 3. 2. Backplates were attached to rock substrata by wider cable ties (0.46cm wide HellermannTyton cable ties, Product N^o T50L, RS Components) locked to a network of 0.6cm strong nylon twine, which was held tightly to the rock surface by means of 5cm nylon tension rings (used for the cod-end in fishing). Backplates remained in the field throughout the settlement season, and mounting plates were changed everyday by cutting the connecting cable ties and replacing the 'old' mounting plate with a 'new' mounting plate with panels that had not been exposed to settlement. This allowed rapid change-over of panel sets in the field, and enabled panels to be safely removed back to the laboratory for analysis. This also meant that the panels were effectively held against the surface of the rock, but the twine lattice allowed minimal movement so as to prevent cracking and breaking of the acrylic, as would occur if using bolts. Panels were usually changed every day (i.e. after two tides), but daily progression in tidal times necessitated that occasionally panels were changed after one tide, in order to maintain daylight-sampling hours.

In the first two seasons backplates and mounting plates were of the same size (Fig.13), but backplates were extended in the final year to incorporate larval traps

(Fig. 31). Throughout the three seasons no mounting plates, backplates, sediment or larval traps were lost or damaged by wave action.

2. 1. 1. 5. *Panel counts*

After exposure in the field the panels were taken back to the laboratory, still attached to the mounting plates, where they were removed and numbers of cyprids counted under a binocular microscope (Leica Wild M8). The panels were placed in the field in a portrait orientation, therefore care was taken to ensure that the upper edge of the panels was noted. Cyprid numbers and location on the panel, and within grooves, were recorded using a grid of 1.0cm divisions (11.0cm x 13.0cm x 0.6cm black acrylic mount, strung with fine monofilament nylon, see Fig. 14). During the first settlement season (2000), *in situ* counts were taken in the field by eye after the first initial tidal exposure and recorded in wet/dry notebooks, with final counts taken after two tides in the laboratory. Whilst tidal data provided information on settlement every ~12 hours, only pooled data of counts after ~24 hours (2 tides) was used in analysis to prevent the estimation of cyprid settlement (Table 1).

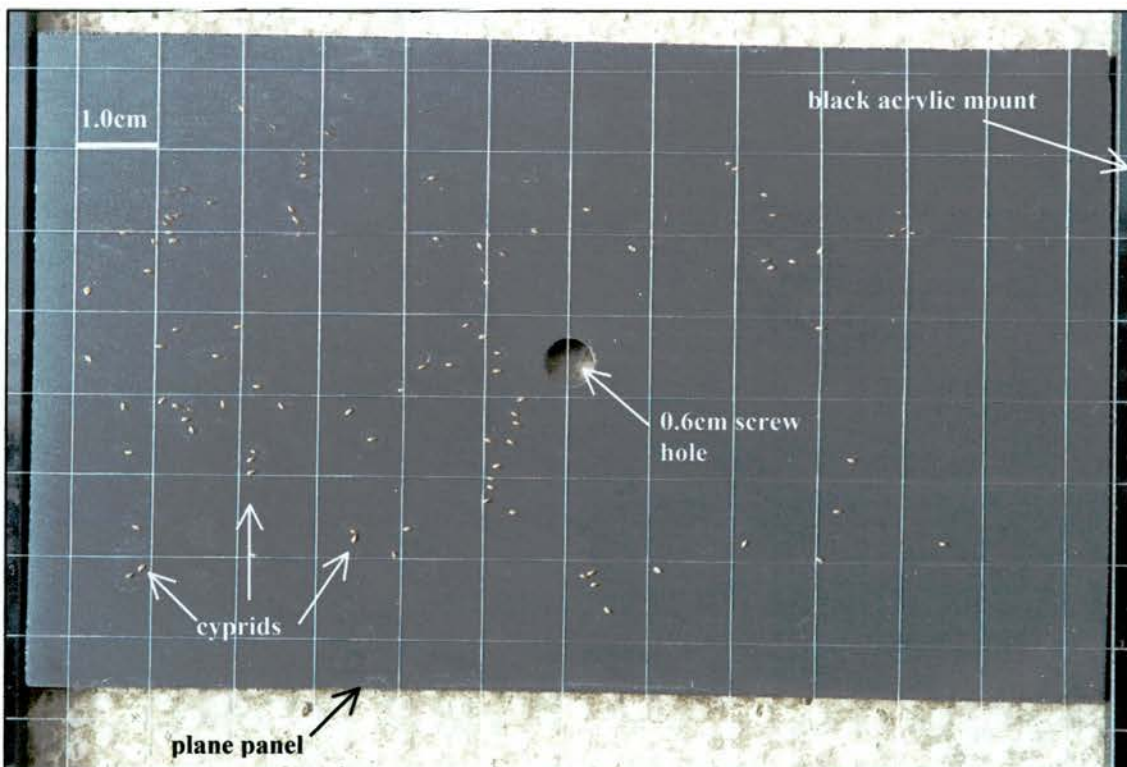


Fig. 14 – Plane sanded settlement panel after exposure in the field; attached cyprids are counted under a binocular microscope and locations recorded using a 1cm² black acrylic mounted grid (11.0 x 13.0 x 0.6cm), strung with fine fishing line.

2. 1. 2. *Settlement quadrats*

During the 2002 season cleared quadrats on natural rock substrata were used to compare larval settlement patterns on natural and artificial substrata, i.e. the pre-described panels. Triplicate quadrats were cleared at each site and adjacent to the panels and were 5.0 x 5.0cm, 25cm², in area. Areas of approximately 7.0 x 7.0cm were cleared before the beginning of the season, leaving barnacles beyond this intact (Fig.15). The 5.0 x 5.0cm squares were then marked in fine permanent marker pen and limpets within an approximate 1m surrounding area were cleared to help ensure that no post-settlement mortalities occurred due to grazer dislodgement. Each day settlement on these quadrats was counted, the cypris larvae removed using fine forceps, and the area scrubbed using a stiff toothbrush to remove the any conspecific larvae. The quadrats were then washed with clean seawater before leaving for an approximate 24-hour period. When necessary the quadrats were redrawn and then rinsed with seawater when dry.

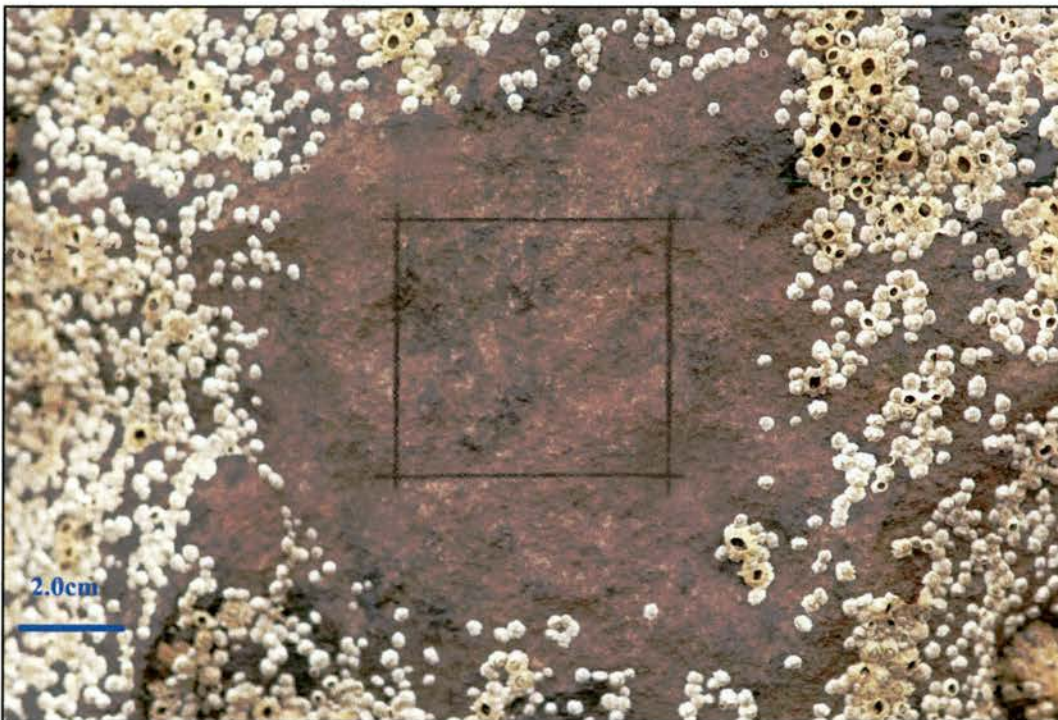


Fig. 15 – Settlement quadrat, taken at Fife Ness mid-way through the 2002 season

2. 2. *Conspecific extract preparation*

A crude aqueous extract of adult *Semibalanus balanoides* barnacles was made each year in April to the same concentration, which is specific to species (Crisp and Ryland 1960). 230g of adult barnacles were scraped using a broad flat blade from recently collected seawater-rinsed intertidal rocks. These were then ground in a pestle and mortar with a small amount of deionised water, which was then made up to a total volume of 1L using more deionised water (230gL^{-1}). This slurry was then allowed to stand for five hours at 10°C , with occasional mixing, before centrifuging at 4000rpm for 30minutes (Beckman, JA10 rotor). The clear, slightly pinkish/orange supernatant purified of the shell fragments and debris was then pipetted into 5ml aliquots, stored in miniature 6ml polyethylene vials (PONY vial Product N^o: 6000292, Packard Bioscience BV, Groningen) and stored at -70°C . Each day the required aliquots were removed and allowed to defrost at room temperature (approx. 20°C) prior to use.

A 1cm chisel-shaped camel hair paintbrush was used to paint the extract onto panels. Two coats were applied, allowing each to dry before application of the second coat or removal to the field. For two coats of extract the plane sanded panels each required $\sim 0.36\text{ml}$ of extract, for horizontal / vertical grooved panels $\sim 0.38\text{ml}$, and for the multiple grooved panels $\sim 0.40\text{ml}$ due to increases in surface area.

2. 3. Larval traps

2. 3. 1. Construction

In order to assess whether observed patterns of settlement were solely a function of larval concentration, traps were used to monitor daily water column fluctuations of larvae. These were as described in Todd (2003, also see Fig. 9a), which were a development of the basic cylinder traps used by Yund *et al.* (1991). The main body of the trap consisted of 57ml capacity conical polypropylene laboratory tissue culture tubes with skirts (Cellstar™, Product N^o 210270 from the Greiner Labortechnik, Germany; <http://www.greiner-lab.com>). Traps were baffled to aid in particle/larval retention, with an aspect ratio of 10.4 and a total volume of 176ml. Four of these 57ml tubes were used in each trap construction which had a 57ml entry chamber, a three-cone baffled middle section of ~39ml, and a basal reception chamber of 80ml. The uppermost two conical baffles had 1.0cm holes in their centre, whilst the last had a 0.6cm hole; this was achieved by the use of a heated steel rod. Two smaller holes of ~0.1cm were melted into the baffles where they join the interior cylinder wall to prevent any air blockages on refilling the traps, which could lead to problems of repeatability of urea volume and spectrophotometric measurements of urea loss. The screw cap at the end of the reception chamber was used for emptying and resealing the trap, which ensured that the trap did not need to be removed from the settlement sites. Cut cylinders were sanded to right angles using a fine-grade sanding wheel, allowing the composite parts to be tightly fitted to each other. These parts were held together using transparent PVC piping sections (2.5cm bore, 0.325cm wall ~3.0cm length, Product N^o TWR-670-292S, Fisher Scientific U.K.); this had been softened in hot water to aid in the trap construction and once cooled it ensured the trap

components were sealed and rigid. To aid in this rigidity the tubes were placed in a freezer for 20 minutes at -20°C (Fig. 16).

2. 3. 2. Trap solution

In order to kill the larvae, and to reduce advection of captured swimming larvae swimming from the traps, a 4M urea in seawater solution was used (made from 98% urea powder, Product N^o U 5378, Sigma. The selected settlement sites were in areas of public access, therefore any conventional killing solutions such as formaldehyde could not be used. To assess the degree of washout in the traps, a 1ppt Bromophenol Blue stock solution (Bromophenol Blue powder, Product N^o B 5525, Sigma) was made in distilled water and stored at 4°C. This was then added to the urea solution and mixed well to provide a final concentration of 10ppm, which would be used in the traps. As described in Todd (2003) the concentration of Bromophenol Blue was spectrophotometrically assessed from trap samples taken after exposure in the field (Shimadzu UV-1601; 594nm absorbance, seawater blank). The readings were then compared to the stock urea with Bromophenol Blue solutions to permit calculation of the percentage urea retention in the traps throughout the season. Therefore this would also prove useful as an indicator of larval capture efficiency in differing wave conditions.

These traps were then firmly mounted onto the extended 0.6cm clear acrylic backplates using 0.35cm width cable ties, and these backplates were then attached to taut nylon ropes on the rock substrata, adjacent to the settlement panels (see Fig. 16 and Fig. 32 in section 2. 6. 1. 3. 2.). The screw cap at the base of the trap was attached below the level of the backplate to aid emptying and refilling in the field. Samples

were emptied daily or tidally into small plastic containers with a maximum capacity of 250ml (kindly donated by Safeway plc.), and the lids secured to prevent leakage before analysis in the laboratory.



Fig. 16 – Larval traps containing 4M Urea 10ppm Bromophenol Blue solution, attached to backplate at Klingsbarns, 2002.

2. 3. 3. Larval counts

Retrieved samples were filtered onto a 50µm nylon mesh screen (Product N^o NY/MO/50/32/1020, Lockertex, Warrington), and then washed into a 10cm diameter plastic petri dish in the laboratory. Samples were then analysed using a Leica Wild M8 dissecting binocular microscope, and different species noted. Dead, decomposing and digested cyprids were noted but not included in later analysis because these larvae would not have been involved in the settlement processes the day prior to observations. During the 2000 season larval sizes were measured using a 1.0cm graticule (10mm/0.1mm Leica graticule, Product N^o 10446447, <http://www.leica-microsystems.com>) and recorded.

2. 4. *Sediment traps*

2. 4. 1. *Construction*

Sediment traps were constructed from two Cellstar™ cell culture tubes (product details as in 2. 3. 1), with a single 0.6cm cone baffle and two air-lock holes located midway down the trap. Sections were joined using PVC tubing sections as for the larval traps, creating a trap 2.8cm wide, 20.8cm long with a trap volume was 120ml (aspect ratio 7.4). As these traps were to be used to provide an indirect measure of wave action, not for trapping larvae, no fixative solution was required and therefore traps were filled with clean, fresh seawater. Samples were collected daily, as this was found to be a reliable measure of wave action (Todd 2003). Samples were emptied daily or tidally into small plastic containers with a maximum capacity of 250ml, and the lids secured to prevent leakage before analysis in the laboratory. Sediment traps were used in the second and third sampled season; initially they were attached adjacent to the panel backplates using nylon cable ties (Fig. 17a, but in the final year they were attached to specially constructed backplates adjacent to the panels (Fig 17b, and Fig. 28 in section 2. 6. 1. 3. 1.)

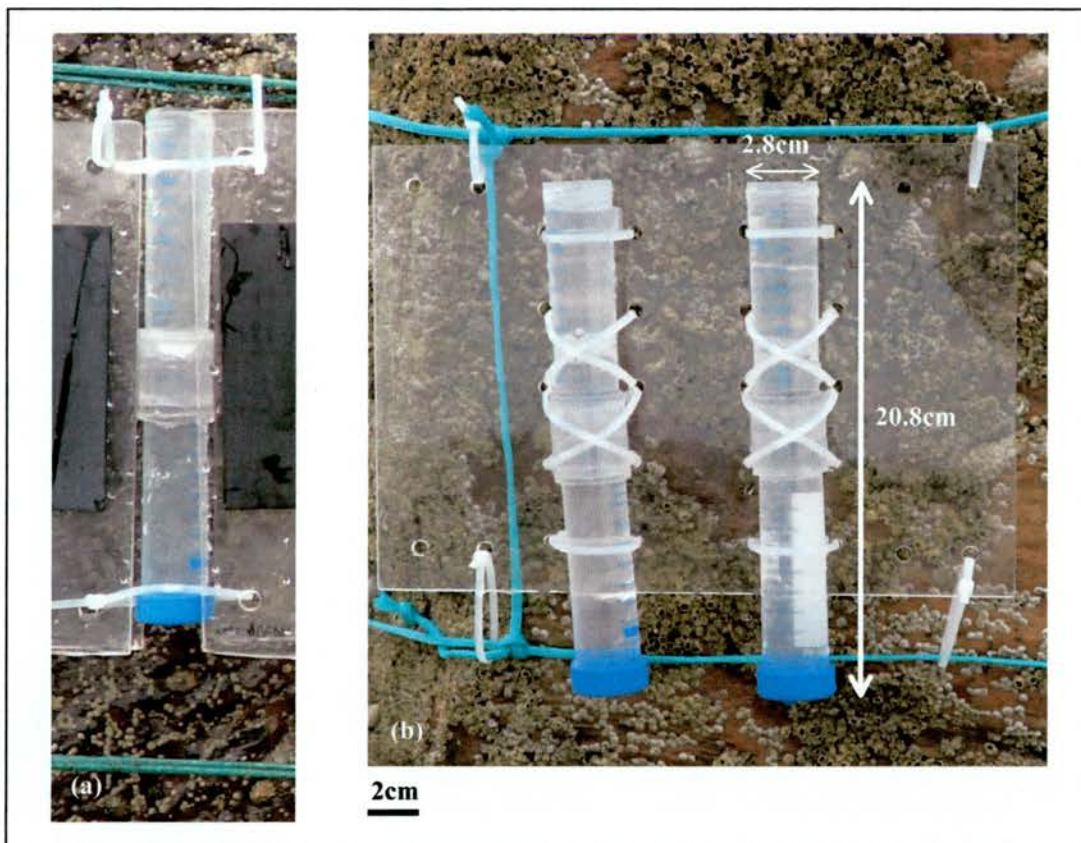


Fig. 17 – (a) Sediment trap attached to backplates, adjacent to panels in 2001 season at Fife Ness; (b) Sediment trap attached to separate backplate, adjacent to panels in 2002 season at Kingsbarns. Scale is the same for both images.

2. 4. 2. *Sediment analysis*

In the laboratory, sediment samples were washed through 50 μ m nylon gauze (Product N^o. NY/MO/50/32/1020, Lockertex, Warrington) to remove mud particles and small organic matter, using a soft 1.0cm chisel-shaped paintbrush. 50 μ m gauze was chosen as this mesh size would retain all the sand fraction (>63 μ m), including that of the finest sand (50 μ m-100 μ m as detailed in the accepted US Department of Agriculture classification, <http://soils.usda.gov/technical/classification/taxonomy>). The use of the paintbrush aided in the washing of fine silt and mud from sand particles, and in the disruption of faecal pellets. Large pieces of drift macroalgal fragments were removed using fine forceps, which were rinsed onto the mesh before removal; this ensured that only the sand fraction was retained upon the 50 μ m screen. Samples were then

transferred into porcelain crucibles (Haldenwanger squat form), which had been weighed prior to use (to nearest mg, Sartorius BL 105 balance), before being oven-dried at 90°C overnight. After being oven-dried, the sediments were re-weighed before ashing at 550°C for 4.5h to remove any remaining organics, and were subsequently weighed again following this process. This process allowed the sand fraction weight to be calculated. Samples were then passed through a 500µm woven aperture wire mesh sieve (brass BS410, 100mm diameter, Endecotts Ltd, Product N^o SIH-360-220S, from Fisher Scientific, U.K.), and the ≤500µm fraction was weighed and retained in glass vials to prevent rehydration of samples (squat glass specimen tube, polyethylene snap cap, 34mm height x 23mm diameter, Product N^o TUL-490-032N, Fisher Scientific, U.K.). The retained sample provided a measure of the coarse and very coarse sand fraction of the sediment composition (coarse sand particle diameter 0.5-1.0mm; very coarse sand diameter 1-2mm as detailed by the U.S.D.A.). As the chosen field sample sites had varying beach substrata (St Andrews sandy, Kingsbarns sand and shell fragments, and Fife Ness being mainly rocky), sediment samples were transferred into proportional values of the maximum recorded settlement as each site, i.e. maximum sediment weight / daily settlement rate.

2. 5. Plankton sampling

Prior to the beginning of the settlement season plankton tows were conducted at East Sands Bay from a boat, using a conical sampling net and cod-end receptacle. Tows lasted for 15 minutes at mid water levels, and 15 minutes at upper water levels. Tow samples were concentrated by passing through a 50µm mesh screen, and the presence of *Semibalanus balanoides* nauplius VI and cyprids were noted using a Leica Wild M8 dissecting binocular microscope. This procedure was used only as indicator for

the commencement of the settlement season, and was not used for quantitatively measuring larval concentrations.

2. 6. *Study sites*

Intertidal study sites with relatively easy accessibility were chosen in the East Neuk of Fife in Scotland, as the need for daily sampling precluded the sites further afield. The 15km coastline from St Andrews to the Fife Ness headland has a north-easterly aspect and winds from the NNW to ESE generate waves, whereas winds originating from the SSE to WNW are offshore winds and generate little or no wave action (Fig.18). As a promontory, the headland at Fife Ness is exposed to wind-generated waves from the NW to the SW, whereas winds from the WNW to the WSW will result in low wave action. Settlement was studied each year for three years, 2000-2002 inclusive. Each year some aspects of the settlement experiment were changed, to improve settlement responses and therefore aid in the interpretation of the observed settlement patterns (see 2. 6. 1 to 2. 6. 4).

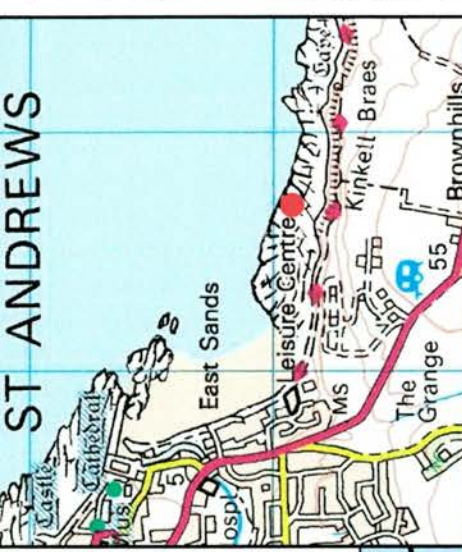
ST ANDREWS



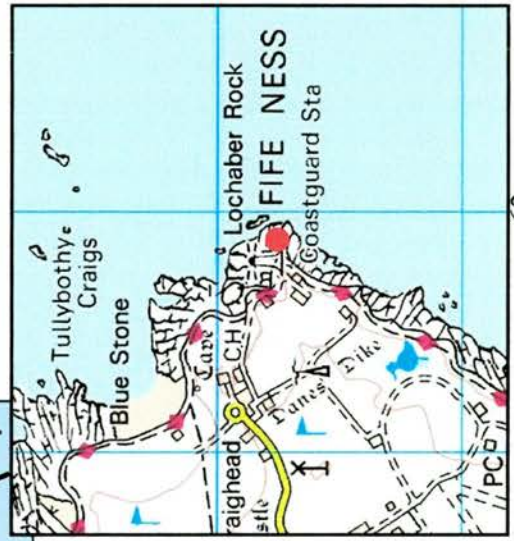
Andrews
OS Grid ref: 529 160
56° 20.1' N 02° 46.2' W



Boarhills site
OS Grid ref: 568 151
56° 19.6' N 02° 42.1' W



Kingsbarns site
OS Grid ref: 603 128
56° 18.3' N
02° 38.7' W



Fife Ness site
OS Grid Ref: 639 097
56° 16.7' N 02° 35.2' W

Fig. 18 – Settlement study sites, locations indicated by red circles. All maps reproduced from the Edina Digimap / JISC supplied service, courtesy of © Crown Copyright Ordnance Survey.

2. 6. 1. Kinkell Braes, St Andrews (56° 20.1' N 02° 46.2' W; OS Grid ref: 529 160)

This is a rocky intertidal site with a north-easterly aspect and dense *Semibalanus balanoides* settlement, especially on vertical surfaces. *Mytilus edulis* (L.) dominated lower midshore beds, with fucoid macroalgae frequently found on horizontal bedrock surfaces. *Laminaria digitata* (Huds.) Lamour was the predominant infralittoral kelp species at this location, which has a mean and maximum spring tidal amplitudes of 4.8m and 6.0m respectively. All experimental sites at Kinkell Braes were immersed on every low tide.

2. 6. 1. 1. First settlement season, year 2000

Initially a textured scrub pad (Vileda Active Wave, 10.0 x 14.0 x 0.7cm, discontinued product) was used as a settlement substratum, because it was thought that the microtextured surface would be ideal for cyprid settlement. However it was soon found that observed settlement was very low, whilst neighbouring rocks had large numbers of settlers; this may be accounted for by the flexibility of the surface, any solvents/detergents that may be present from the manufacturing process, and the depth of the surface pits. Therefore the choice was then made to use the aforementioned black acrylic panels, and the sampled settlement season for this year was May 6th to June 4th (observed settlement began 19th April).

2. 6. 1. 1. 1. Sites A and B

Site A faces west and Site B faces southeast on the same triangular-shaped rock in the upper intertidal region, ~ 1.5m from the bedrock. *Semibalanus balanoides* cover was dense, approaching 100%, and the substratum was also populated by limpets and *Littorina* species (see Fig. 19). This location was closer to the East Sands beach than

any other at Kinkell Braes, with the other locations being further down the shore (Sites C-G, T). As seen in Fig. 19 this is not a ‘stand alone’ rock, and on two sides is surrounded by rocks of similar heights. This site was used in the first year only, with four plane panels with extract and four plane panels without extracted routinely deployed (as in Fig. 13 and Fig. 19). Counts of settlers were made *in situ* after one tide, and then panels were removed to the laboratory for final counts and re-preparation of the panel surfaces. These sites were used for a period of six tides (May 6th pm – May 9th am) during which it became apparent that this site had very low settlement; although in the mid intertidal region, the local hydrodynamics caused by the adjacent rock formations may be the cause of such low observed settlers.

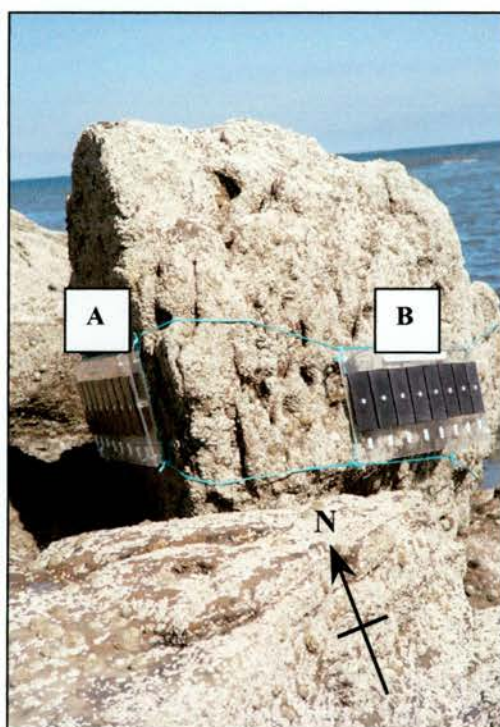


Fig. 19 – Sites A and B at Kinkell Braes, St Andrews (OS Grid ref: 529 160). Site A is to the left, and faces west towards East Sands. Site B faces southeast towards the cliff face of Kinkell Braes. Backplate length is 71.0cm, for scale.

2. 6. 1. 1. 2. *Sites C, D and E*

Sites C, D and E all were situated on the same vertical rock ~ 1.5m in height, located in the intertidal region at Kinkell Braes and facing southwest (Fig. 20). This aspect meant that although the rock was exposed to waves, it was protected from direct wave crash upon the panels. Again *Semibalanus balanoides* cover was almost entire upon the upper part of the rocks, but declined to ~5% at the rock surface adjacent to the bedrock, and the dominant community species were the same as for A and B. Site C was the middle block, at a mid-intertidal height, Site D the upper block at an upper intertidal height, and Site E the lower panel block at a lower intertidal height (Fig. 20). These three sites were used to examine differences in settlement patterns with small differences in tidal height (= exposure to settling cyprids), and were counted *in situ* after one tide and in the laboratory after exposure to two tides. Each set (or block) of plates were directly underneath each other, with D being vertically separated from C by ~28cm screw-hole to screw-hole, C to E by ~38cm, and D to E by ~54cm (Fig.20). Backpanels and mounting panels were 71.0 x 24.0 x 0.6 cm clear acrylic sheets, and each settlement site was enumerated for eight black acrylic panels daily during the season (Fig.13). Sites D and E involved four plane panels with extract and four plane panels without extract (see Fig. 20); both sites were sampled between May 9th pm to the 24th May pm. Site C also included four plane panels with extract and four without for the majority of the sampled season (May 6th pm –May 26th am, May 30thpm – June 4th pm), apart from the six tides between May 7th pm to May 10th am where four plane panels with extract, two new smooth (unsanded) panels with extract and two without (painted with seawater) were deployed. These data were used to compare larval settlement behaviour with surface texture (Fig. 21).

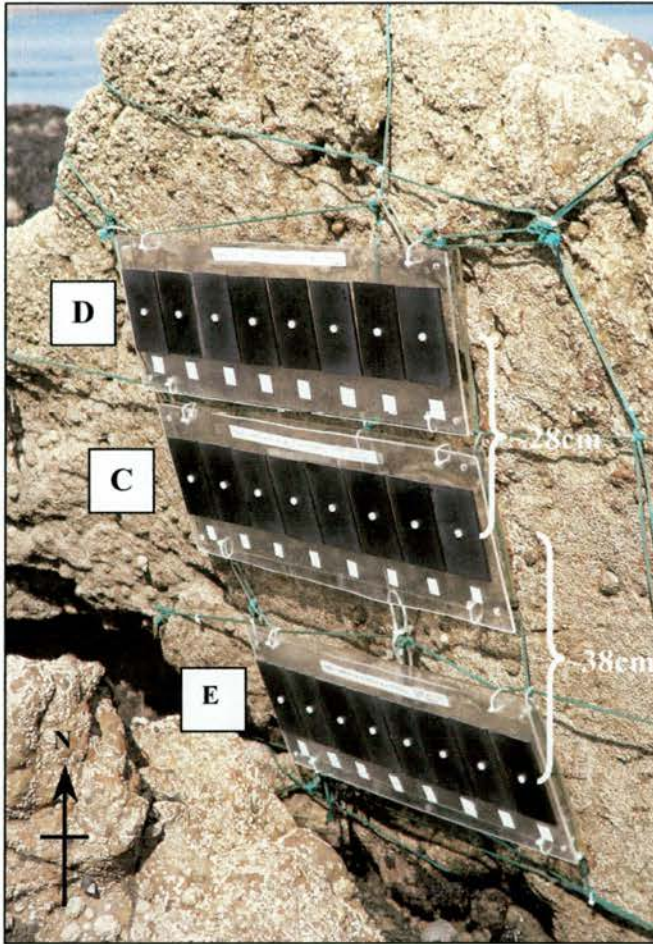


Fig. 20 – Vertical rock face used for Sites C – E in experiments of tidal height with larval settlement patterns, at Kinkell Braes. Each panel set consists of four plane panels with painted extract, and four without, screwed to a mounting sheet and attached to a backplate (each sheet 71.0cm x 24.0cm x 0.6cm clear acrylic). 0.35cm width white nylon cable ties secure the section together, and to the twine lattice on the rock face.

As can be seen from the above photograph, there is a rock outcrop in close proximity to Site E. This would cause water flow to be channelled through the gully between the panels and the outcrop, and may affect the observed settlement.

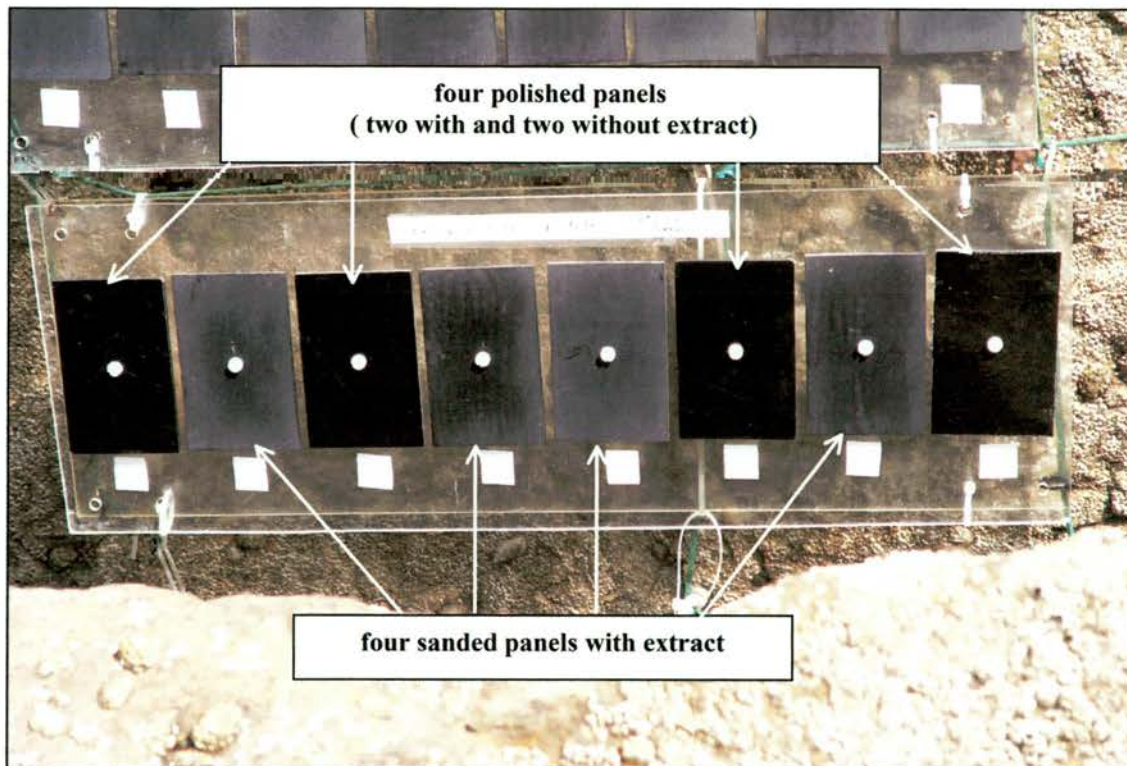


Fig. 21 – Experimental set-up for studies of substratum type with larval settlement at Site C, Kinkell Braes. Attached to the 71.0cm x 24.0cm x 0.6cm clear acrylic mounting and backing plates are four plane sanded panels with extract, two polished (unsanded) panels with extract, and two polished panels without extract (seawater painted).

2. 6. 1. 1. 3. Sites F and G

Sites F and G were located on two opposing rock faces within a narrow gully, located in the low intertidal region of Kinkell Braes, approximately 10m from the rock bearing panel sets C-E (Fig. 22). These locations were at the same height at Site E, with the latter rock being ~40cm in height from the bedrock. *Semibalanus balanoides* coverage was dense upon the upper levels of the rock but, as can be seen in Fig. 22, encrusting algae and young *Fucus serratus* plants covered the lower half of the rocks (~20cm - 0cm). Backplates were tied halfway up this rock to a twine lattice, therefore the panels straddled both the barnacle and the algal areas. Site F faced northerly (seawards) towards the incoming tide, whereas Site G faced southerly, towards the Kinkell shore (Figs.23 and 24). The floor of the gully between the sites contained many large, loose pebbles and rock surfaces also were inhabited by limpets and *Littorina* species.

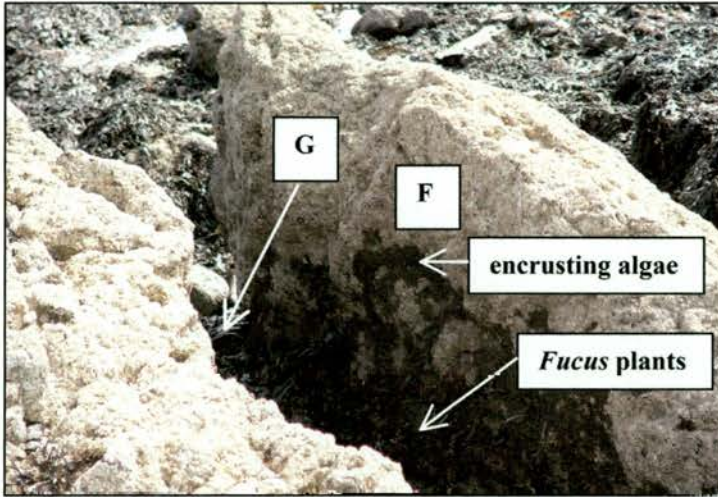


Fig. 22 – Bare rock face which housed Site F; upper half of rock shows dense *Semibalanus balanoides* cover whereas lower half of rock is dominated by encrusting algae and *Fucus serratus*. Sites shown without panels to display rock substratum and associated species.

At both Sites F and G four plane sanded panels with extract and four plane panels without extract were deployed. These sites were sampled daily (*in situ* and final counts) in the period between May 9th pm and May 15th pm (12 tides).

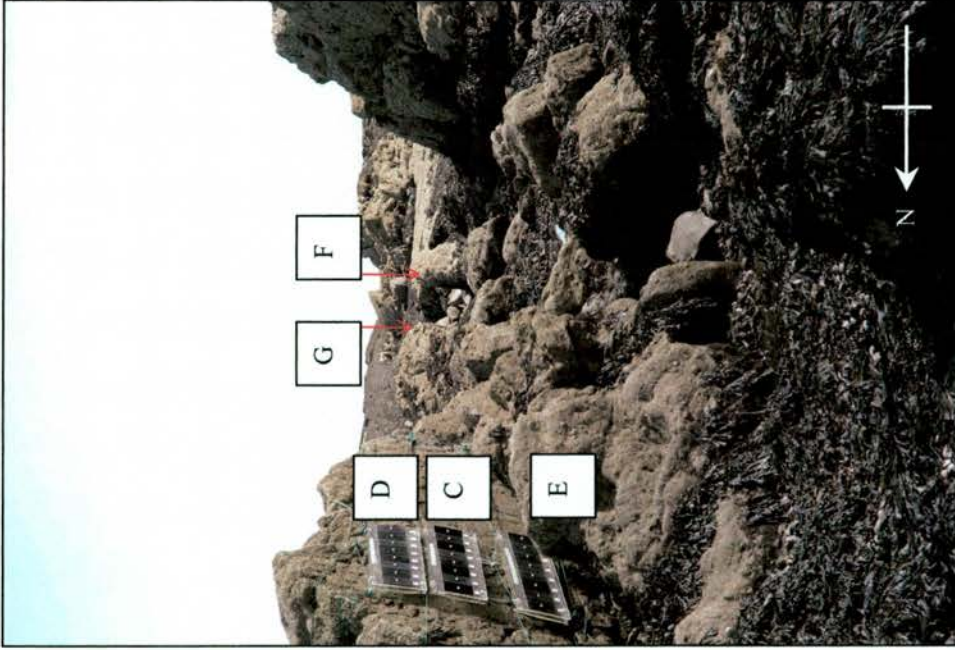


Fig. 23 – Study sites F and G in relation to Sites C – E at Kinkell Braes. Site G faces towards the shore, whereas F faces north towards the incoming tide.

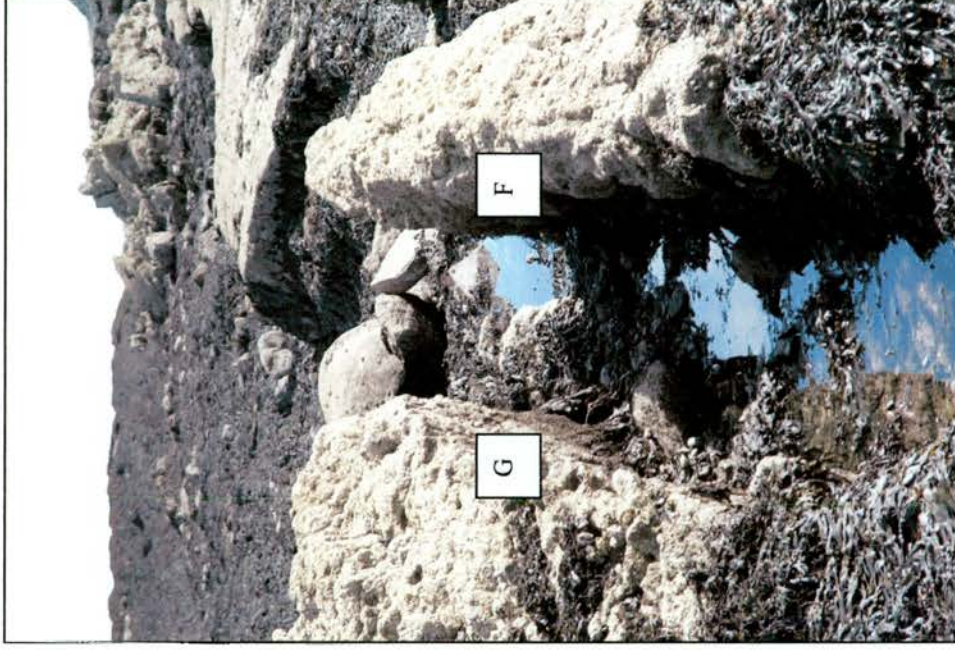


Fig. 24 – Settlement study Sites F and G, Kinkell Braes, separated by a gully containing loose stones. Panels not shown to clarify rock structure.

2. 6. 1. 2. *Second settlement season, 2001*

2. 6. 1. 2. 1. *Sites C, D and E*

The same vertical rock was used again for Sites C, D and E at Kinkell Braes in 2001 (Fig. 20, 25a and b), with as before four plane panels with extract and four plane panels without extract being deployed daily. Panels were deployed in the field between the 22nd April and the 2nd June for Sites C and D, with only final counts taken after two tides in the laboratory. Site E was sampled between the 27th April and the 13th of May. Mounting plates and backplates were of the typical dimensions, and again nylon screws and wing nuts secured the panels to the mounting plates. Sediment traps were secured at each end of the panel backplates, using 0.35cm width nylon cable ties, at the same height as the panels. One trap was located on the left and one trap on the right of each panel backplate, providing a total of six sediment traps for Sites C – E (25a and 25b). These were filled with seawater and emptied each time the panels were retrieved and replaced. Therefore they were emptied daily (or occasionally after one tide when necessary) into small plastic food containers with a maximum capacity of 250ml, and the lids were secured. Sediment traps were refilled daily with fresh, clean seawater and any algal biofilm was cleaned from the inside of the trap using a stiff toothbrush.

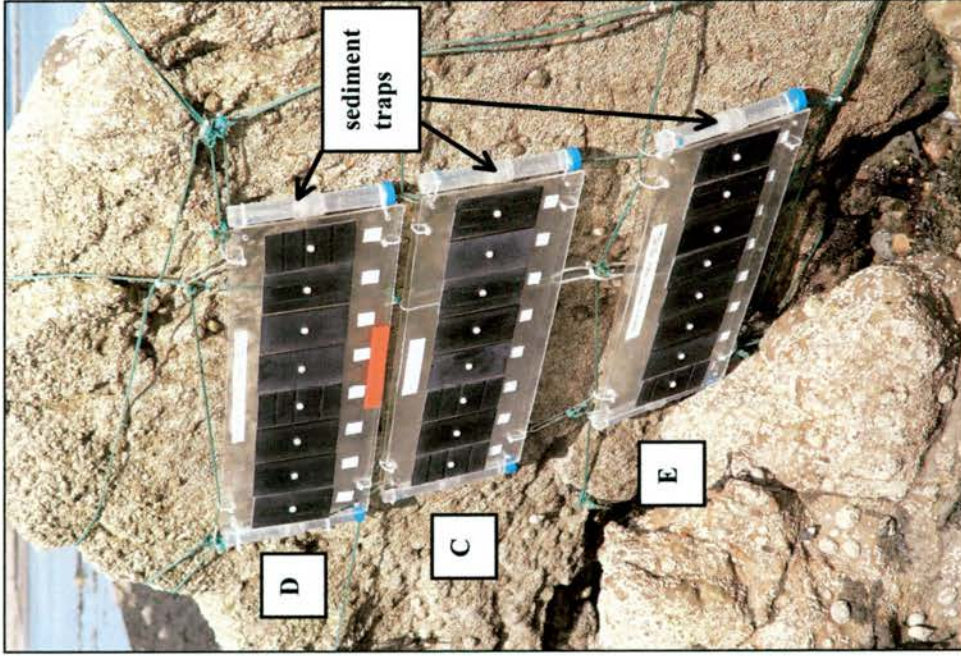


Fig. 25a – Sites C, D and E with sediment traps located at each side of the panel backplates, 2001. Backplates and mounting plates 71.0 x 24.0 x 0.6cm clear acrylic for scale.

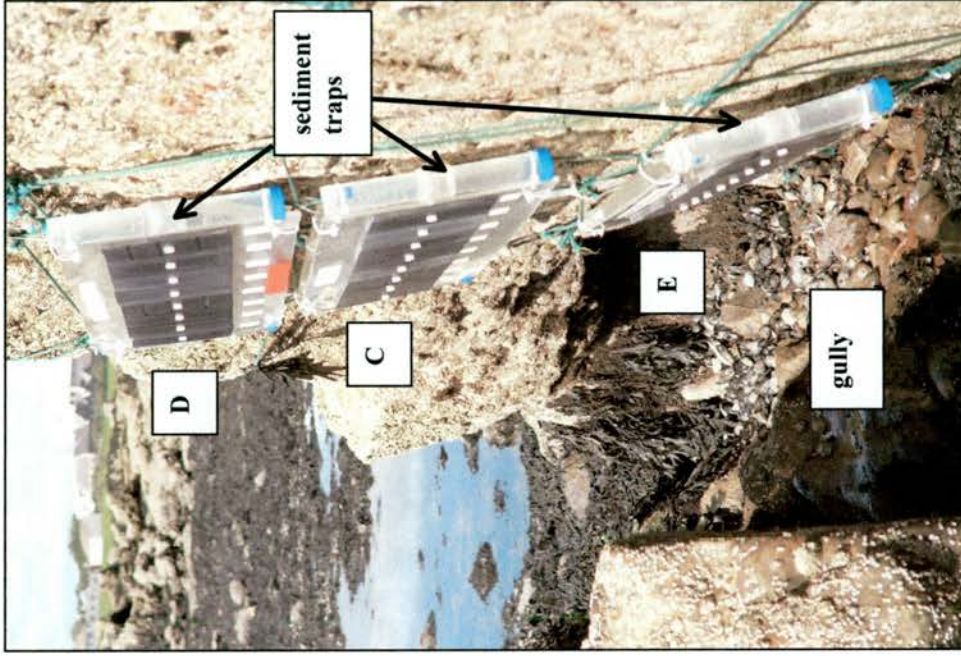


Fig. 25b - Sites C, D and E with sediment traps, 2001. Photo taken from a side angle to display the gully between site E and the opposing rock. Backplates and mounting plates 71.0 x 24.0 x 0.6cm clear acrylic for scale.

2. 6. 1. 2. 2. *Site T.*

Site T was a rock outcrop, with a vertical face of $\sim 0.75\text{m}$ height by $\sim 1.1\text{m}$ width, facing due north and without protection from wave exposure. This rock was located approximately 30m southeast of Sites C / D / E and 15m south of Sites F and G. Therefore it was higher upshore towards the Kinkell Braes cliffs than the other sites in the area, and with a higher vertical position $\sim 30\text{cm}$ above Site C. Directly in front of this site was a flat slab of bedrock, with small tidal pools, covered in encrusting red algae and *Fucus* spp. Limpets and *Littorina* spp. again were present in moderate to high numbers (Fig. 26). Each panel set consisted of three plane sanded panels, three horizontal grooved panels and three vertical grooved panels, all painted with barnacle extract (Fig. 27); this site was sampled daily between the 4th of May and the 6th of June, with no *in situ* counts.

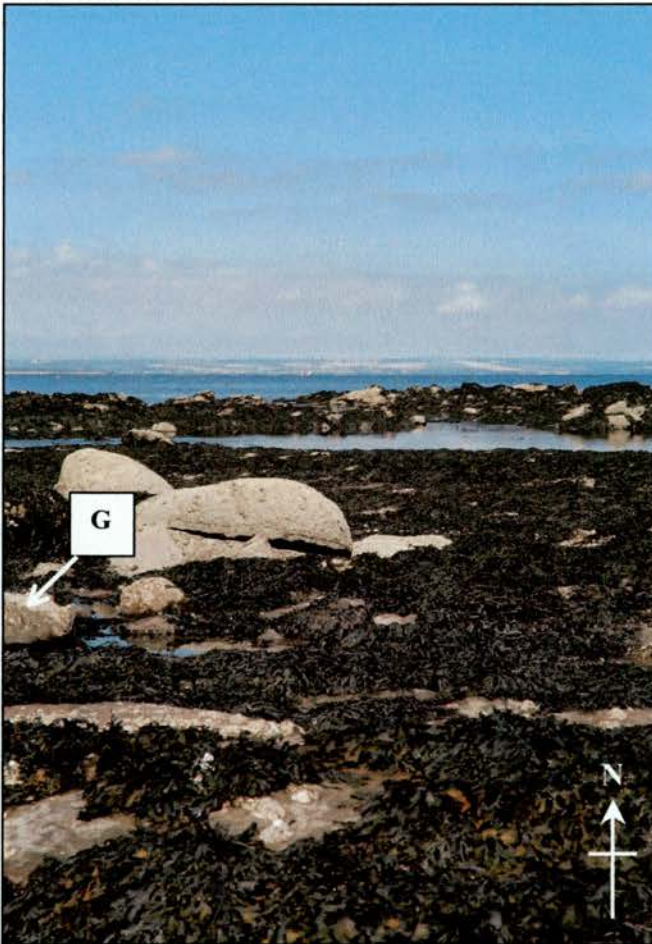


Fig. 26 – View from Site T, Kinkell Braes facing due north towards the incoming tide, 2001. Rock housing Site T projects vertically from a wide, flat rock ledge that is indispersed with shallow rockpools and *Fucus serratus* plants.

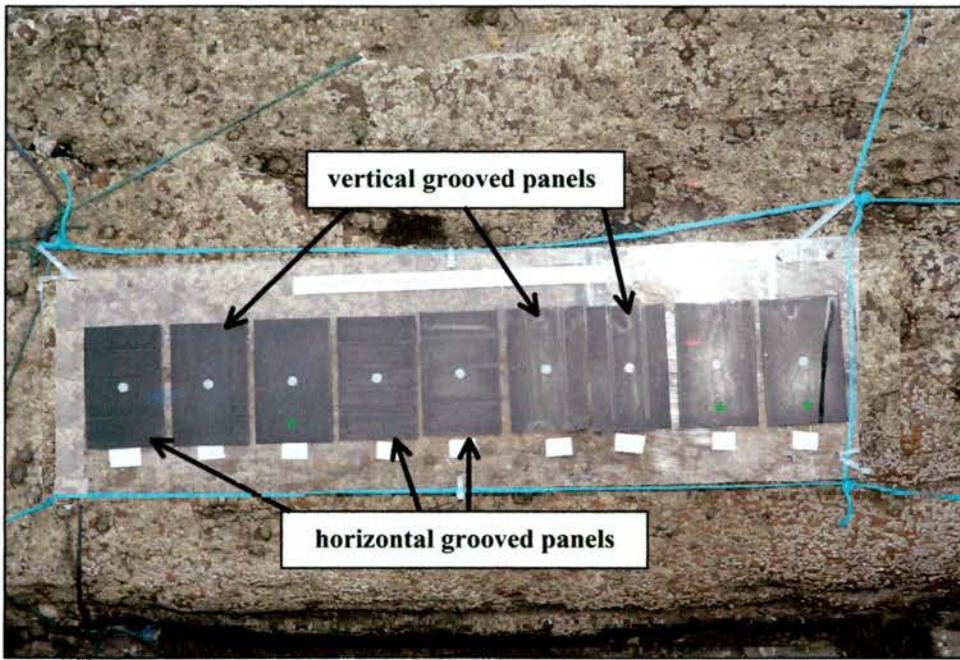


Fig. 27 – Site T panel set-up 2001; three horizontal grooved panels, three vertical grooved panels and three plane sanded panels (*), all painted with barnacle extract. Photograph taken between seasons, therefore the twine lattice is not secured as for experimental work. Backplates and mounting plates 79.5 x 24.0 x 0.6cm clear acrylic.

2. 6. 1. 3. *Third settlement season, year 2002*

2. 6. 1. 3. 1. *Sites C left, C right and D*

In the final settlement season it was decided that the vertical rock, which had in previous years provided Sites C–E, could accommodate an additional panel backplate adjacent to Site C. Therefore the original Site C was renamed Site C left, and the new adjacent backplate to its right was named C right. At C left and C right four multiple grooved panels (see 2. 1. 1. 3. 2.) and four plane sanded panels, all with extract, were deployed daily and tidally when necessary (Fig. 28). Again these were attached using nylon screws and wingnuts to 71.0 x 24.0 x 0.6cm clear acrylic mounting plates, which were then attached to backplates of the same dimensions in the field using 0.35cm width nylon cable ties. C left and right therefore provided replicate blocks at the one tidal height and these panels were sampled between the 19th of April and the 2nd of June, 2002.

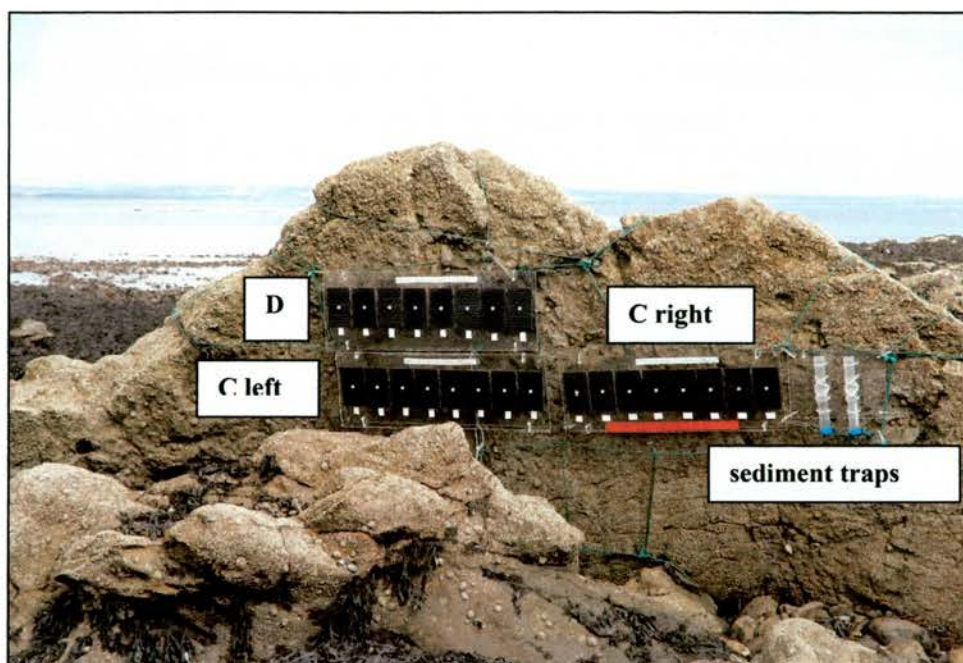


Fig. 28 – Sites C left, C right, D and sediment traps on a separate backplate at Kinkell Braes, 2002. Mounting plates and backplates was 71.0 x 24.0 x 0.6cm clear acrylic sheets, whereas the sediment trap backplate was 29.0 x 20.5 x 0.6cm clear acrylic sheets.

Site D was sampled between the 19th of April and 2nd June, as for C left and right, but panel composition changed during the season; from 19th April to the 10th of May four multiple grooved and four plane sanded panels with extract were deployed, whereas from the 11th May to the 2nd of June four multiple grooved panels with extract and four multiple grooved panels without extract were deployed (see Figs. 29a and 29b).

Sediment traps were attached with cable ties to a separate backplate for sampling in this final season (Fig.28). This was made from 29.0 x 20.5 x 0.6 cm clear acrylic and 0.7cm drilled holes in the backplate were used to attach the sediment traps to the backplate by using 0.35cm width nylon cable ties. These were then attached to the twine lattice in the field by using further cable ties. This enabled the sediment traps to be firmly secured and remained more rigid than if they had been independently secured to the twine lattice (Figs. 17a and 30).

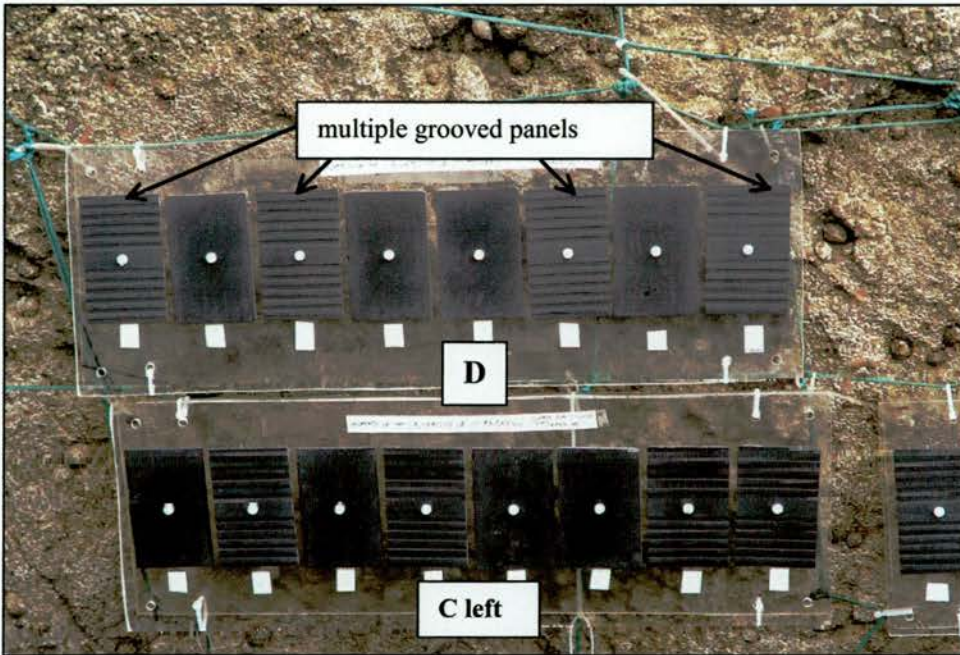


Fig. 29a – Sites C left and D at Kinkell Braes, 2002. Site D shows panel configuration used from the 19th April to the 10th of May; four plane sanded panels with extract and four multiple grooved panels with extract. Backplates and mounting plates are 71.0 x 24.0 x 0.6cm clear acrylic sheets.



Fig. 29b – Site D at Kinkell Braes, 2002, showing latter panel configuration of four grooved panels with extract (*) and four grooved panels without extract (no star). This panel combination was used from the 11th of May to the 2nd of June. Backplates and mounting plates are 71.0 x 24.0 x 0.6cm clear acrylic sheets.

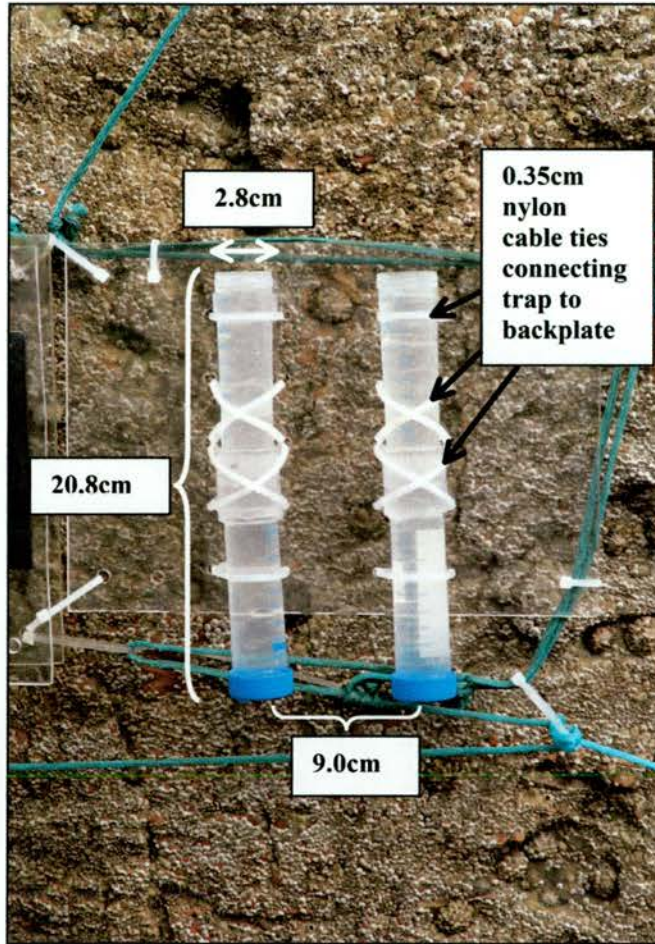


Fig. 30 – Sediment traps and backplates as used in the 2002 settlement season at all sites. Backplate is 29.0 x 20.5 x 0.6cm clear acrylic, to which the sediment traps are attached via 0.7cm drilled holes and 0.35cm width nylon cable ties.

2. 6. 1. 3. 2. *Site T*

Site T was used again in the final settlement year, see 2. 6. 1. 2. 2. for details. For the 2002 season, the backplates were extended to accommodate two larval traps at either end (107.0 x 27.0 x 0.6 cm clear acrylic), as seen in Figs. 31 and 32a. From the 19th of April to the 23rd of April panel sets of four multiple grooved panels and four plane sanded panels, all with extract, were deployed daily (see Figs. 31, 32a). From the 24th of April until the end of the season on the 2nd June the panel configuration was changed to four multiple grooved panels and four horizontally grooved panels daily (Fig. 32b). Larval traps were emptied at the same time as the panel set-up was

changed, with traps labelled 1-4 from the left to the right of the backplate, as viewed by the observer.

Three 5.0 x 5.0 cm quadrats on the natural substratum to the left, right and middle of the backplates, were counted and re-scrubbed each day from the 15th of May to the end of the settlement season. These were sampled daily at the same time as panels and traps were changed. No sediment traps were deployed at Site T in 2002, due to limited rock space.

5.0cm

107.0

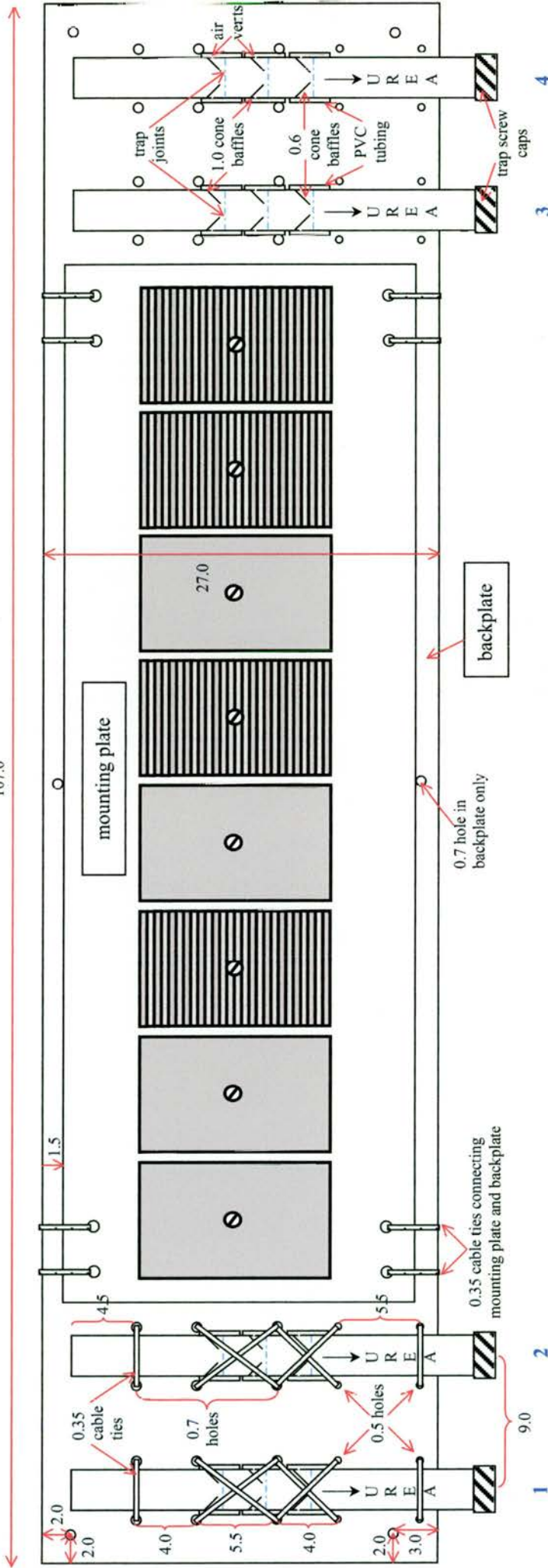


Fig. 31 – Extended backplate used in the third settlement year, incorporating four larval traps with mounted panels in the centre. The backplate with the larval traps remains in the field, while the mounting plate is changed daily by cutting and replacing cable ties. The two larval traps at the left of the diagram show cable tie positions, whereas they are not included on those on the right to display trap construction. The large section of PVC tubing that was used to encase each trap is also omitted, again to clearly show trap details. Mounting plate details as in Fig. 13.

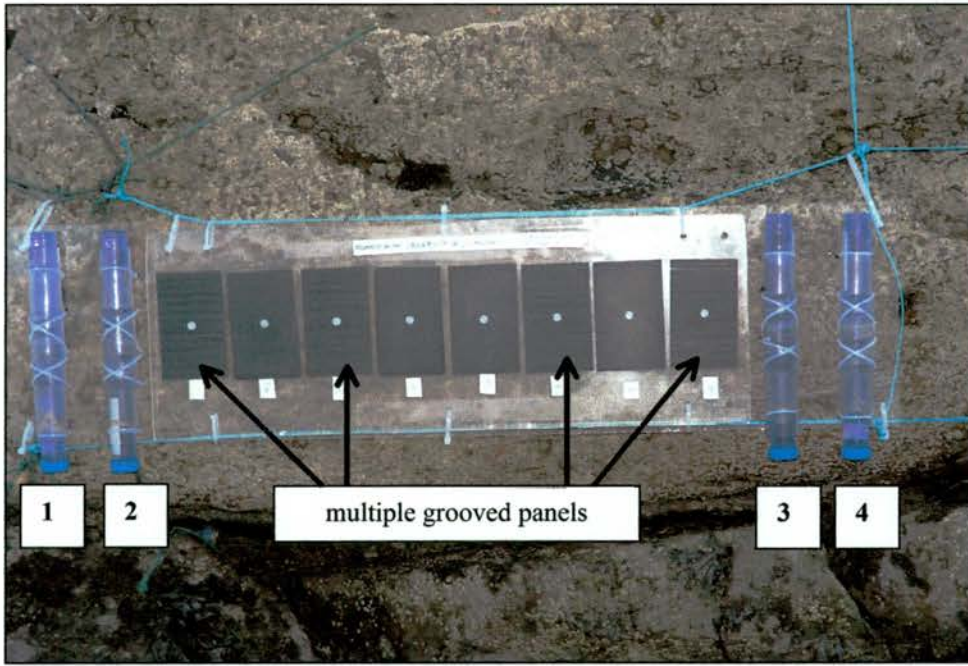


Fig. 32 a – Site T showing initial panel configuration used in 2002; four plane sanded panels and four multiple grooved panels, all painted with adult barnacle extract. Backplate 107.0 x 27.0 x 0.6cm clear acrylic.

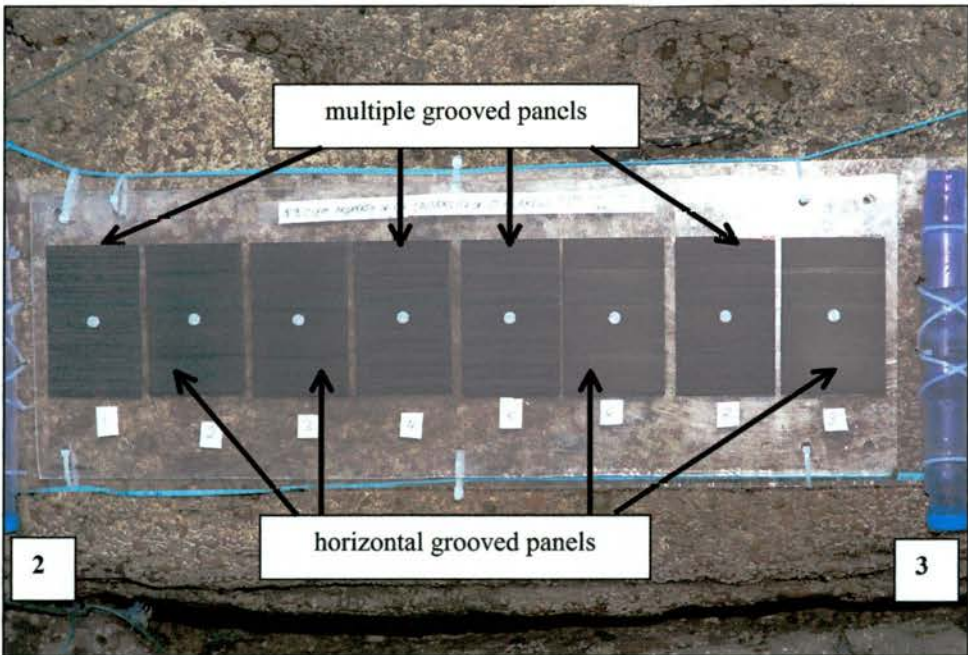


Fig. 32 b – Site T showing latter panel configuration used in 2002; four horizontally grooved panels and four multiple grooved panels, all painted with adult barnacle extract. Backplate 107.0 x 27.0 x 0.6cm clear acrylic.

2. 6. 2. Boarhills (56° 19.6'N 02° 42.1'W; OS Grid ref: 568 151)

The site chosen at Boarhills is a rocky intertidal area facing towards the northwest, with many vertical skerries running northeast to southwest. *Semibalanus balanoides* settlement is dense upon horizontal and vertical flat surfaces in the mid intertidal region, with sparser settlement on lower surfaces and large loose boulders on the bedrock. Sand and shingle collect in the little embayments between the skerries, while *Fucus* plants and filamentous green algae occur in the low intertidal with *Laminaria digitata* (Huds.) Lamour occurring further down the shore. Littorinid snails and limpets were common upon the rock faces. This experimental site was covered by every high tide, and has a mean and maximum spring tidal height of 4.8m and 6.0m respectively.

2. 6. 2. 1. First settlement season, 2000

Boarhills was only used in the first settlement season for studies, although plans had been made to return in the second year. The only access to the site was through farmland and fields of cows, and as the second sampled year coincided with the foot-and-mouth disease outbreaks it was not possible to use this site in that year. Subsequently another site was chosen further down the coast (2. 6. 3.), which proved to be of easier access and therefore Boarhills was not sampled again.



Fig. 33 – Sites H and I, immediately adjacent to one another, at Boarhills. For scale, combined backplates are 142cm in width.

2. 6. 2. 1. 1. *Sites H and I*

Sites H and I were monitored with two ‘blocks’ of panels, immediately adjacent to each other in the mid intertidal region of the shore (Fig. 33). The panels faced southeasterly, and were therefore protected from any direct wave action, on a sloping triangular faced rock with a vertical front section (~2.7m wide, 0.7m high). Immediately in front of the rock harbouring the panels was a large flat rock (Fig. 34); both were densely covered with previous *Semibalanus balanoides* settlement. For each experimental block four plane sanded panels painted with extract, and four sanded panels without extract were deployed daily (or tidally when necessary), and *in situ* counts were made after one tidal exposure. Panels were mounted onto 71.0 x 24.0 x 0.6cm clear acrylic sheets, as in Fig. 13, using 0.6cm nylon screws and wingnuts and were then cable-tied to acrylic backplates of the same dimensions attached to 0.6cm nylon twine around the rocks (Fig. 34). Panels were deployed at Site H

between 19th May am and the 4th June pm, while panels at Site I ran between the 19th May am and the 24th of May pm.

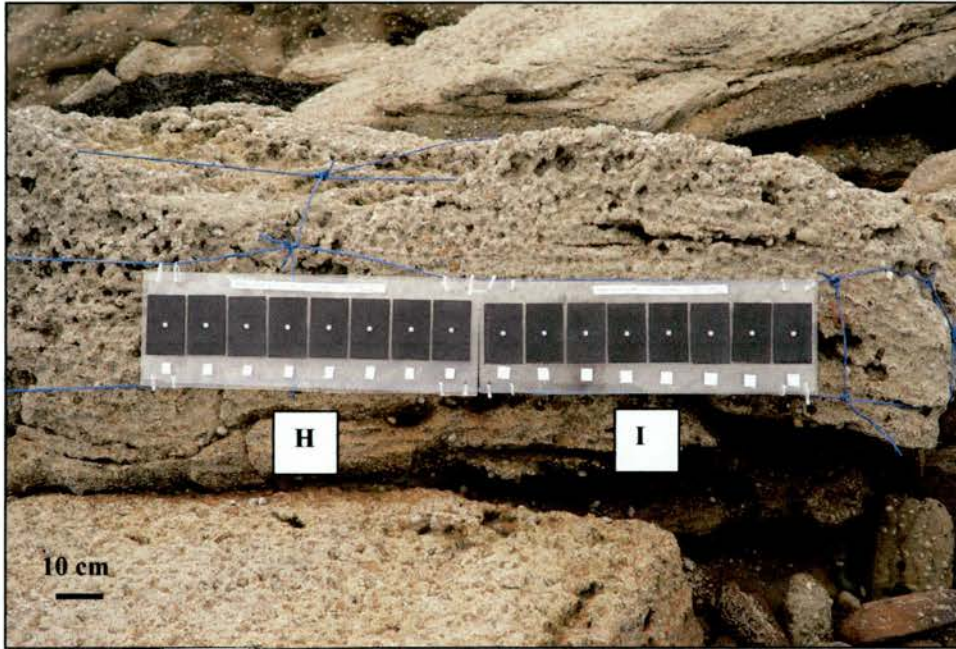


Fig. 34 – Sites H and I deployed at the field site in Boarhills, 2000. Four plane sanded panels painted with extract and four plane sanded panels without extract were daily exposed to settlement.

As can be seen in Fig. 34 no sediment or larval traps were deployed at this site, nor were any settlement quadrats cleared and monitored.

2. 6. 3. *Cambo, Kingsbarns* (56° 18.3'N 02° 38.7'W; OS Grid ref: 603 128)

The Kingsbarns site was similar to that of Boarhills, being a rocky intertidal site with vertical skerries running northeast to southwest, separated by small shingle and sand bays. *Semibalanus balanoides* settlement is dense, almost at 100%, on most rocks in the intertidal, again with limpets and littorinids also being present. *Fucus* plants were more abundant here on the lower intertidal rocks than at Boarhills, with *Laminaria digitata* (Huds.) Lamour as the dominant kelp species on the infralittoral fringe. The

chosen site has mean and maximum tidal amplitudes of 4.8m and 6.0m respectively, and is covered by every high tide.

2. 6. 3. 1. Second settlement season, 2001

2. 6. 3. 1. 1. Sites L and M

A vertical-faced mid intertidal rock ~ 1.5m wide and ~0.6m high, projecting ~2.0m from the bedrock was chosen as a site to accommodate two adjacent backplates, each 71.0 x 24.0 x 0.6cm in size and made from clear acrylic. Each backplate held eight 13.0 x 8.0 x 0.6cm black acrylic panels and were changed daily or tidally when necessary. The panel sets faced NNW and were therefore unprotected from wave exposure, with a horizontal flat section of rock ~ 2.0m wide in front. The centre of the panels is 3.1m above chart datum and therefore the panels were covered by water at each high tide (Fig 35a).

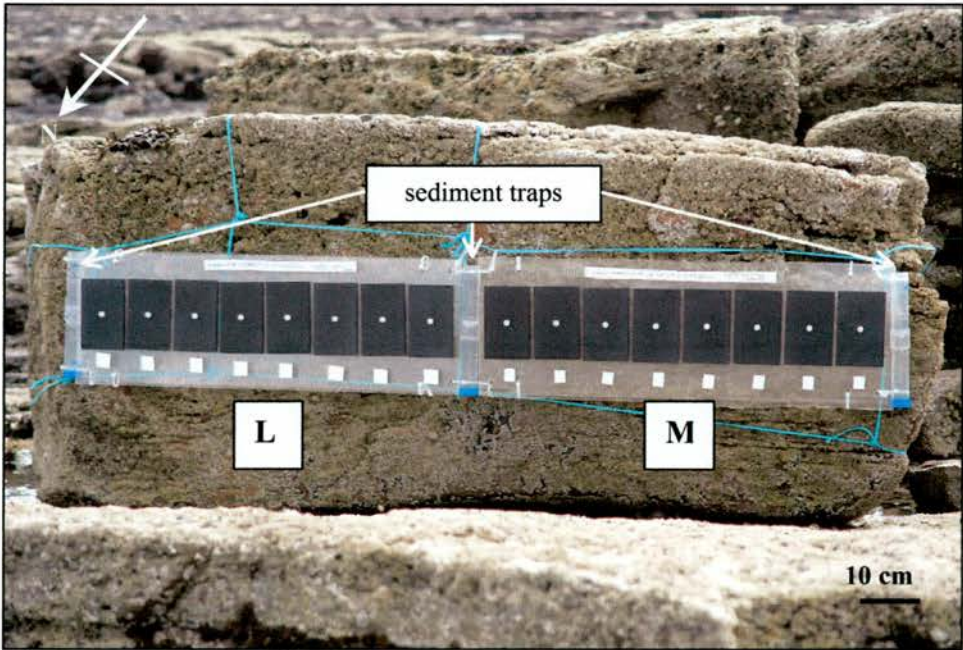


Fig. 35a – Sites L and M at Kingsbarns, in 2001 initial panel configuration. Three sediment traps were also deployed at this site.

Site L was sampled between the 22nd of April and the 6th of June, 2001, with four sanded panels with extract and four sanded panels without extract. At Site M four sanded panels with extract and four without were exposed for settlement between the 22nd April and the 19th of May. Thereafter the panel composition was changed to two horizontally grooved panels with extract, two vertically grooved panels with extract, two sanded panels with extract and two sanded panels without extract. This panel set-up was maintained until the end of the season on June 6th (Fig, 35b).

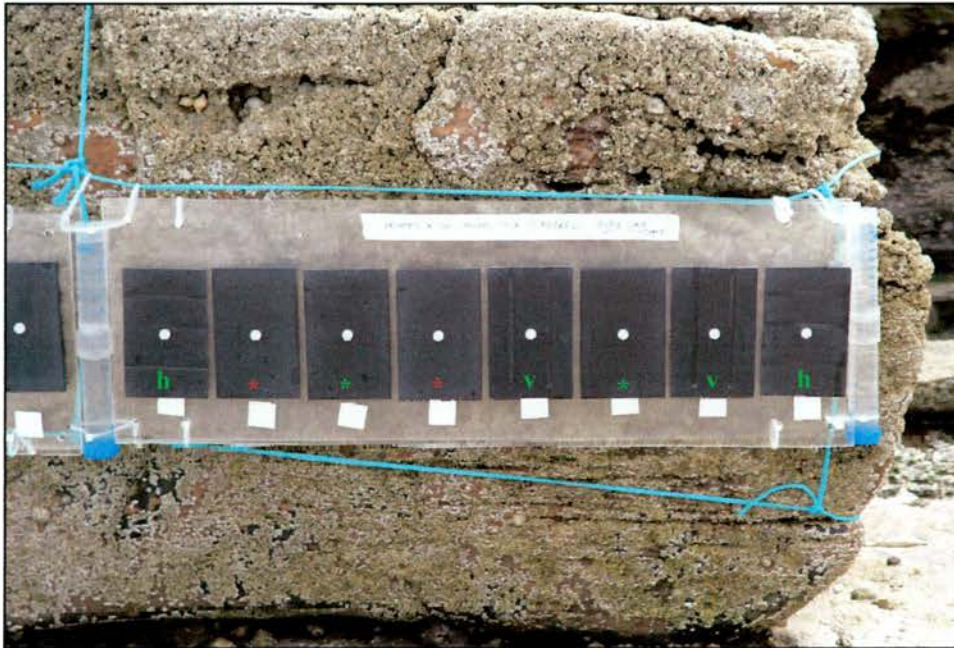


Fig. 35b – Site M at Kingbarns with panel composition as used for the second half of the 2001 season (20th May to June 6th). Two plane panels with extract (*), two plane panels without extract (*), two horizontal panels with extract (h) and two vertical panels with extract (v).

Sediment traps were also deployed at this site, attached using 0.35cm width nylon cable ties to the panel backplates and nylon twine around the rock. These were emptied and refilled with fresh seawater each time the mounting plates were changed; care was taken to ensure all sediment was washed into the collection pots each time they were emptied.

2. 6. 3. 2. *Third settlement season, 2002*

2. 6. 3. 2. 1. *Site L/M*

In the final settlement season the rock previously used in 2001 to accommodate Site L and M panels was integrated into a single site, named L/M. In this final year larval traps were also deployed at this site, and therefore an extended backplate was used; because available rock space was limited, only one set of panels could be attached at this site (Fig. 36). Four plane sanded panels and four multiple grooved panels, all painted with adult barnacle extract, were attached to a 71.0 x 24.0 x 0.6cm clear acrylic mounting plate using nylon wing nuts and screws as before. This mounting plate was in turn attached to a permanently fixed backplate in the field (107.0 x 27.0 x 0.6cm clear acrylic), using 0.35cm width nylon cable ties (see Fig. 31). Four larval traps, labelled 1 to 4 from the left to right, were attached to the extended backplate. These were carefully emptied into collection pots whenever the panel sets were changed in the field. In addition to the eight panels and larval traps, two sediment traps were located at the left of Site L/M, attached to the nylon twine via a 29.0 x 20.5 x 0.6cm clear acrylic backplate (Figs. 17b and 36).

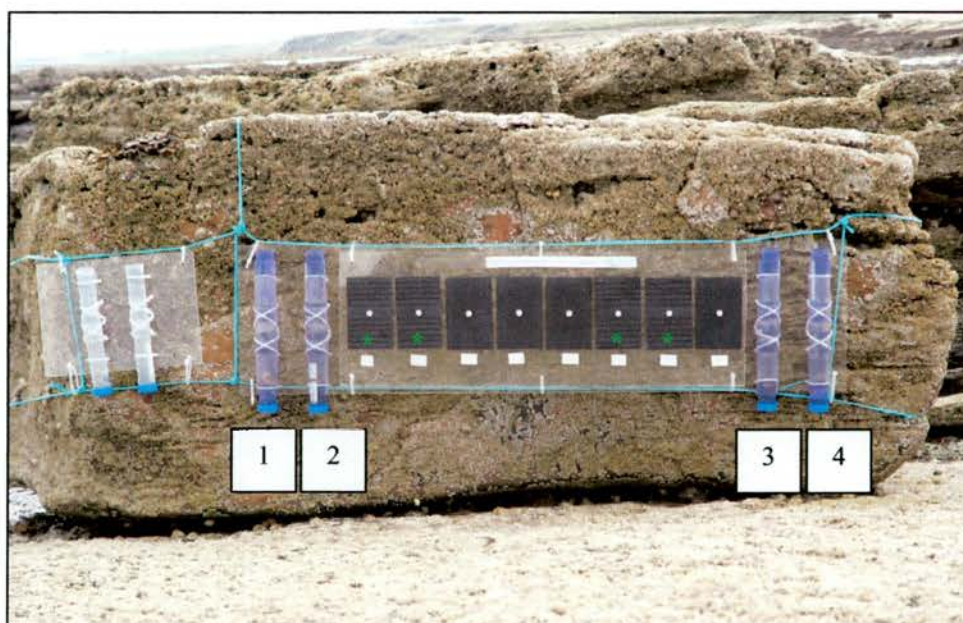


Fig. 36 – Site L/M as used in the third settlement season in 2002. Four larval traps and two sediment traps are fixed to backplates, with four multiple grooved panels (*) and four plane panels all painted with adult extract are attached to the mounting plate. Extended backplate 107.0 x 27.0 x 0.6cm, for scale.

This site was sampled between the 19th of April and the 29th of May 2002. Unfortunately this site was vandalised on two occasions, May 19th and May 21st, which resulted in lost or partial data. Additionally as the vandalism occurred at periods where more people accessed the beach, it was decided not to deploy any panels or traps for the weekend of the 24th of May to the 26th of May.

Three settlement quadrats were cleared on the 14th of May at the left, middle and right of the backplate at the same height as the panels (25cm² area). These were counted and cleared whenever the panels were sampled, using fine forceps to remove the cyprids as they were counted. The areas were then scrubbed with a stiff toothbrush and rinsed in clean seawater. These were sampled until the 8th of June, except for the 21st of May where quadrats had been damaged by vandalism.

2. 6. 3. 2. 2. *Site Beta*

As the rock where Site L/M could only accommodate one set of panels, another site was chosen ~1.5m to the left of L/M. This rock was ~ 2.0m from the bedrock and projected out over one of the embayments between the skerries, and the vertical face to which the panels were attached was ~1.5m wide and ~0.7m high. Named Site Beta, the panel block attached here was at the same approximate tidal height as Site L/M, with a northwesterly direction and was subject to wave exposure (Figs. 37 and 38).

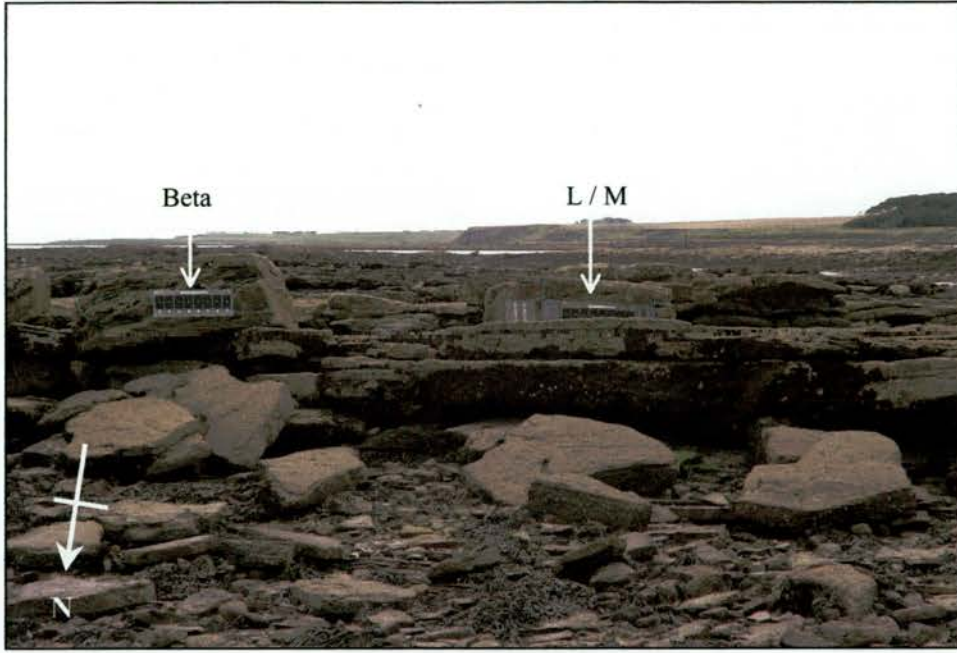


Fig. 37 – Sites L / M and Beta at Kingsbarns, 2002. Beta backplate 71.0 x 24.0 x 0.6cm, for scale.

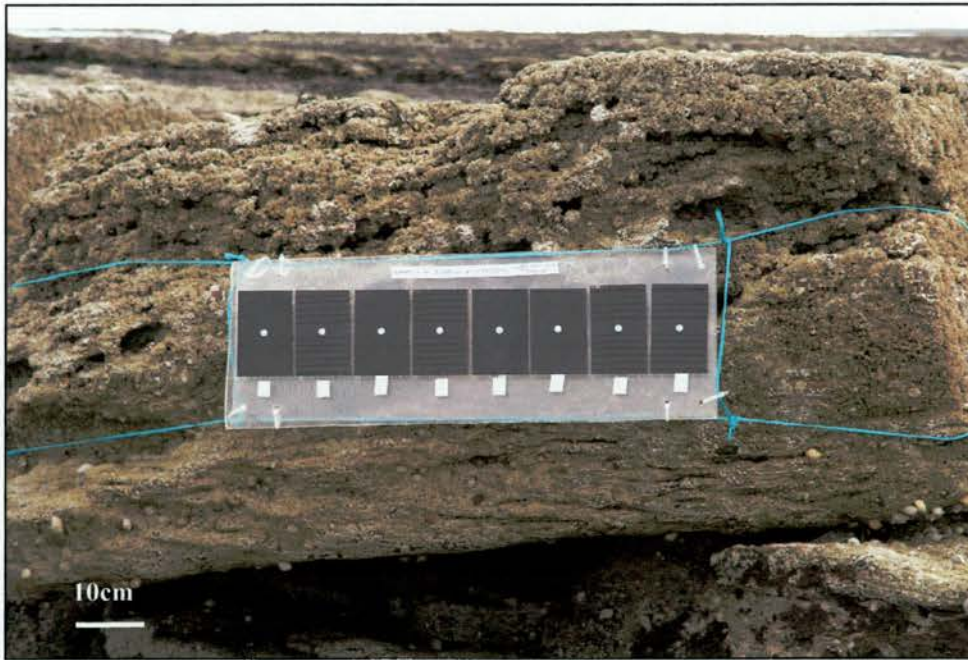


Fig. 38 – Site Beta at Kingsbarns, 2002. Four multiple grooved panels and four plane sanded panels, all painted with extract were deployed daily. Beta backplate 71.0 x 24.0 x 0.6cm, for scale.

Throughout the season four multiple grooved panels and four plane sanded panels, both painted with extract, were put in the field for settlement studies on a daily or tidal basis. Site Beta was sampled between the 19th of April and the 29th of May, as for Site L/M, but no larval or sediment traps were deployed here, nor quadrats

cleared. Additionally, due to its close proximity to L/M it also was vandalised on the 19th and 21st of May, and again panels were not deployed over the weekend of 24th – 26th May.

2. 6. 4. Fife Ness (56° 16.7'N 02° 35.2'W; OS Grid ref: 639 097)

Fife Ness is located on the most easterly point of Fife, called the East Neuk. This promontory is exposed to winds from the northwest to southwest, whereas winds from the WNW to WSW will provide calmer waters. This is a rocky intertidal site, with areas of flat bedrock between higher rocky outcrops. Unlike Boarhills and Kingsbarns, no sand or shingle is found here, with the bedrock being occupied by dense *Fucus serratus* (L.) plants. At the end of the rocky promontory the rocks steeply drop into deep water, where dense kelp beds are found (*Laminaria digitata* (Huds.) Lamour is the most dominant species). Large tidal pools are common, filled with littorinid snails and filamentous green algae. The many vertical rock surfaces in the mid intertidal were dominated by *Semibalanus balanoides* settlement, on average comprising approximately 40-50% in coverage. Mean and maximum spring tidal amplitudes are 4.8m and 6.0m respectively, with all experimental sites covered by each high tide.

2. 6. 4. 1. Second settlement season, 2001

2. 6. 4. 1. 1. Sites J and K

Sites J and K were located on a mid intertidal rock with a vertical face ~1.5m wide by 0.7m high and facing due east. Two backplates were attached to nylon twine cords, tension-tied around the rock (each 71.0 x 24.0 x 0.6cm clear acrylic). Onto these

backplates two mounting plates were cable-tied, as were three sediment traps at the left, middle and right sides of the panel backplates. These traps were tied at the same height as the panels. Approximately 1.5m in front of the panels is a large tidal pool, separated from the study plates by flat bedrock. At the height of the screw holes in the panels, this site was 3.5m above chart datum and covered at each high tide.

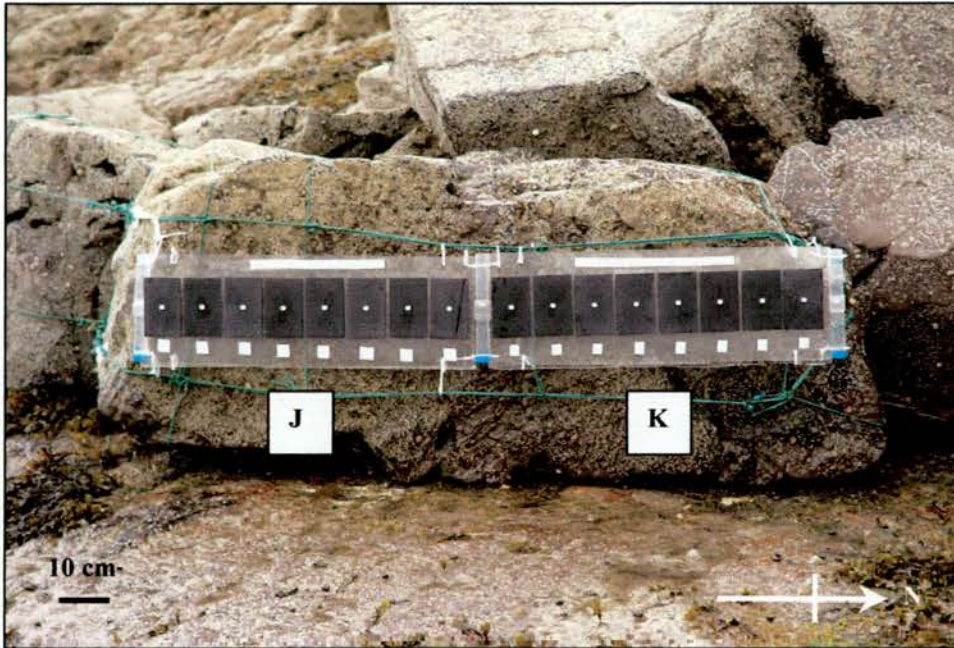


Fig. 39 – Settlement study Sites J and K at Fife Ness, 2001. Four plane panels painted with extract and four without are shown on each mounting plate with sediment traps located in the middle and at either end of the backplates.

At Site J four plane sanded panels with painted extract and four plane sanded panels without extract were attached to mounting plates and daily put out in the field between the 22nd of April and the 6th of June. Initially at Site K four plane panels with and without extract were deployed, but from the 20th of May until the 6th of June the panel set composition was changed to two horizontally grooved panels with extract, two vertically grooved panels with extract, two plane sanded panels with extract and two plane sanded panels without extract (Fig. 40).

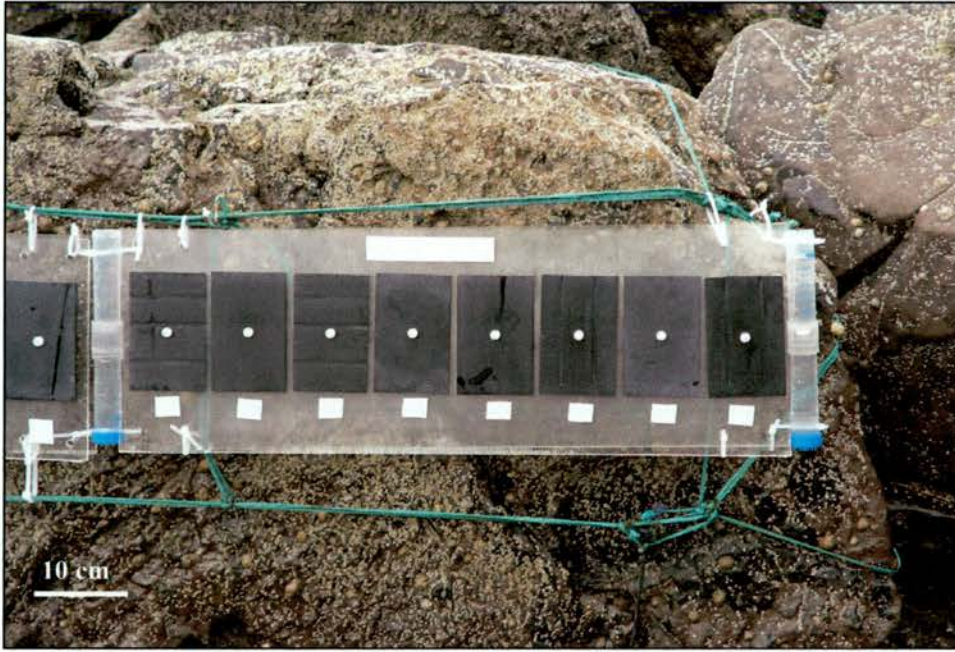


Fig. 40 – Site K at Fife Ness with panel composition as used for the second half of the 2001 season (20th May to June 6th). Two plane panels with extract (*), two plane panels without extract (*), two horizontal panels with extract (h) and two vertical panels with extract (v).

Sediment traps were emptied each time the mounting plates were exchanged, and refilled again with clean fresh seawater.

2. 6. 4. 2. *Third settlement season, 2002*

2. 6. 4. 2. 1. *Site J / K*

In the final settlement season, extended backplates were used to incorporate larval traps alongside the black acrylic panels (Fig. 31). Therefore a 107.0 x 27.0 x 0.6cm clear acrylic backplate with four attached larval traps was cable-tied onto the nylon twine tightly tied around the rocks. These were labelled 1-4, from left to right and were carefully emptied and refilled when panels were daily exchanged in the field. Four multiple grooved panels and four plane sanded panels, all painted with extract, were daily deployed at Site J / K from the 19th of April until the 2nd of June.

Additionally two sediment traps were cable-tied to a 29.0 x 20.5 x 0.6cm clear acrylic backplate, which was then attached to the nylon ropes at the end of the rock nearest to left (Fig. 41). Three settlement quadrats (25cm² sampled area) were cleared to the left, middle and right of the backplate and were sampled between the 14th of May and the 8th of June. Each time the panels were changed over the settlement quadrats were counted and cyprids removed using fine forceps. The areas were then scrubbed with a stiff toothbrush and rinsed in clean seawater.

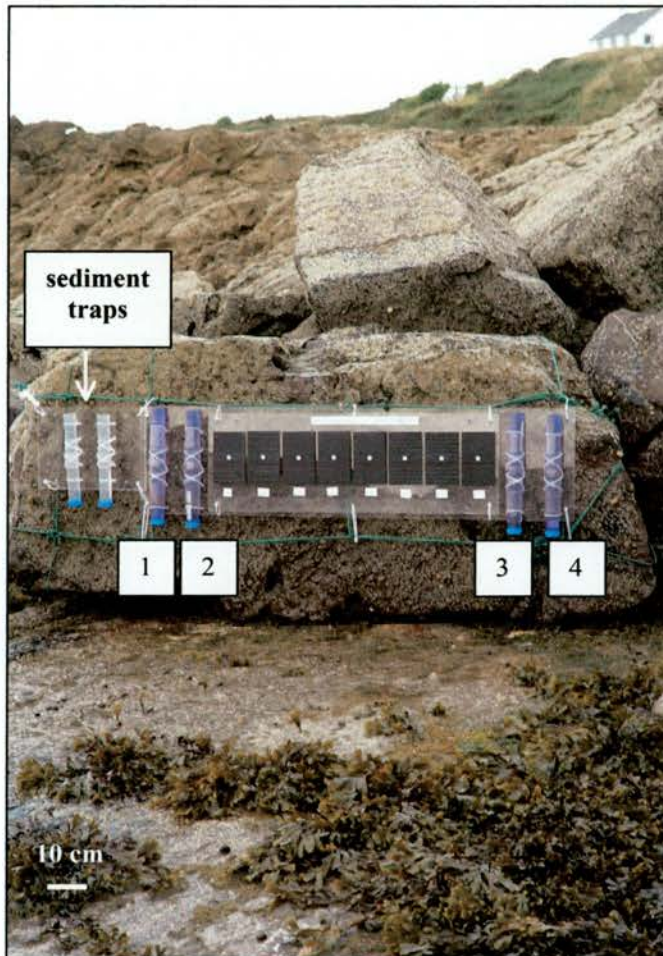


Fig. 41 – Extended backplate incorporating four multiple grooved panels, four plane panels and four larval traps used at Site J / K in 2002. To the left of the picture two sediment traps are attached to a separate, smaller backplate.

2. 6. 4. 2. 2. *Site Alpha*

As an extended backplate had been used at Site J / K, another set of panels could not be deployed at this site owing to there not being enough free rock space available. Therefore another nearby site was located, named Alpha, on the boulder adjacent to J / K but ~50cm further upshore, again facing towards the east and with no protection from wave crash (Fig. 42). Here four multiple grooved panels and four plane sanded panels, all with extract, were deployed daily, and tidally when necessary. Because this rock was approximately 74cm wide by 68cm in height, only the panel backplate could be housed here, thus no larval or sediment traps were attached at this location.

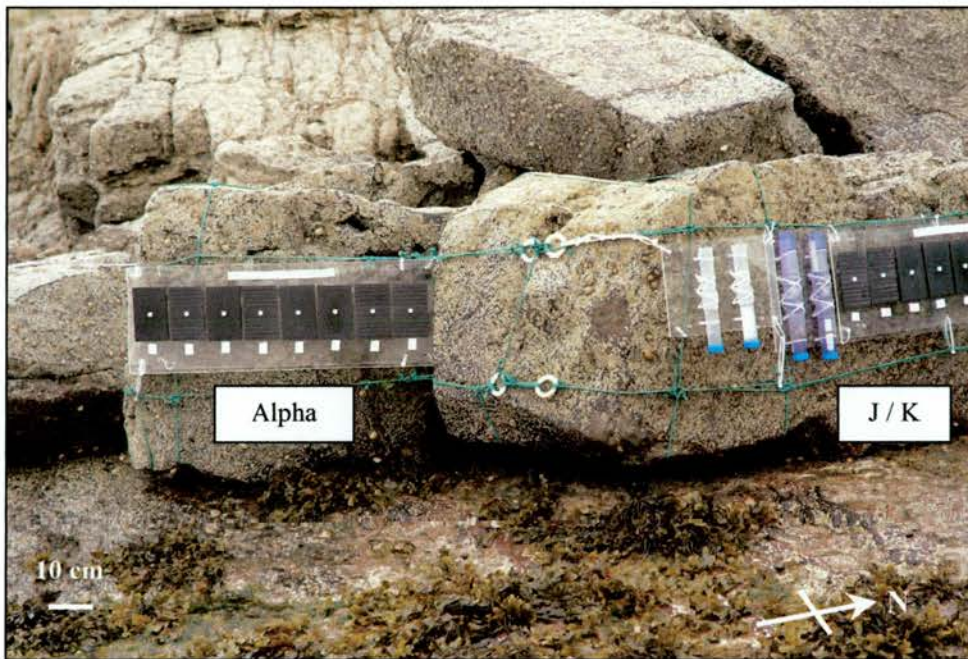


Fig. 42 – Site Alpha at Fife Ness, located approximately 50cm behind Site J / K, which was used in the final settlement season of 2002.

Panels were carefully placed at the same tidal height as J / K, and were therefore also 3.5m above chart datum and covered by each high tide. This site was sampled between the 19th of April and the 2nd of June in 2002.

2. 7. *Wind data*

For the first settlement season in 2000, wind median and maximum gust direction (°) and median and maximum speed (knots) were kindly provided by the Central Climate Unit of the Met Office from their Leuchars station (56°38'N 02°86'W; OS Grid Ref: 346 7209N; 10m altitude). Hourly averages were then used to calculate predominant wind directions with median and maximum force for each sampling period. In the subsequent settlement years wind strength (ms^{-1}) and direction were recorded using a 1-Wire™ Weather Instrument Kit V3.0 (Tecnología Aplicada, Mexico), which was mounted on the roof of the laboratory, located approximately 500m from the Kinkell Braes settlement sites. Data were logged every 10 minutes as averages for that period, and wind direction with its median and maximum strengths over each sampling frequency were derived. Wind strength data were converted into Beaufort Scale because this provided a standardised descriptive scale of wind velocity that is linked to sea state.

2. 8. *Data analyses*

All data were checked for normality using Kolmogorov-Smirnov normality tests and homogeneity of variances were checked using Barlett, Levene's and F-ratio tests where necessary. All cyprid counts of panels, traps and quadrats were $\log x + 1$ transformed prior to ANOVA and regression analysis, with urea percentage retention data requiring arcsine transformation before use in analysis. Factorial ANOVAs included panel treatments (extract, panel texture) as fixed factors, with Site and Day being considered random. Nested GLM ANOVAs included groove and panel half as fixed factors, again with Site considered random. Where interactions occurred, S-N-K and Tukey tests were used to determine its source and aid in the determination of

main effects (Underwood 1997; Quinn and Keough 2002). ANCOVA was used for comparison of supply and settlement relationships between sites. Further details of analyses used will be provided in the results text.

Summary Table 1 – Panel composition and sample information for each site through the three settlement seasons.

Year	Site	Panel type and replication	Dates sampled
2000	A and B (St Andrews)	4 sanded plane with extract 4 sanded plane without extract	06/05 – 09/05
	C (St Andrews)	4 sanded plane with extract 4 sanded plane without extract	06 + 07/05, 10/05 – 26/05, 30/05 – 04/06
	C (St Andrews)	4 sanded plane with extract 2 unsanded plane with extract 2 unsanded plane without extract	07/05 – 10/05
	D (St Andrews)	4 sanded plane with extract 4 sanded plane without extract	09/05 – 24/05
	E (St Andrews)	4 sanded plane with extract 4 sanded plane without extract	09/05 – 24/05
	F and G (St Andrews)	4 sanded plane with extract 4 sanded plane without extract	09/05 – 15/05
	Site H (Boarhills)	4 sanded plane with extract 4 sanded plane without extract	19/05 – 04/06
	Site I (Boarhills)	4 sanded plane with extract 4 sanded plane without extract	19/05 – 24/05
2001	C and D (St Andrews)	4 sanded plane with extract 4 sanded plane without extract	22/04 – 02/06
	E (St Andrews)	4 sanded plane with extract 4 sanded plane without extract	27/04 – 13/05
	T (St Andrews)	3 sanded plane with extract 3 sanded horizontal grooved with extract 3 sanded vertical grooved with extract	04/05 – 06/06
	Site J (Fife Ness)	4 sanded plane with extract 4 sanded plane without extract	22/04 – 06/06
	Site K (Fife Ness)	4 sanded plane with extract 4 sanded plane without extract	22/04 – 19/05
	Site K (Fife Ness)	2 sanded plane with extract 2 sanded plane without extract 2 sanded horizontal grooved with extract 2 sanded vertical grooved with extract	20/05 – 06/06
	Site L (Kingsbarns)	4 sanded plane with extract 4 sanded plane without extract	22/04 – 06/06
	Site M (Kingsbarns)	4 sanded plane with extract 4 sanded plane without extract	22/04 – 19/05
	Site M (Kingsbarns)	2 sanded plane with extract 2 sanded plane without extract 2 sanded horizontal grooved with extract 2 sanded vertical grooved with extract	20/05 – 06/06
2002	C left and C right (St Andrews)	4 sanded plane with extract 4 sanded multiple grooved with extract	19/04 – 02/06
	D (St Andrews)	4 sanded plane with extract 4 sanded multiple grooved with extract	19/04 – 10/05
	D (St Andrews)	4 sanded multiple grooved with extract 4 sanded multiple grooved without extract	11/05 – 02/06
	T (St Andrews)	4 sanded plane with extract 4 sanded multiple grooved with extract	19/05 – 23/04
	T (St Andrews)	4 sanded horizontal grooved with extract 4 sanded multiple grooved with extract	24/04 – 02/06
	Sites J / K and Alpha (Fife Ness)	4 sanded plane with extract 4 sanded multiple grooved with extract	19/04 – 02/06
	Sites L / M and Beta (Kingsbarns)	4 sanded plane with extract 4 sanded multiple grooved with extract	19/04 – 29/05 (minus 19/05 + 21/05 vandalism, 24-26/05)

CHAPTER 3

RESULTS



3. Results

3. 1. First settlement season, 2000

As mentioned in 2. 1. 1. 5., for analysis tidal data was pooled into daily data to avoid potential non-independence of results in the 2000 season at all sites.

3. 1. 1. Kinkell Braes, 2000

3. 1. 2. Sites A and B

Although Sites A and B were initially chosen as experimental locations, very poor levels of settlement were observed when compared to Site C (Fig. 43, Table 1).

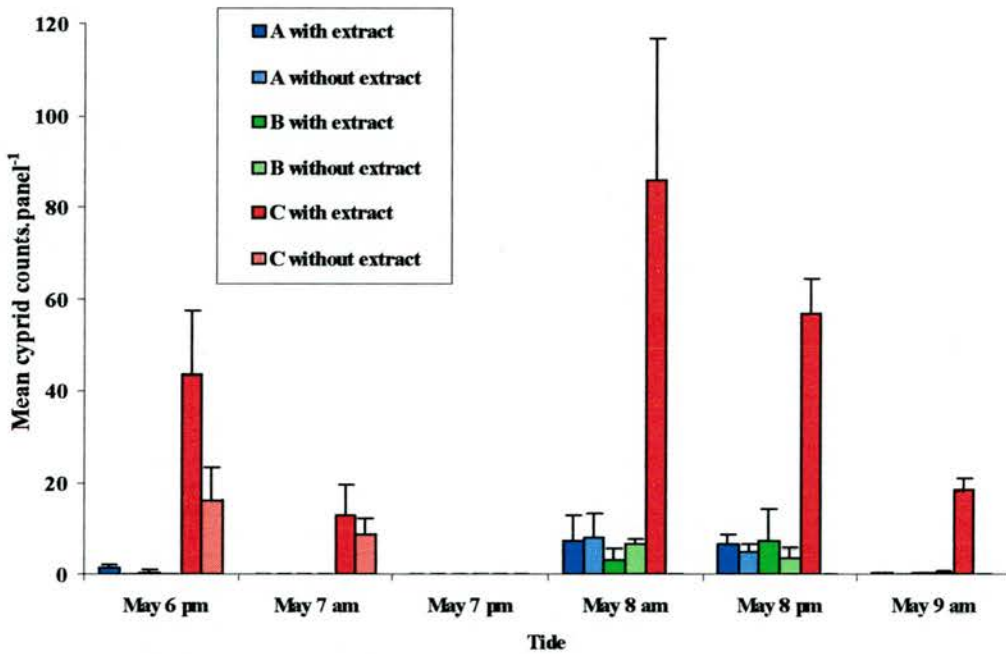


Fig. 43 – Observed tidal *S. balanoides* cyprid settlement at Sites A, B and C at Kinkell Braes for a six tide period, from May 6th pm to May 9th am. No counts were made May 7th pm, n=4 for each bar observation with vertical lines representing S.E.M.

Site C was found to have consistently higher settlement over the tidal period studied. For example, while Site C had a mean settlement of 86 ± 31 cyprids for panels with extract sites on the May 8th am tide, Sites A and B had means of 7 ± 6 and 3 ± 2 larvae respectively for the same panel treatment. Different numbers of cyprid settlers were seen on each tide, as expected, due to variance in larval flux. ANOVA analysis of daily recorded cyprid counts on positive panels across the sites (Table 1) confirmed

that Site was significant, Day was not significant and with no significant interaction between the two factors over this time period.

Table 1
Settlement panels: site and daily comparisons

Source	<i>df</i>	SS	MS	<i>F</i>	<i>p</i>
Site	2	13.130	6.564	93.03	<0.001
Day	2	0.793	0.400	5.62	0.069
Site x Day	4	0.282	0.071	0.31	0.866
Error	27	6.072	0.225		
Total	35	20.277			

ANOVA for cyprids (log $x+1$) settlement on panels with extract. Both factors Site and Day were random.

A Scheffe test for comparisons ($\alpha = 0.05$) of the sites revealed that Site C was significantly different to Site A and B ($p < 0.001$), while Sites A and B were not different to one another ($p = 0.276$). It is likely that local hydrodynamics around the triangular-shaped rock upon which Sites A and B were located is responsible for the reduced settlement observed (Fig.19).

3. 1. 3. Sites C, D and E.

The mid-intertidal Site C was sampled from May 6th pm to May 26th am, and then from May 30th pm to June 4th; the settlement season had effectively finished by May 26th, with only one cyprid settling on May 31st during the second sampling period. Observed settlement began during this 2000 season on the 19th April, but due to preliminary experimentation using other settlement panels, Site C was not sampled until the 6th May pm. Therefore although two main peaks of settlement are seen in this year (Fig. 44), the presence or absence of any larger settlement periods remains unknown. The first observed settlement peaks occurs between the May 6th pm – to May 9th pm, reaching a mean maximum of 86 ± 31 cyprids per panel with extract on May 8th am with a Beaufort Force 2 N wind. The second, and larger, settlement peak begins on the 14th May am tide and finishes on the May 17th am with a maximum

observed mean settlement of 191 ± 37 cyprids on panels with extract on the May 15th am tide. This peak occurs after a six-tide period of predominant winds from the N or NNE (11th am – 14th am May), and ceases when the wind turns to the WSW on May 17th pm. Settlement panels with extract are consistently higher than those without painted extract, except for settlement on May 15th pm where mean cyprid counts were 181 ± 28 on panels without extract compared to a mean count of 164 ± 41 on panels with extract. The May 15th am tide represents an *in situ* count, whereas the pm tide was a final count after the panels had been exposed to two tides in the field. Therefore it is probable that the high settlement seen on the first tide on panels with extract (i.e. preferred substratum) may have caused cyprids to select the unpainted panels due to lack of available space, or the presence of conspecifics in the nearby area was sufficient to promote settlement.

Site D was located in the upper intertidal above Site C and was sampled from the 9th May pm and the 24th May pm inclusive (Fig. 45). One main peak of settlement was observed during this season, from the 14th May am tide to the 17th May pm, which correlated with the main peak at Site C. The maximum mean settlement occurred on May 15th pm, where panels without extract (553 ± 78) had higher numbers of cyprid settlers than those with extract (454 ± 27). This peak occurred after a period of N / NNE winds, and settlement dropped sharply with the change of wind direction to the WSW on the 17th May pm. Again as for Site C, the May 15th pm tide was a final settlement count, not an interim settlement count after one tide, therefore the high settlement at Site C during the previous (*in situ*) count may have stimulated settlement at Site D through the presence of conspecifics or lack of available space at Site C. Higher settlement on unpainted panels is also seen on the 14th May pm, 202 ± 30

compared to 150 ± 73 cyprids, which again may be related to increased settlement at Site C for the corresponding period (129 ± 15 settlers with extract, 118 ± 8 settlers without extract).

Site E was located in the lower intertidal, directly beneath Site C, and was sampled between May 9th pm and the 24th May pm inclusive. Only one main settlement peak was seen, from May 14th am to May 16th am, therefore corresponding to the settlement peak seen at Sites C and D, and occurring after the six tides of predominant NE / ENE winds from the 11th am to the 14th May am (Fig. 46). Settlement counts were much lower at this Site E with the maximum tidal average of 41 ± 12 cyprids occurring on panels with extract at the 15th May pm tide; for this same tide and panel type recorded tidal average counts were 164 ± 41 and 454 ± 27 settlers at Sites C and D respectively. Again observed settlement greatly decreased from May 17th pm (predominant WSW winds) until the end of the sampled period.

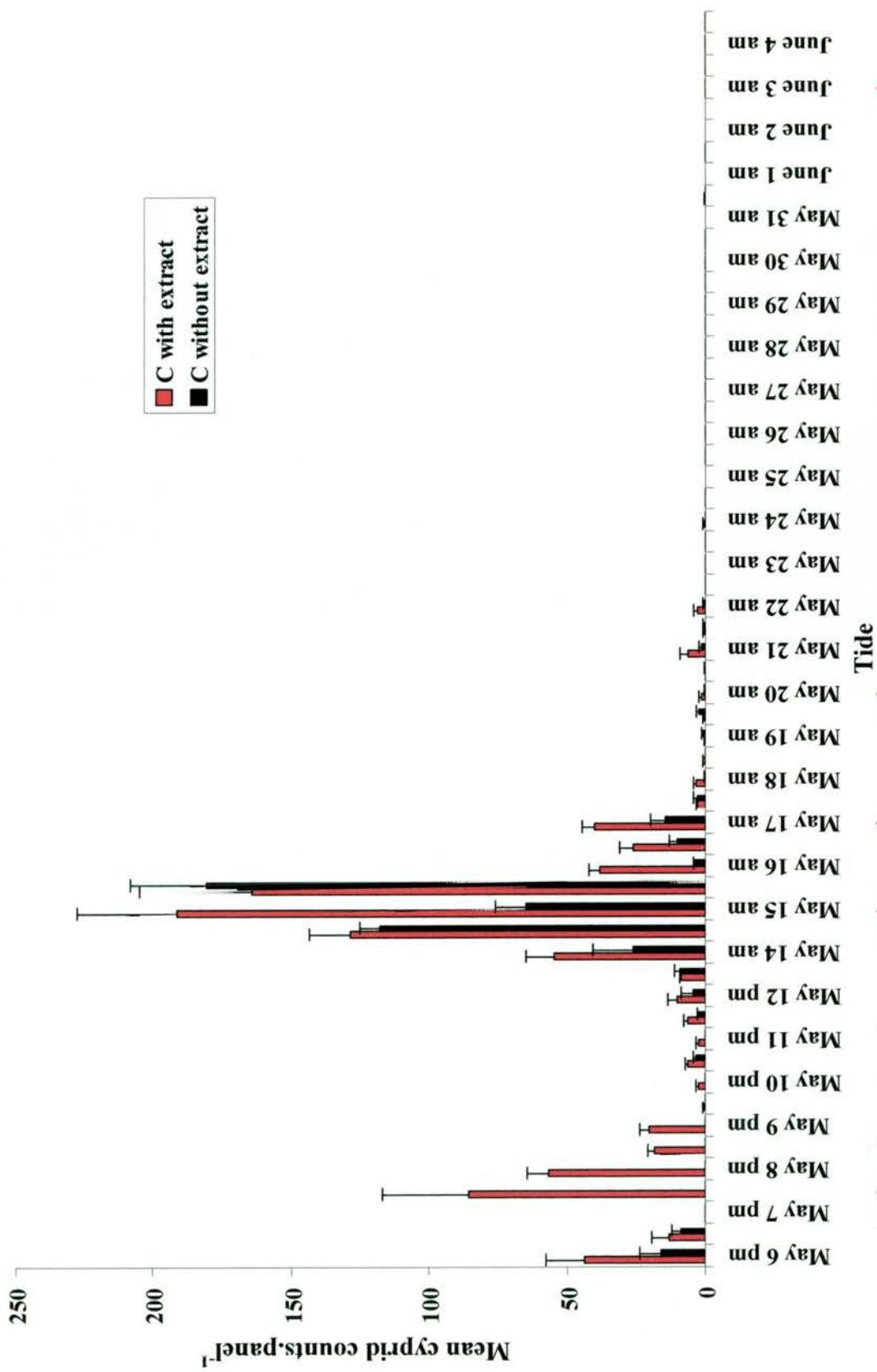


Fig. 44 – Mean tidal settlement of *S. balanoides* cyprids on plane panels, with and without extract, at Site C during the 2000 season. n=4 for each bar observation, with vertical lines representing S.E.M. Wind data shown as maximum Beaufort strength and predominant direction over each tidal period, calculated from hourly averages.

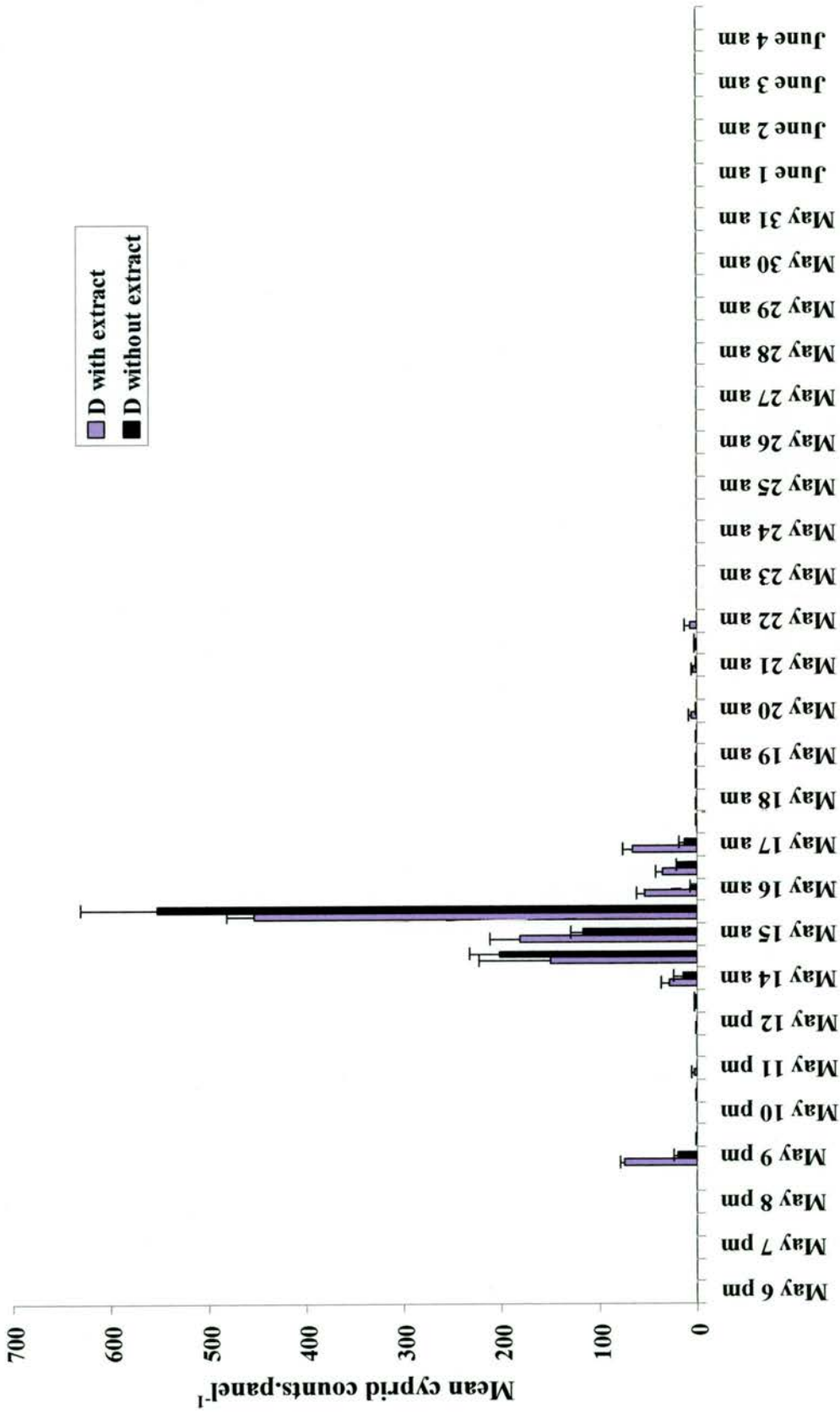


Fig. 45 – Mean tidal settlement of *S. balanoides* cyprids on plane panels, with and without extract, at Site D during the 2000 season. n=4 for each bar observation, with vertical lines representing S.E.M. Wind data shown as maximum Beaufort strength and predominant direction over each tidal period, calculated from hourly averages.

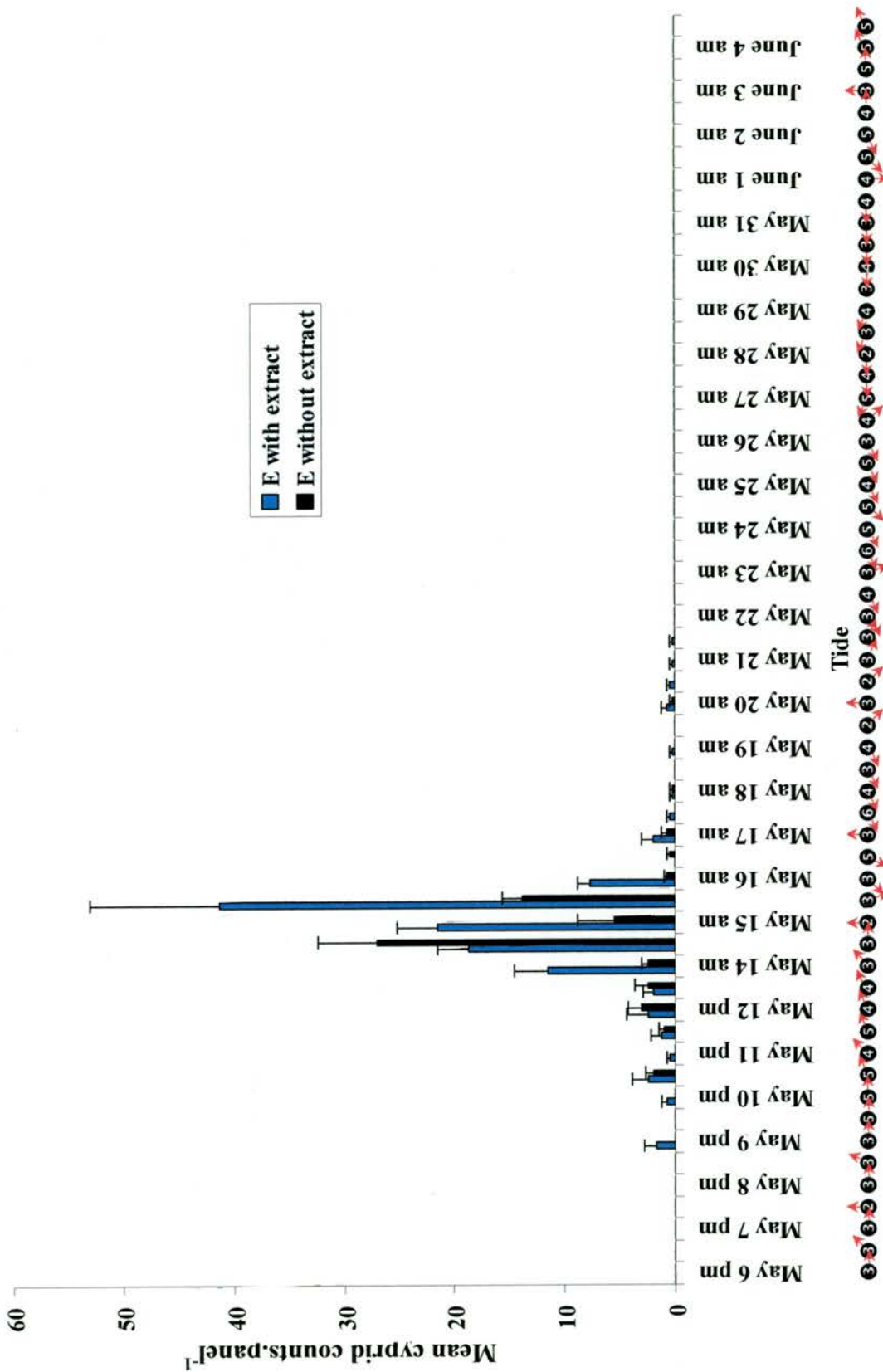


Fig. 46 – Mean tidal settlement of *S. balanoides* cyprids on plane panels, with and without extract, at Site E during the 2000 season. n=4 for each bar observation, with vertical lines representing S.E.M. Wind data shown as maximum Beaufort strength and predominant direction over each tidal period, calculated from hourly averages.

3. 1. 3. 1. Settlement response with tidal height at Sites C - E.

The peaks of settlement seen at Sites C – E were found to be temporally correlated with one another during the sampled period of 24 tides from May 10th pm to May 22nd pm (Spearman $r_s = 0.7213$ for C to D, $r_s = 0.6631$ C to E, $r_s = 0.5477$ D to E; $p < 0.001$ and $n=192$ for all comparisons from eight panels; see also Fig. 47). Settlement was seen to vary significantly with Day, as was expected (One-way ANOVA tide $F_{13,383} = 68.20$, $p = < 0.001$).

Table 2
Settlement panels: extract and between tidal height comparisons for Sites C-E, 2000

Source	df	SS	MS	<i>F</i>	<i>p</i>
Extract	1	4.862	4.862	7.95	0.005
Tidal height	2	19.881	9.940	16.26	<0.001
Extract x Tidal height	2	0.551	0.276	0.45	0.637
Error	378	231.032	0.611		
Total	383	256.326			

ANOVA for cyprids ($\log x + 1$) settlement on plane panels with and without painted extract. Factors were Extract (fixed) and Tidal height (random). $n = 64$ for each treatment at each site.

ANOVA analyses of cyprid counts on panels in the presence or absence of extract at Sites C – E revealed that both Extract and Tidal height are of significant influence to cyprid settlement, but that settlement response to the extract does not differ with location as shown by the lack of interaction (Table 2). An interaction bar plot emphasises that settlement on panels without extract is consistently lower than those with extract, and that the low intertidal Site E has significantly less settlement than the other two sites (Fig. 48). Additionally although extract had a significant effect on settlement when grouped over all the sites, a Tukey-Kramer unplanned multiple comparisons test revealed that the presence or absence of extract was not significant within sites for Sites C and E, which may be due to the May 15th am and pm tides.

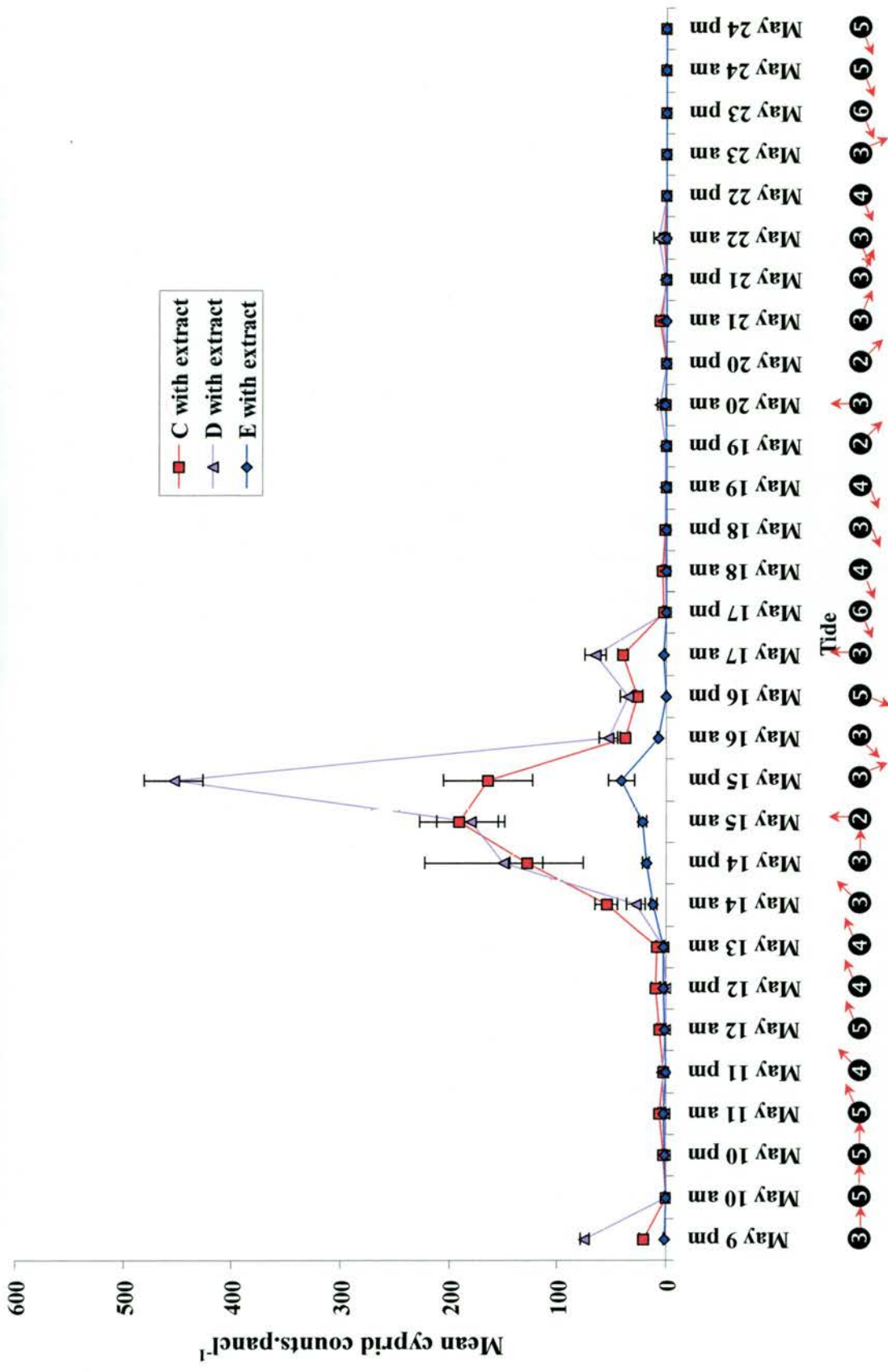


Fig. 47 – Mean tidal settlement of *S. balanoides* cyprids on plane panels with extract, at Sites C- E during a 26 tidal period in 2000. n=4 for each data point, with vertical lines representing S.E.M. Wind data shown as maximum Beaufort strength and predominant direction over each tidal period, calculated from hourly averages.

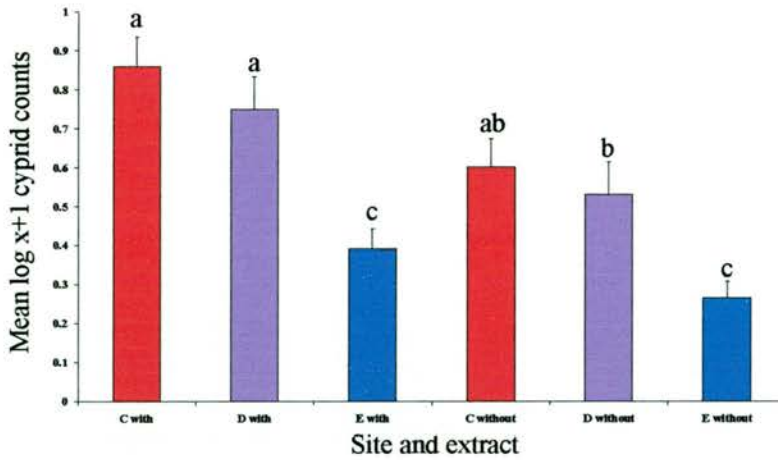


Fig. 48 – Mean counts of log $x+1$ cyprid settlement on plane panels with and without extract at Sites C, D and E for 24 tides, from the 10th May pm tide to the 22nd May pm tide 2000. Vertical bars represent S.E.M., with $n=96$ for each bar. Letters denote statistical groupings from a Tukey-Kramer multiple comparisons ($\alpha = 0.05$).

3. 1. 4. 1. Sites F and G

Sites F and G were two opposing panel blocks, situated in a low intertidal gully at the same tidal height as Site E. Site F faced towards the oncoming tide, whereas Site G faced inland towards the cliffs. These sites were sampled tidally between May 9th pm and May 15th pm for a period of 12 tides during the peak in settlement seen at Sites C – E. Settlement at Site F (Fig.49) peaks on the 14th May pm with a maximum average of 17 ± 4 cyprids on plane panels with extract. This coincided with a Force 3 E wind, after a previous period of NE / ENE winds. Settlement on the following N Force 2 tide (May 15th am) approaches that of the previous day, with a mean settlement of 15 ± 5 cyprids on plane panels with painted extract. In contrast the maximum observed mean on plane panels for Site G (Fig. 50) occurred on the 15th May pm, two days after the maximum seen at Site F even though they were only separated by a gully of approximately 40cm. On May 15th am the predominant wind direction was from the north, and cyprid counts on panels with extract were 15 ± 5 and 13 ± 14 at Site F and G respectively. When the wind shifted to a southerly direction (SSE) on the 15th pm tide, mean cyprid counts on panels with extract were 7 ± 1 and 32 ± 14 for Site F and

G respectively. This suggests that when the wind direction is from the south, the south facing Site G has a higher settlement response and vice versa with northerly winds for Site F. However as the standard errors are large and the sampling period was short, it was not possible to confirm such observations.

3. 1. 4. 2. *Settlement response with tidal height, Sites C-G.*

Sites F and G were located at the same tidal height at Site E, in the low intertidal region of the Kinkell Braes shore. Spearman rank correlation analysis revealed that all sites were temporally correlated over the sampling period ($p = <0.001$, $n=48$ for all sites).

Table 3
Settlement panels: between-site comparisons, Sites C-G, over 6 days

Source	<i>df</i>	SS	MS	<i>F</i>	<i>p</i>
Extract	1	2.270	2.270	10.73	0.024
Site	4	17.243	4.311	2.71	0.058
Day	5	84.485	16.900	10.61	<0.001
Extract x Site	4	0.571	0.143	1.96	0.140
Extract x Day	5	0.709	0.142	1.94	0.132
Site x Day	20	30.473	1.524	20.88	<0.001
Extract x Site x Day	20	1.460	0.073	1.37	0.145
Error	180	9.616	0.053		
Total	239	146.826			

ANOVA for cyprid ($\log x+1$) settlement on plane panels with and without conspecific extract. $n=4$ for each panel type at each site on each tide. Factors were Extract (fixed), Site (random) and Tide (random).

The presence or absence of the conspecific Extract is again seen to be of significant effect, whilst Site is not, with no significant interaction effect between the two factors. However on examination of the Tukey comparison tests in Fig. 51 suggests this mildly non-significant p value of 0.058 for the Site factor is probably due to the fact that Sites E, F and G are all at low tidal heights in comparison to Sites C and D in mid and upper-intertidal areas respectively. Table 2 indicates that tidal height is of significant influence in the settlement seen ($F_{2,570} = 7.95$, $n = 64$, $p <0.001$). Day is a

significant factor, as would be expected, and is the main source of the interaction between Site and Day. Tukey-Kramer multiple comparisons of panel treatment and site are shown in Fig. 51.

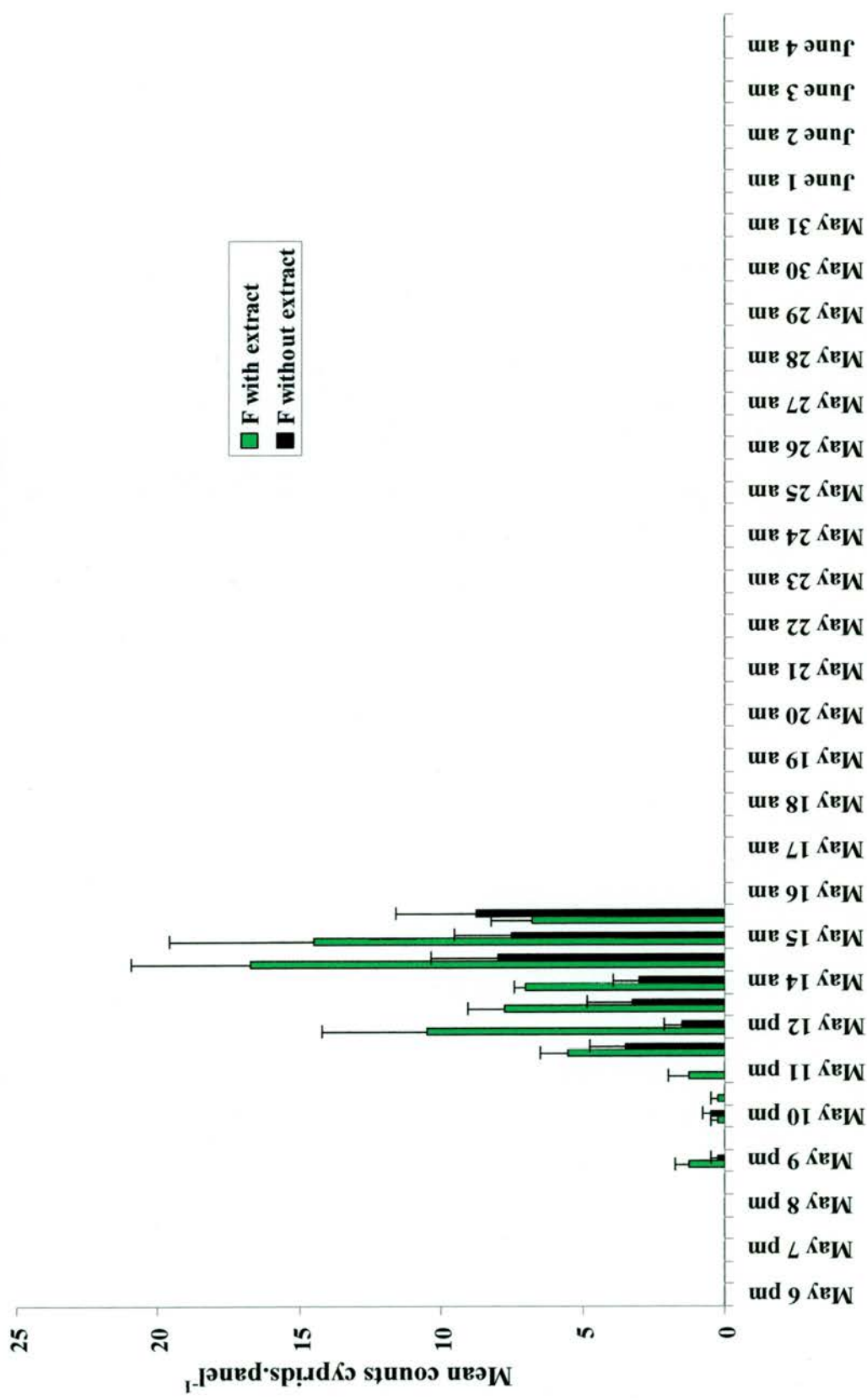


Fig. 49 – Mean tidal settlement of *S. balanoides* cyprids on plane panels, with and without extract, at Site F during the 2000 season. n=4 for each bar observation, with vertical lines representing S.E.M. Wind data shown as maximum Beaufort strength and predominant direction over each tidal period, calculated from hourly averages. Site sampled between May 9th pm and May 15th pm (12 tides).

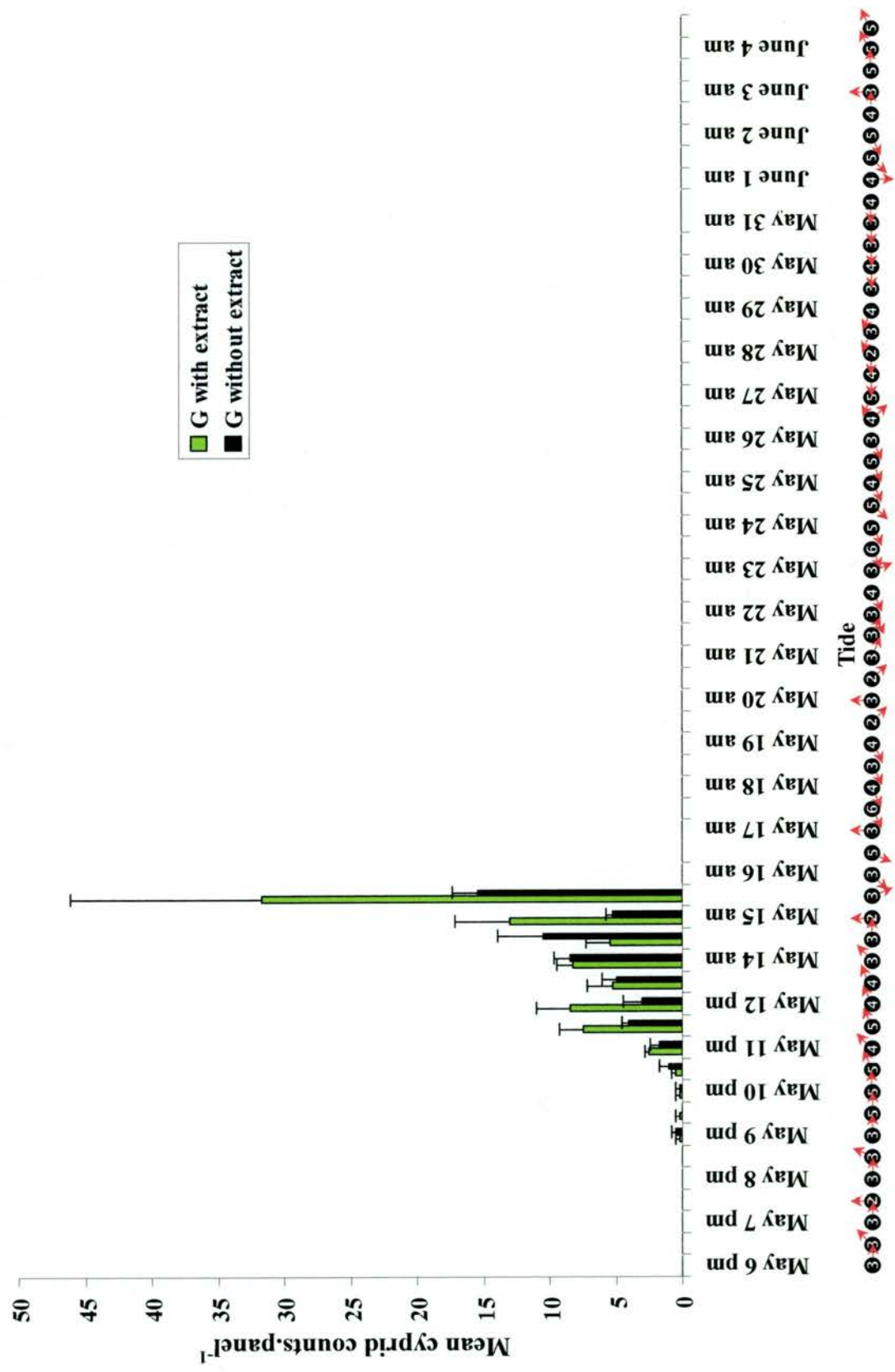


Fig. 50 – Mean tidal settlement of *S. balanoides* cyprids on plane panels, with and without extract, at Site G during the 2000 season. n=4 for each bar observation, with vertical lines representing S.E.M. Wind data shown as maximum Beaufort strength and predominant direction over each tidal period, calculated from hourly averages. Site sampled between May 9th pm and May 15th pm (12 tides).

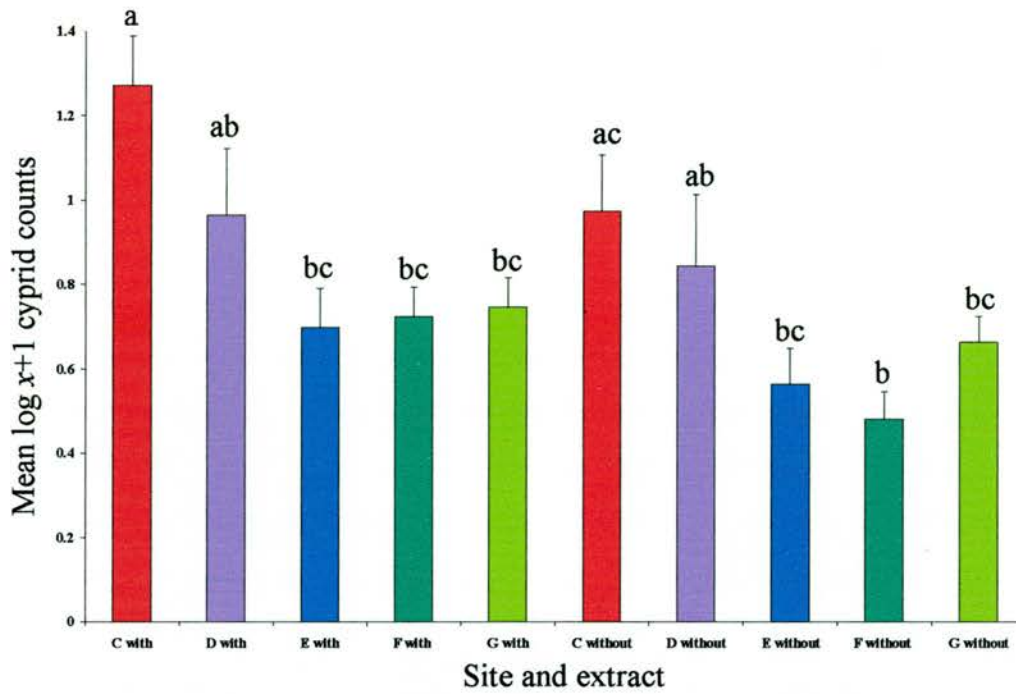


Fig. 51 – Mean counts of log $x+1$ cyprid settlement on plane panels with and without extract at Sites C-G for 10 tides, from the 10th May pm tide to the 15th May pm tide. Vertical bars represent S.E.M., with $n=80$ for each bar. Letters denote statistical groupings from a Tukey-Kramer multiple comparisons test ($\alpha = 0.05$).

As can be seen in Fig. 51, the presence of extract has a positive effect on settlement over the sites, with Site C panels with extract recording the highest mean settlement over the 10-tide period. Low intertidal sites (E-G) are significantly different from panels with extract at the mid-intertidal Site C.

3. 1. 5. *Boarhills, 2000*

3. 1. 5. 1. *Sites H and I*

Sites H and I were located immediately adjacent to one another in the mid intertidal region at Boarhills. Site H was sampled in two settlement periods between May 19th am to May 25th pm, and then from the 31st May pm to 4th June pm. One settlement peak is seen at this site between May 20th pm and May 22nd am, after which mean cyprid counts drop sharply and do not rise above 1 therefore indicating the settlement season can be considered finished by the 25th May pm tide (Fig.52). The maximum

mean cyprid count for this site occurred on the May 21st am tide (16 ± 6) during a three-tide period of SE winds.

Site I panels were situated in a block next to Site H (Fig. 33), and had the same settlement peak as that observed for Site H, running from the May 20th pm tide to the May 22nd am tide, with a maximum mean cyprid count of 9 ± 1 over the four replicate panels with extract. Again this peak coincided with winds from the SE (Fig. 53).

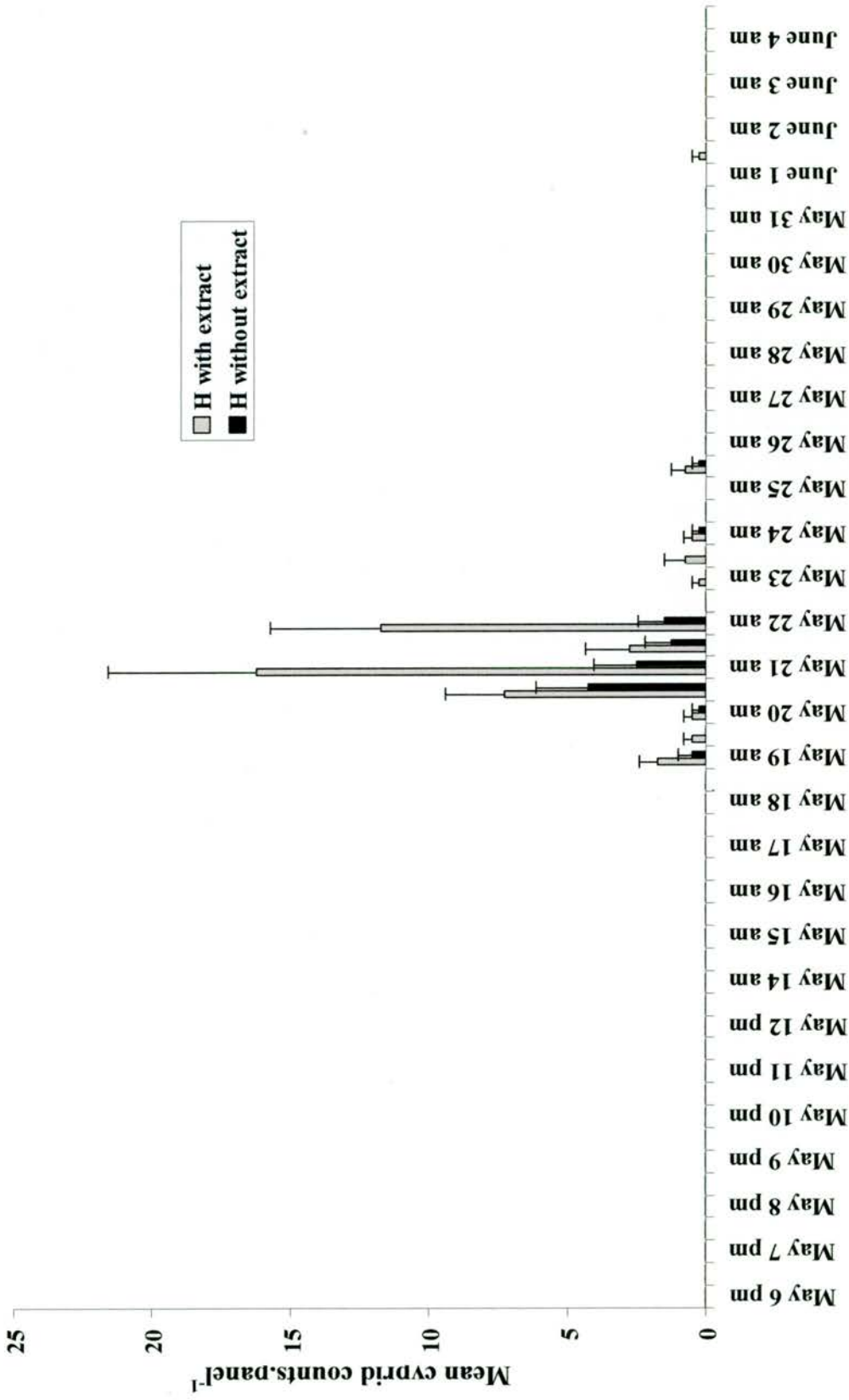


Fig. 52 – Mean tidal settlement of *S. balanoides* cyprids on plane panels, with and without extract, at Site H during the 2000 season. n=4 for each bar observation, with vertical lines representing S.E.M. Wind data shown as maximum Beaufort strength and predominant direction over each tidal period, calculated from hourly averages. Site sampled in two periods; between May 19th am and May 25th pm (14 tides), and May 31st pm to June 4th pm (9 tides)

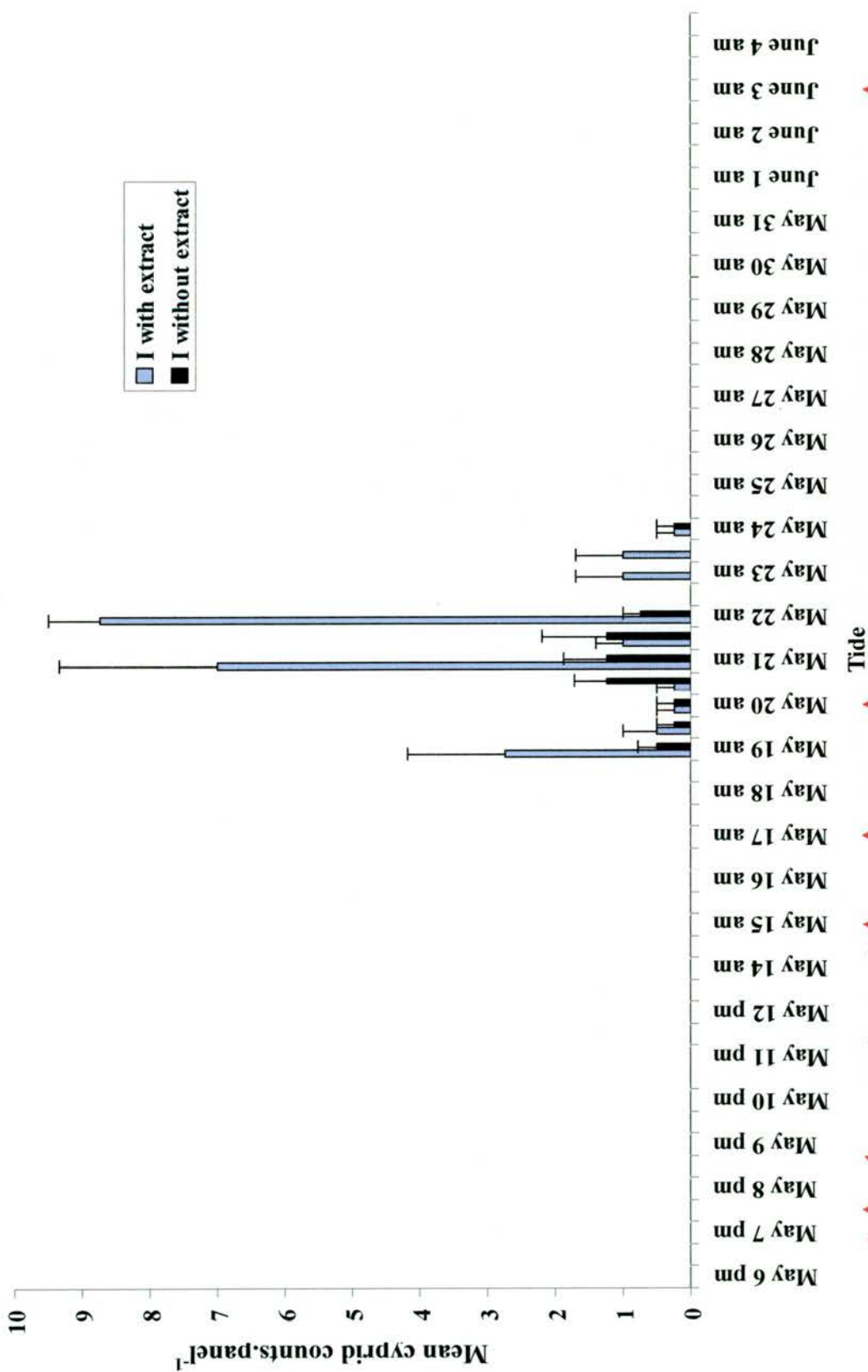


Fig. 53 – Mean tidal settlement of *S. balanoides* cyprids on plane panels, with and without extract, at Site I during the 2000 season. n=4 for each bar observation, with vertical lines representing S.E.M Wind data shown as maximum Beaufort strength and predominant direction over each tidal period, calculated from hourly averages. Sites sampled from May 19th am to May 24th pm (12 tides).

3. 1. 5. 2. *Settlement response with site, sites C, H and I.*

Spearman tests of $\log x+1$ cyprid counts at the mid intertidal sites of C, H and I through the 12 tide period between May 19th am and May 24th pm revealed that the sites were temporally correlated (C to H $r_s = 0.3912$; C to I $r_s = 0.3900$; H to I $r_s = 0.4807$; $n=96$ for each site, $p < 0.001$ for all comparisons). Settlement at Site C during this period had virtually ceased with a maximum mean settlement of 7 ± 1 cyprids (Figs.44 and 54).

Table 4
Settlement panels: extract, day and between-site comparisons for Site C, H and I over 5 days.

Source	<i>df</i>	SS	MS	<i>F</i>	<i>p</i>
Extract	1	2.057	2.057	3.69	0.127
Site	2	1.040	0.520	1.91	0.288
Day	4	5.403	1.351	2.38	0.184
Extract x Site	2	0.375	0.188	1.68	0.245
Extract x Day	4	1.927	0.482	4.32	0.037
Site x Day	8	1.573	1.197	1.76	0.220
Extract x Site x Day	8	0.891	0.111	1.56	0.149
Error	90	6.441	0.072		
Total	119				

ANOVA for cyprid ($\log x+1$) settlement on plane panels with and without extract. $n=4$ for each panel type at each site on each tide. Factors were Extract (fixed), Site (random) and Day (random).

ANOVA revealed that the presence or absence of conspecific extracts did not have a significant effect on settlement ($p=0.127$) but the low observed cyprid counts suggest that this observation is unreliable. Additionally this analysis is derived from data at the end of the season and therefore the fitness of larvae may be questionable. This is confirmed by the lack of significance of the Day factor ($p = 0.184$), as input was consistently low over the 5 days studied. Cyprid counts did not differ with Site ($p = 0.288$); all sites were in the mid intertidal region of the shore, but again low counts cannot confirm this relationship. Moreover Sites H and I face SE and the sampled

time period was during a period of SE winds, and Site C faces SW and low settlement responses were observed during periods of southerly winds (Fig. 44). Therefore the apparently similar settlement at Sites C, H and I may not be a function of tidal height, but rather of low count numbers caused by wind direction. Tukey-Kramer comparisons ($\alpha = 0.05$) found that only panels with extract at Site H were significantly different from all other pairings of site and extract presence or absence.

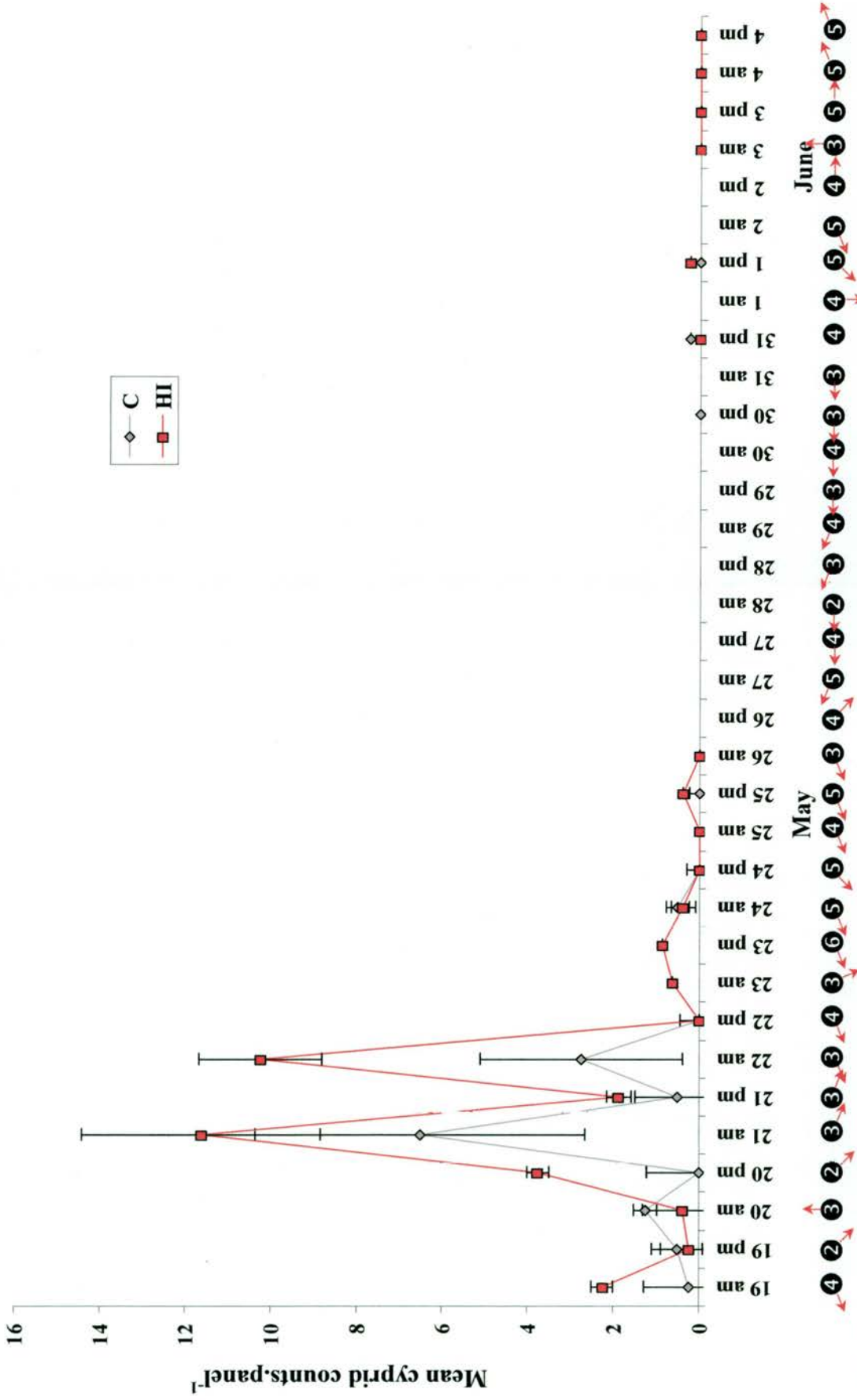


Fig. 54 – Mean tidal settlement of *S. balanoides* cyprids on plane panels, with extract only, at Sites C, and pooled sites H and I during the 2000 season. n=4 for each data point observation, with vertical lines representing S.E.M. Wind data shown as maximum Beaufort strength and predominant direction over each tidal period, calculated from hourly averages. Sites not sampled between May 26th pm and May 30th am inclusive.

3. 1. 6. Settlement panel type and influence of extract.

At Site C cyprid settlement response to differing panel substratum, with or without extract, was investigated over a six tide period from May 7th pm to May 10th am. At each tide four plane sanded panels with extract, two unsanded panels with extract and two unsanded panels without extract were counted either *in situ* or in the laboratory, producing five sets of tidal data as the panels were not deployed until May 7th pm. For analyses the four plane sanded panels with extract at each tide have been randomly selected into two pairs, which were then averaged to produce two replicates to ensure balanced analysis. It was necessary to maintain the greater number of sanded panel replicates as this site was sampled throughout the season with four sanded replicates with extract and four without, in order to prevent the break in any settlement patterns. As each backplate could only hold eight panels in total, no panel data is available for cyprid counts on plane panels without extract. Therefore for data analysis the effect of extract with panel type could not be examined across all groups, hence the effect of extract was examined on polished panels, and the effect of panel type (sanded or unsanded, Table 5) was determined using panels with extract only (Table 6).

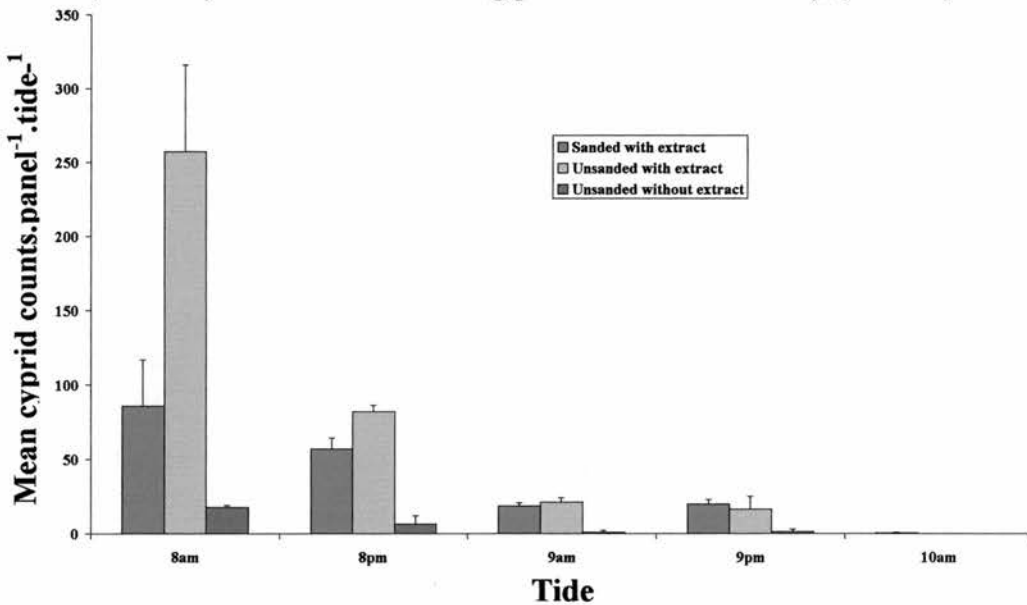


Fig. 55 – Mean tidal settlement of *S. balanoides* cyprids at Site C on sanded panels with extract and unsanded panels, with and without extract. For each bar observation n=4 on sanded panels, with n=2 on unsanded panels; vertical lines represent the S.E.M

3. 1. 6. 1. Effect of extract on unsanded panels, Site C.

Unsanded panels without extract had significantly lower cyprid settlement counts than those with extract (Fig. 56a, $p = 0.017$ Table 5a) with means of 23 and 2 cyprids respectively.

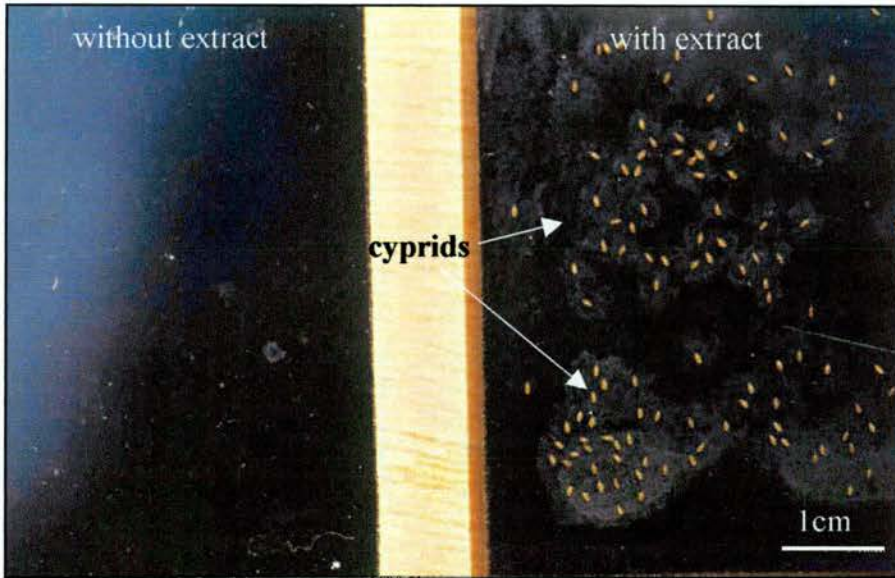


Fig. 56a – Cyprid settlement on unsanded panels without painted conspecific extract (left) and with conspecific extract (right) from Site C.

Tide was also seen to have a significant effect on settlement ($F_{4,10} = 7.57, p = 0.038$). Additionally a significant interaction occurred between the two factors which was attributable to very high settlement on the 8th May am tide on unsanded panels with extract (Tukey-Kramer multiple comparison test, $\alpha = 0.05, p = 0.005$).

Table 5a
Comparison of settlement on unsanded panels with extract over 5 tides, Site C.

Source	<i>df</i>	SS	MS	<i>F</i>	<i>p</i>
Extract	1	3.858	3.858	15.40	0.017
Tide	4	7.581	1.900	7.57	0.038
Extract x Tide	4	1.002	0.251	3.61	0.045
Error	10	0.695	0.070		
Total	19	13.137			

ANOVA for cyprid ($\log x+1$) settlement on unsanded plane panels with and without conspecific extract. Factors were Extract (fixed) and Tide (random).

3. 1. 6. 2. Settlement on sanded and unsanded panels.

Settlement on sanded and unsanded panels, both painted with extract, was found to be not significant for five tidal observations (Table 5b). Additionally although Tide was found to be of influence to cyprid settlement ($F_{4,10} = 16.61, p = 0.009$), it did not significantly affect the relationship between panel type (Table 5b).

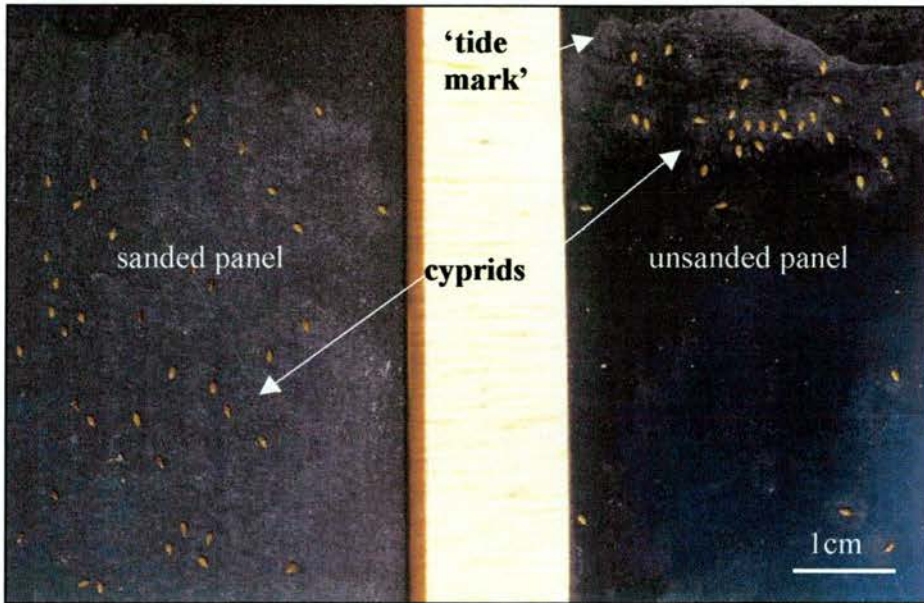


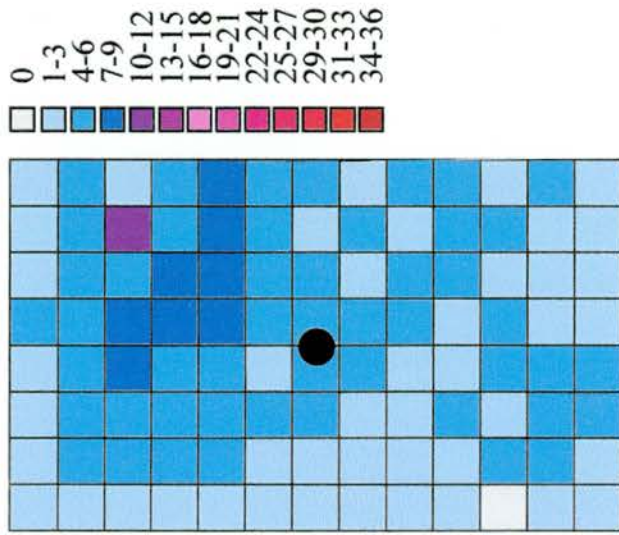
Fig. 56b – Settlement patterns of *S. balanoides* cyprids on sanded (left) and unsanded (right) settlement panels at Site C, both painted with a conspecific extract. Panel orientation as deployed in field.

Although cyprid counts were not seen to differ significantly with panel type, the pattern of settlement appears dissimilar (Fig.56b). While cyprids appear more randomly spaced on the sanded panels, cyprids appear to congregate towards the upper edge of the panel on smooth panels (Fig. 56b and 57b).

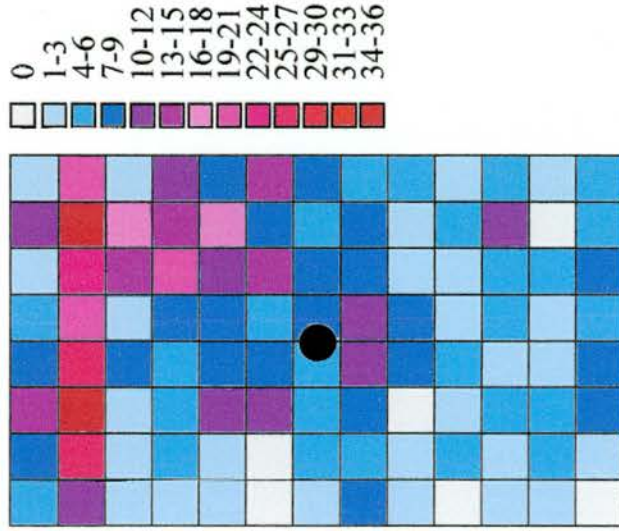
**Table 5b
Comparison of settlement with panel texture and extract over 5 tides, Site C.**

Source	<i>df</i>	SS	MS	<i>F</i>	<i>p</i>
Texture	1	0.121	0.121	0.86	0.405
Tide	4	9.306	2.326	16.61	0.009
Texture x Tide	4	0.560	0.140	2.35	0.124
Error	10	0.595	0.060		
Total	19	10.582			

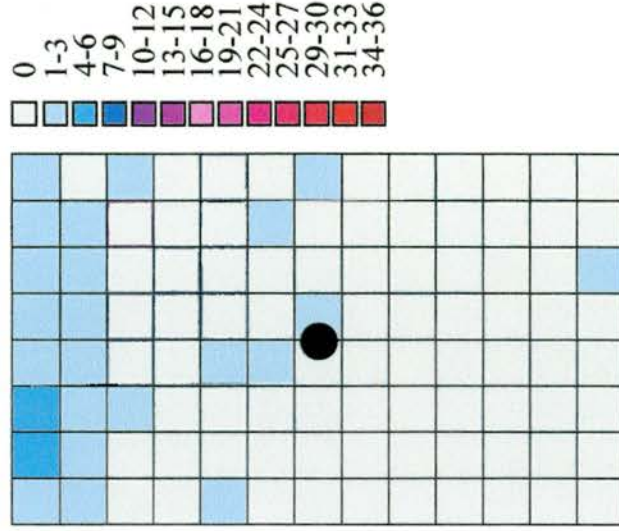
ANOVA for cyprid (log $x+1$) settlement on sanded and unsanded panels with conspecific extract. Factors were Texture (fixed) and Tide (random).



(a) Sanded with extract



(b) Unsanded with extract



(c) Unsanded without extract

Fig. 57 – Diagrammatic representation of total cyprid counts on unsanded panels with and without extract, and sanded panels with extract taken from final laboratory counts. Coloured blocks represent the total cyprid counts observed in that cm^2 over the sampled five tide period of 8th May am to 10th May am. (a) For each tide the four sanded replicates were randomly averaged into two replicates for representational comparisons with the unsanded panels; therefore panel n=6, total cyprid counts n=131. (b) Total cyprid counts = 761 for n=6 panels (c) Total cyprid counts = 53 for n=6 panels. Panels shown in portrait orientation as were deployed in field.

When panels were retrieved and counted in the laboratory it was noticed that cyprids appeared congregated at 'tide-marks' on unsanded panels with extract (Fig. 56); these 'tide-marks' were often observed on the upper edge of these panels, and were not present on sanded panels with extract. When the panels were painted before deployment in the field, they were allowed to dry lying horizontally on benches, therefore the 'tide-mark' was not due to any vertical orientation in the drying process. Additionally although settlement was low on the unsanded panels without extract, those cyprids that have settled are found upon the upper edges of the panels suggesting that these congregations around the 'tide-marks' may be due to the panel type itself, such as increased upward exploratory motion by the cyprids on the smooth surface, rather than as a function of any concentrated lines of painted extract. Therefore these marks may be caused by the cyprids themselves, through exploratory movement or leaking of cellular materials on drying, and indeed marks like 'haloes' can be seen around individual cyprids in Fig. 56. However, as these panel types were investigated over a relatively short period with little replication and during a period of E / NE winds, no conclusions can be made concerning general larval behaviour regarding any patterns of upward movement on smoother surfaces.

3. 2. *Second settlement season, 2001*

3. 2. 1. *Kinkell Braes, 2001*

3. 2. 1. 1. *Site C*

Throughout the 2001 season settlement at Site C was examined daily using four plane sanded panels with extract and four plane sanded panels without. Three peaks of settlement were seen during this season (Fig. 58), although only lasting for one day unlike that seen in 2000. The first peak is seen on May 12th with a mean cyprid count of 53 ± 6 on panels with extract and coincides with a Force 7 E wind, after four previous days of NE winds. Panels without extract on this date have a mean of 4 ± 1 cyprids over the four replicates, over 13 times less than painted panels. The second settlement peak occurs on the 15th of May, with a mean settled count of 48 ± 17 settlers on panels with extract and 12 ± 6 on panels without extract after 8 days of onshore NE / E winds. The final and greatest settlement peak occurs on the 17th of May (119 ± 28 mean cyprid count on panels with extract, 20 ± 4 on panels without extract) after 10 days of predominantly NE onshore winds (Fig. 58). As sampling took place daily rather than tidally during the 2001 season, it was expected that the peak would appear 'steeper', with less gradual increases and decreases than those seen in 2000. Additionally, unlike in 2000, during the peaks of settlement panels with extract consistently showed a greater settlement response than those without.

Plots of mean ash weight of sediment samples (n=2) alongside the panel data (Fig. 58) also show three major peaks on the 30th April ($0.093\text{g} \pm 0.002$), 11th May ($0.007\text{g} \pm 0.014$) and the 15th May ($0.101\text{g} \pm 0.013$). All increases in trapped ashed sediment weight occurred during NE winds with a median Beaufort strength of Force 4. Additionally, as can be seen in Fig. 58, the increases in captured sediment weight

appear either the day before (30th April, 11th May) or on the same day (15th May) as the increases in settlement on the panels. While a Spearman Rank Correlation test of settlement on positive panels with sediment weight (n=2 per day) showed no significant correlation when compared as in Fig. 58 ($r_s = 0.1860$, $n = 36$, $p = 0.2773$), it was found that with a lag of one day (i.e. April 28th becomes April 29th) the sediment data produced a very significant correlation ($r_s = 0.4559$, $n = 36$, $p = 0.005$). This lag indicates that the NE winds are transporting the larvae onshore because of large amounts of water movement, leading to a subsequent settlement response.

3. 2. 1. 2. Site D

During the 2001 season at Site D, large mean cyprid settlement was observed on panels with extract on May 12th (186 larvae \pm 47) and May 15th (42 \pm 13), coinciding with Force 7 E and Force 5 NE winds correspondingly (Fig. 59). Unlike in 2000 at this site, panels without extract did not have a greater settlement response than those with extract (Figs. 45 and 59). As with Site C three large sediment peaks were seen on April 30th (0.042g \pm 0.010), May 11th (0.050g \pm 0.040) and 15th May (0.038g \pm 0.002), which corresponded to periods of onshore NE winds with median Beaufort strengths of Force 4. Spearman Rank Correlation analysis of mean painted panel counts with mean sediment weight revealed no correlation ($r_s = 0.0527$, $n = 36$, $p = 0.7604$). Additionally correlation analysis of the mean painted panel counts with 'sediment weight + 1 day' proved not quite significant ($r_s = 0.2985$, $n = 36$, $p = 0.077$); only two peaks of settlement were seen at the upper intertidal Site D unlike 3 at Site C, which will have contributed to the lack of significance.

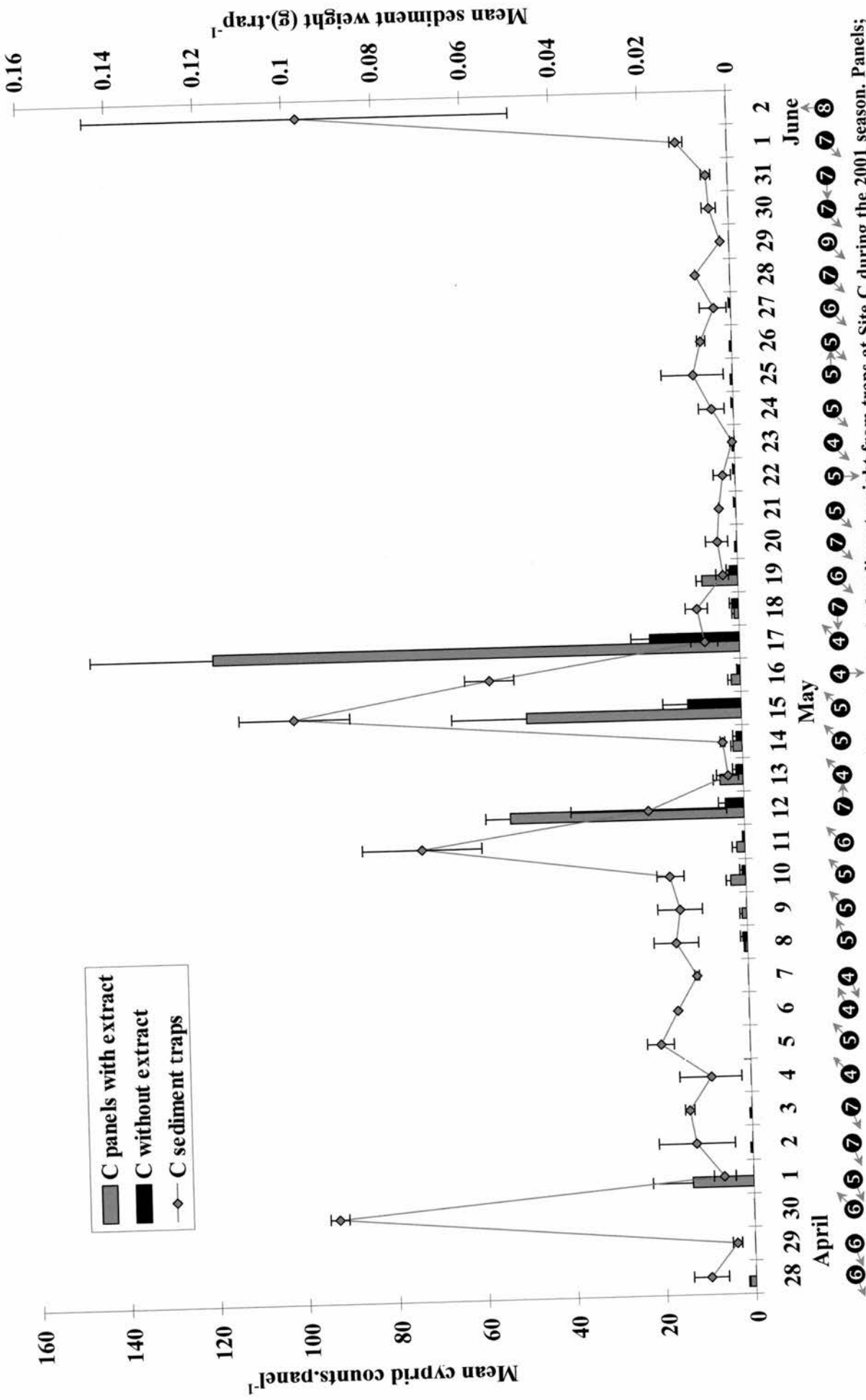


Fig. 58 – Mean daily settlement of *S. balanoides* cyprids on plane panels with captured ashed sediment weight from traps at Site C during the 2001 season. Panels; painted with extract or unpainted (n=4 each treatment each day). Sediment traps were ~71 cm apart on the backplate; emptied daily (n=2 each day). Vertical lines represent S.E.M. Wind data shown as maximum Beaufort strength and predominant direction over each daily period, calculated from 10 minute averages.

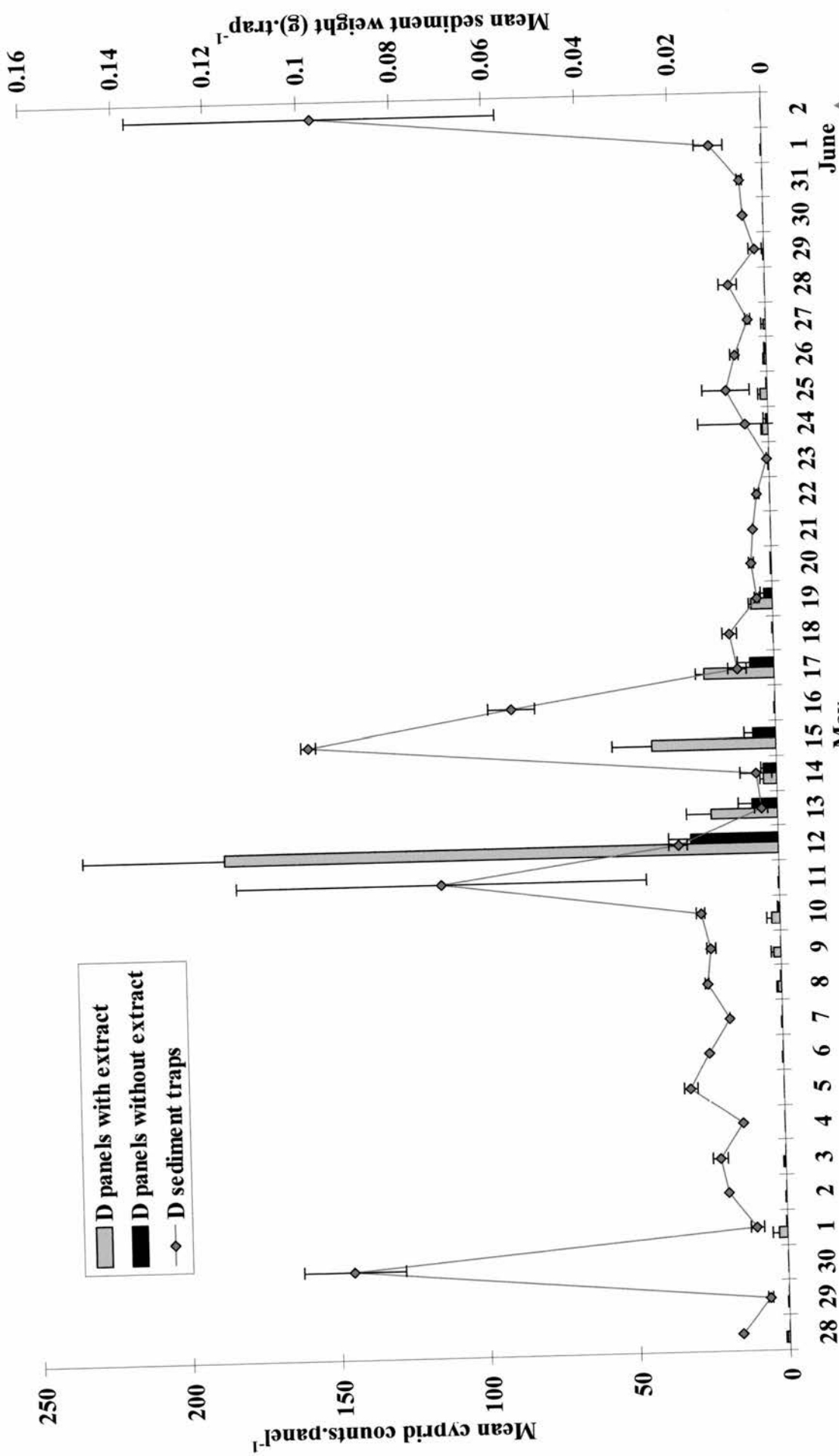


Fig. 59 – Mean daily settlement of *S. balanoides* cyprids on plane panels with captured ashed sediment weight from traps at Site D during the 2001 season. Panels; painted with extract or unpainted (n=4 each treatment each day). Sediment traps were ~71 cm apart on the backplate; emptied daily (n=2 each day). Vertical lines represent S.E.M. Wind data shown as maximum Beaufort strength and predominant direction over each daily period, calculated from 10 minute averages.

3. 2. 1. 3. *Site E*

Site E was sampled daily with four plane panels with extract and four plane panels without extract from the 28th April until the 13th May. Only one peak appears, on May 12th coinciding with the same peak of settlement seen at sites C and D (panels with extract 2 ± 0.4 cyprid counts, panels without extract 1 ± 0.5 cyprids, Fig. 60). However counts are so low compared to that of Site C, at approximately 20 times less, that sampling at this site was discontinued on the 13th May. Both panel and sediment samples were only taken daily from the 28th April until the 3rd of May; again an increase in captured sediment weight occurred during NE winds on the day before a settlement increase on the 1st May (Fig. 61). However as the coinciding period was so short no correlation analysis was performed.

3. 2. 1. 4. *Settlement with tidal height, Kinkell Braes 2001*

ANOVA analyses of $\log x+1$ cyprid counts over 16 days (28th April to 13th May inclusive) at Sites C, D and E showed a significant effect of Site (Table 6), due to the significantly lower settlement at Site E when compared to Sites C and D (Tukey-Kramer test; $\alpha = 0.05$, $n=128$ for each site, $p < 0.01$; see also Fig. 62). Therefore settlement was found to be significantly lower in the low intertidal region than in the mid and upper intertidal region. A significant difference was observed with Day, as expected (Table 6, Fig. 62), which was the main contributor to the significant interaction seen between the two factors. As can be seen in Fig. 62, while there is a significant difference over the season, it was not consistent throughout the season as in periods of low or zero settlement the relationship is not seen. The plot of mean cyprid counts on panels with extract over the season at Sites C, D and E (Fig. 62) indicates that on May 12th settlement was much higher on panels with extract at Site

D than Site C (53 ± 6 and 186 ± 47 mean cyprid counts respectively). This occurred during a direct onshore E wind of Force 7 and therefore increased wave action and splash may have contributed to the higher settlement on an upper intertidal area than a mid intertidal region. As settlement was so low at Site E, it was not included in analysis of the relationship between settlement and presence / absence of extract. However when the effect of Extract was analysed at Sites C and D, the cyprid settlement response was found to significantly greater on panels with extract during this 16 tide period ($F_{1,252} = 15.08, p < 0.001$).

Table 6
Within-site comparisons of settlement with tidal height at Sites C, D and E from 28th April to 13th May, 16 days 2001.

Source	<i>df</i>	SS	MS	<i>F</i>	<i>p</i>
Height	2	3.048	1.524	4.30	0.023
Day	15	30.701	2.047	5.77	<0.001
Height x Day	30	10.634	0.354	6.96	<0.001
Error	336	17.115	0.051		
Total	383	61.497			

ANOVA for cyprid ($\log x+1$) settlement on plane panels at Sites C, D and E. Height was a fixed factor and Day a random factor.

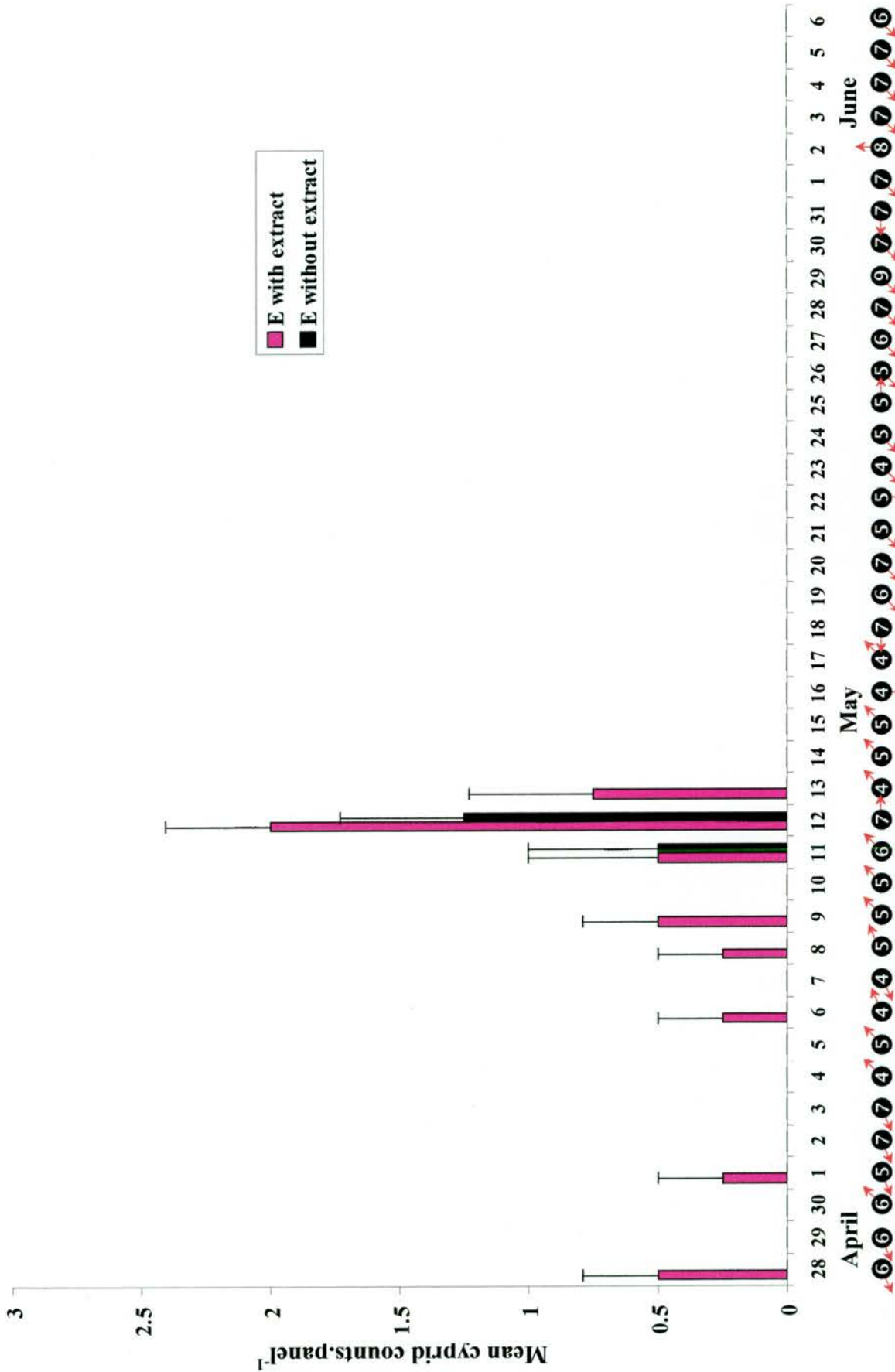


Fig. 60 – Mean daily settlement of *S. balanoides* cyprids on plane panels with and without extract at Site E during the 2001 season. Panels; painted with extract or unpainted (n=4 each treatment each day). Vertical lines represent S.E.M. Wind data shown as maximum Beaufort strength and predominant direction over each daily period, calculated from 10 minute averages.

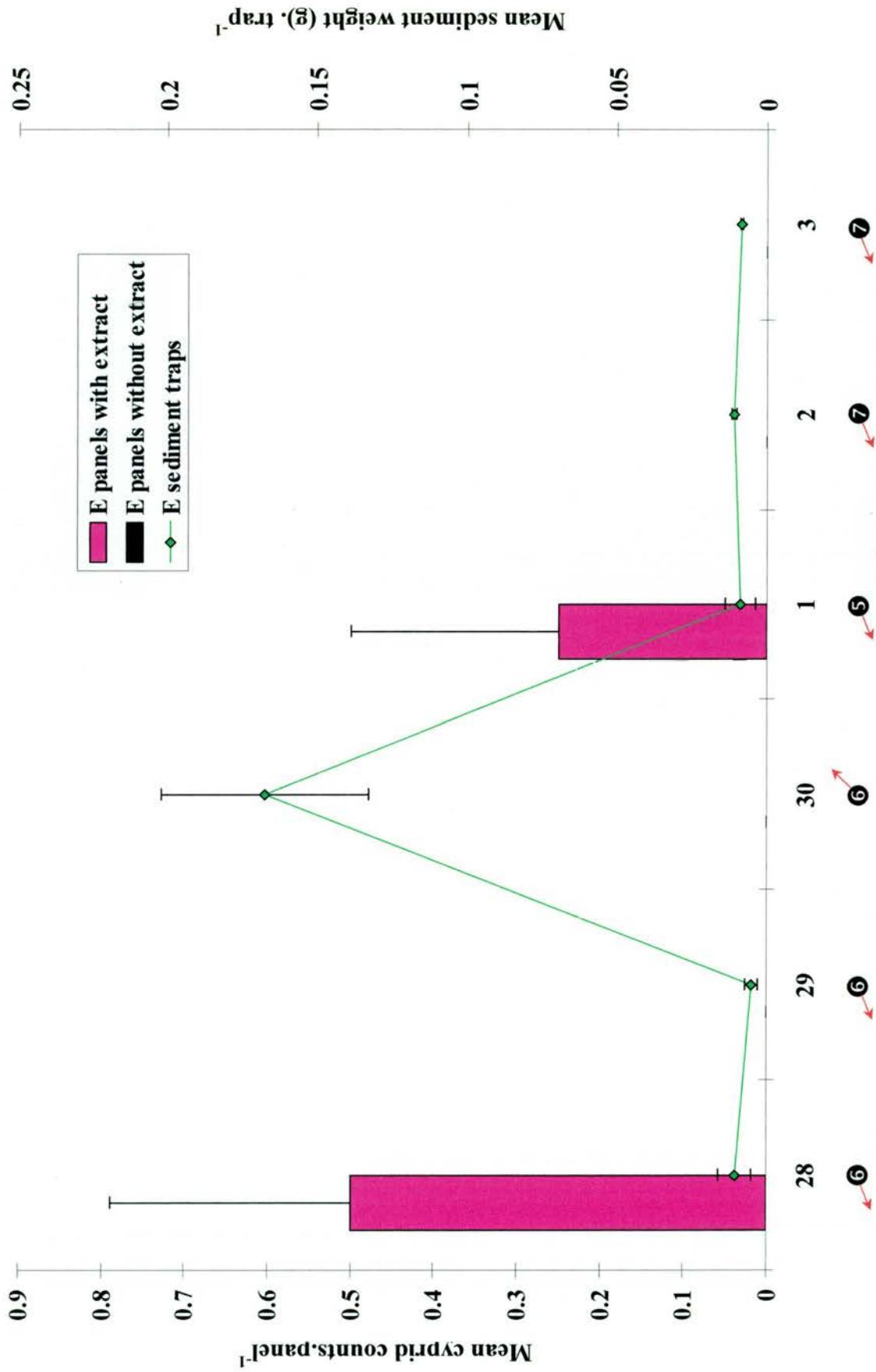


Fig. 61 – Mean daily settlement of *S. balanoides* cyprids on plane panels with captured ashed sediment weight from traps at Site E during the 2001 season. Panels; painted with extract or unpainted (n=4 each treatment each day). Sediment traps were ~71 cm apart on the backplate; emptied daily (n=2 each day). Vertical lines represent S.E.M. Wind data shown as maximum Beaufort strength and predominant direction over each daily period, calculated from 10 minute averages.

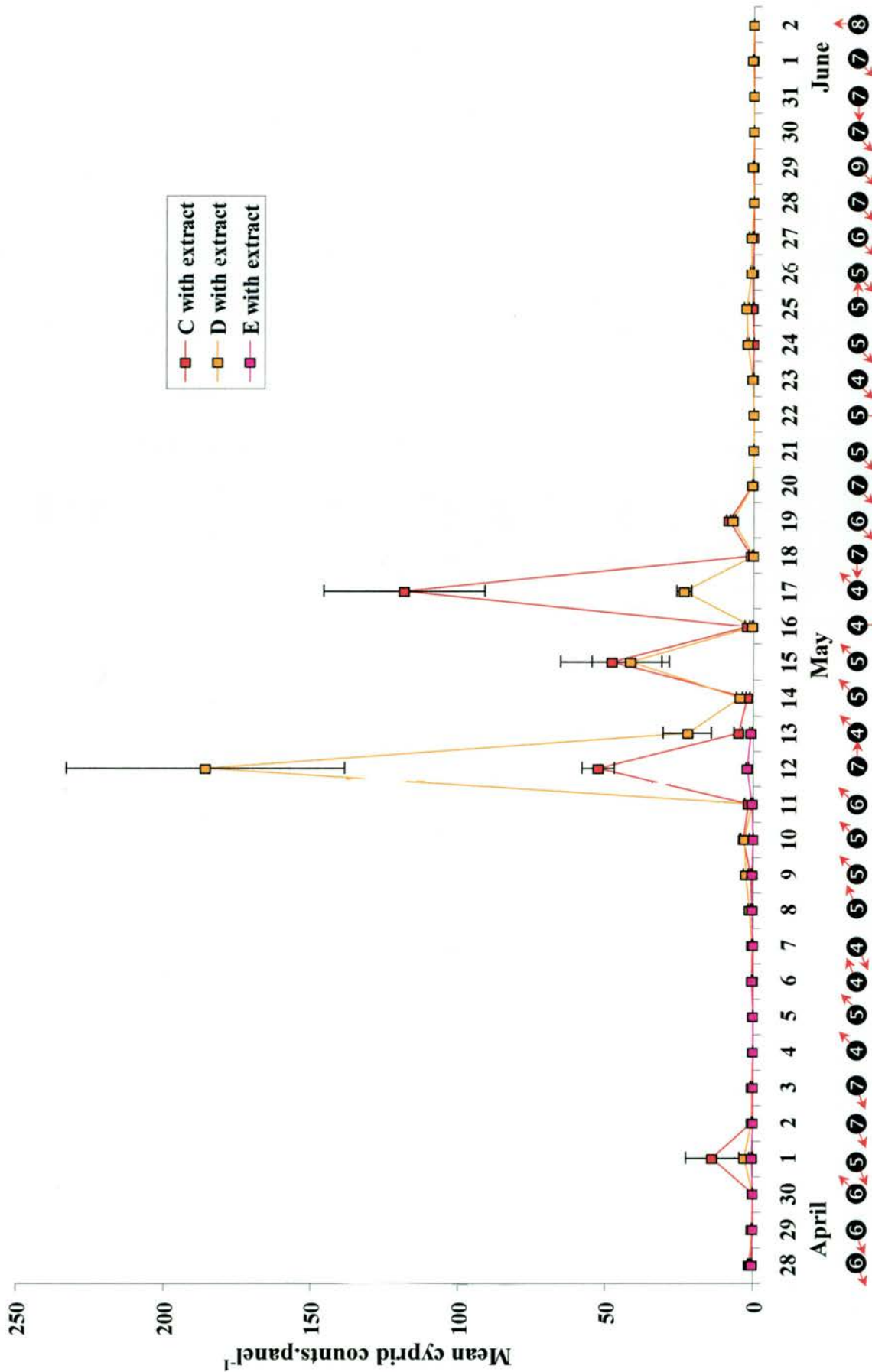


Fig. 62 – Mean daily settlement of *S. balanoides* cyprids on plane panels with extract at Sites C, D and E during the 2001 season. n=4 for each data point observation, with vertical lines representing S.E.M. Wind data shown as maximum Beaufort strength and predominant direction over each daily period, calculated from hourly averages.

3. 2. 2. Site T – Effects of panel type on settlement

From 5th May to the 6th June Site T was sampled daily with triplicate painted plane, horizontally grooved and vertically grooved panels (Fig. 63 and 64). Two observed peaks of settlement occurred on the plane panels, with maximum mean cyprid counts of 6 ± 1 cyprids and 8 ± 3 cyprids on the 10th May and 17th May respectively (Fig. 63). At Site C maximum recorded means occurred on the 12th of May, rather than the 10th, with one large observation per peak (Fig. 58). However at Site T these peaks lasted for three days, with the maximum recorded mean observed on the first day (10th May); large standard errors of the mean counts over this three day period, especially with the grooved panels, show no comparative difference in settlement. During these three days the wind was predominantly from the NE / E and therefore such observed differences between settlement at Site C and Site T is most probably related to their position towards the wind. As the panel block at Site T faces northerly towards the incoming tide, the cyprids would be pushed in the direction of the panels during NE winds. Conversely although settlement would still occur at southeast-facing Site C during NE winds, it is relatively protected from direct wave action in such conditions and therefore it is only when the wind veers towards the east, resulting in water movement across the front of the panels, that the high settlement peak is seen.

Corresponding peaks of settlement at Site T also occurred on the horizontally and vertically grooved panels on the 10th and 17th May; mean maximum cyprid counts on horizontally grooved panels were 48 ± 27 cyprids and 161 ± 30 cyprids, with maximum counts on vertically grooved panels of 52 ± 11 and 103 ± 3 on the 10th and 17th of May respectively (Fig 64). The normality of the data distribution allowed Pearson correlation analysis to be performed, which confirmed that the settlement

peaks on different panel types were temporally correlated ($r^2 = 0.7494$ horizontal to vertical, $r^2 = 0.4585$ plane to vertical, $r^2 = 0.4193$ vertical to plane; $p < 0.001$, $n=96$ for all comparisons). The 10th –12th May settlement increase is seen after 8 days of predominantly NE winds, and that of the 17th May after 10 days of predominantly NE winds, indicating that wind direction is an important influence in the settlement response (Fig. 63 and 64). Additionally after the 19th May settlement dropped markedly, which coincided with the change in wind direction to the SW, where it chiefly remained until the end of the season.

Cyprid settlement densities were generally higher on horizontal panels than on the vertical grooved panels, even though the groove settlement area was 12cm² on each type (Fig. 64). Although the plane panels were statistically temporally correlated to the grooved panels, settlement only reached a mean maximum of 8 ± 3 cyprids (17th May, panels with extract) and therefore this panel type performed poorly at this site during this season. Settlement on the grooved panels were concentrated on the grooved areas, with approximately 98% of cyprid counts occurring in the milled sections and the remainder settling on the 92cm² area of plane area.

Comparisons of settlement on the different panel types over the sampled 32 days (5th May to 6th June, except for 4th June when no sampling occurred) revealed the expected significant Day and Panel type effect. Additionally a significant interaction occurred due to the persistent low settlement on the plane panels, even when high settlement was observed on the grooved panels (Table 7).

Table 7
Settlement panels: between-treatment comparisons, Site T 2001, 32 days.

Source	<i>df</i>	SS	MS	<i>F</i>	<i>p</i>
Panel type	2	24.923	12.461	69.89	<0.001
Day	31	49.521	1.597	51.41	<0.001
Panel type x Day	62	11.055	0.178	5.74	<0.001
Error	192	5.966	0.031		
Total	287	91.465			

ANOVA for cyprid (log $x+1$) settlement on different panel treatments (plane, horizontal and vertical grooves, all with extract, $n=3$ for each treatment per day). The factors were Panel type (fixed) and Day (random).

As plane panel densities were so low, and influential in the observed interaction (Table 7), the ANOVA analysis was repeated for only the grooved treatments (Table 8).

Table 8
Settlement panels: comparisons of groove orientation, Site T 2001, 32 days.

Source	<i>df</i>	SS	MS	<i>F</i>	<i>p</i>
Groove orientation	1	0.566	0.566	12.20	0.001
Day	31	54.123	1.746	44.32	<0.001
Panel type x Day	31	1.439	0.046	1.18	0.260
Error	128	5.042	0.039		
Total	191	61.169			

ANOVA for cyprid (log $x+1$) settlement on triplicate horizontally and vertically grooved panels over 32 days. The factors were Panel type (fixed) and Day (random).

Settlement was again found to be significantly different with panel type, with horizontally grooved panels having higher settlement densities than the vertically grooved panels. Day was a significant influence on settlement, as expected, but no interaction occurs when the plane panels are omitted from the analysis. Therefore although settlement temporally varies, the preference of cyprids for horizontally grooved panels does not alter.

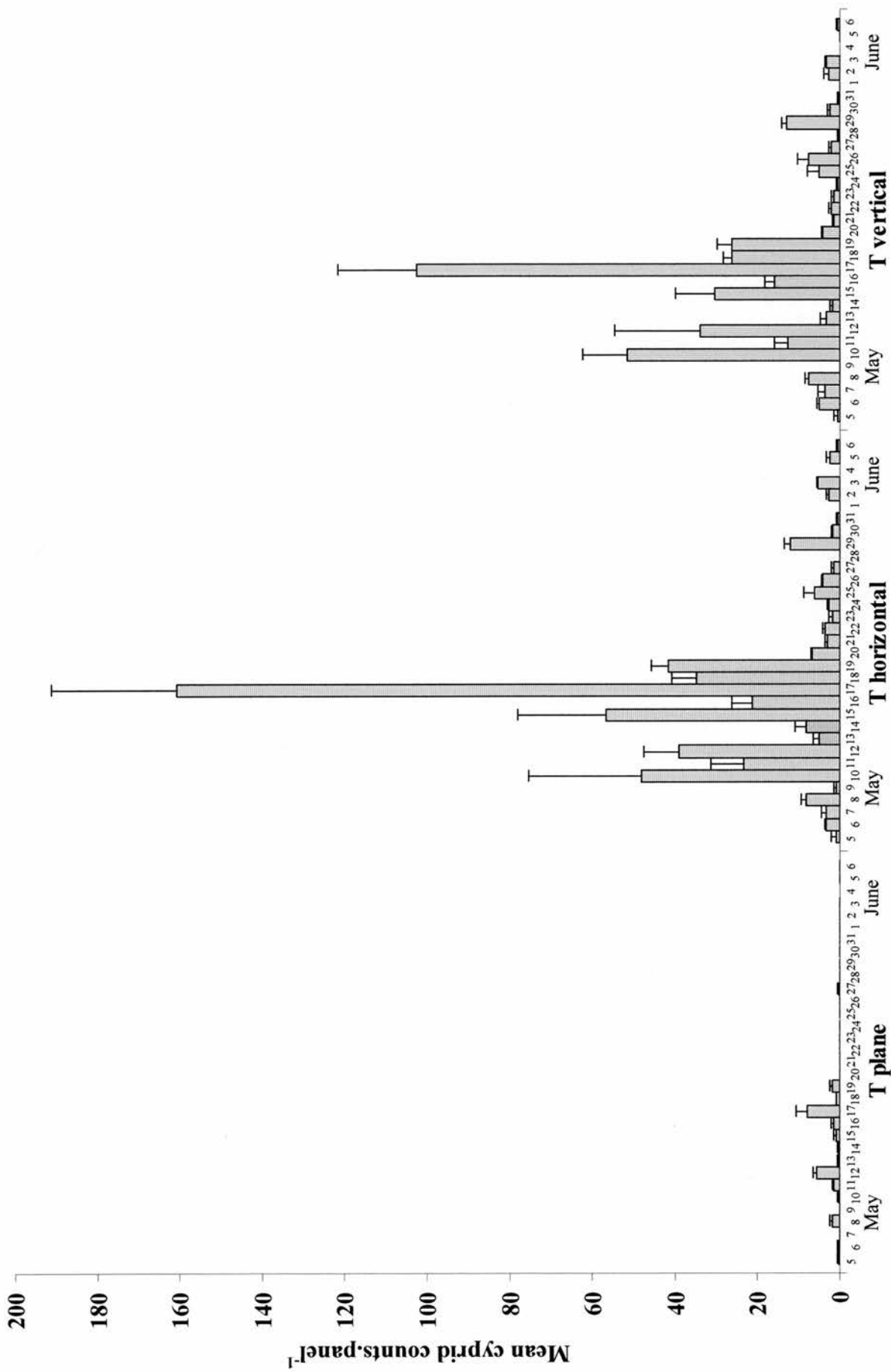


Fig. 63 – Mean daily settlement of *S. balanoides* cyprids on plane, horizontal and vertically grooved panels at Site T from 5th May to 6th June 2001 (33 days). All panels painted with extract (n=3 each panel type per day). Vertical lines represent S.E.M.

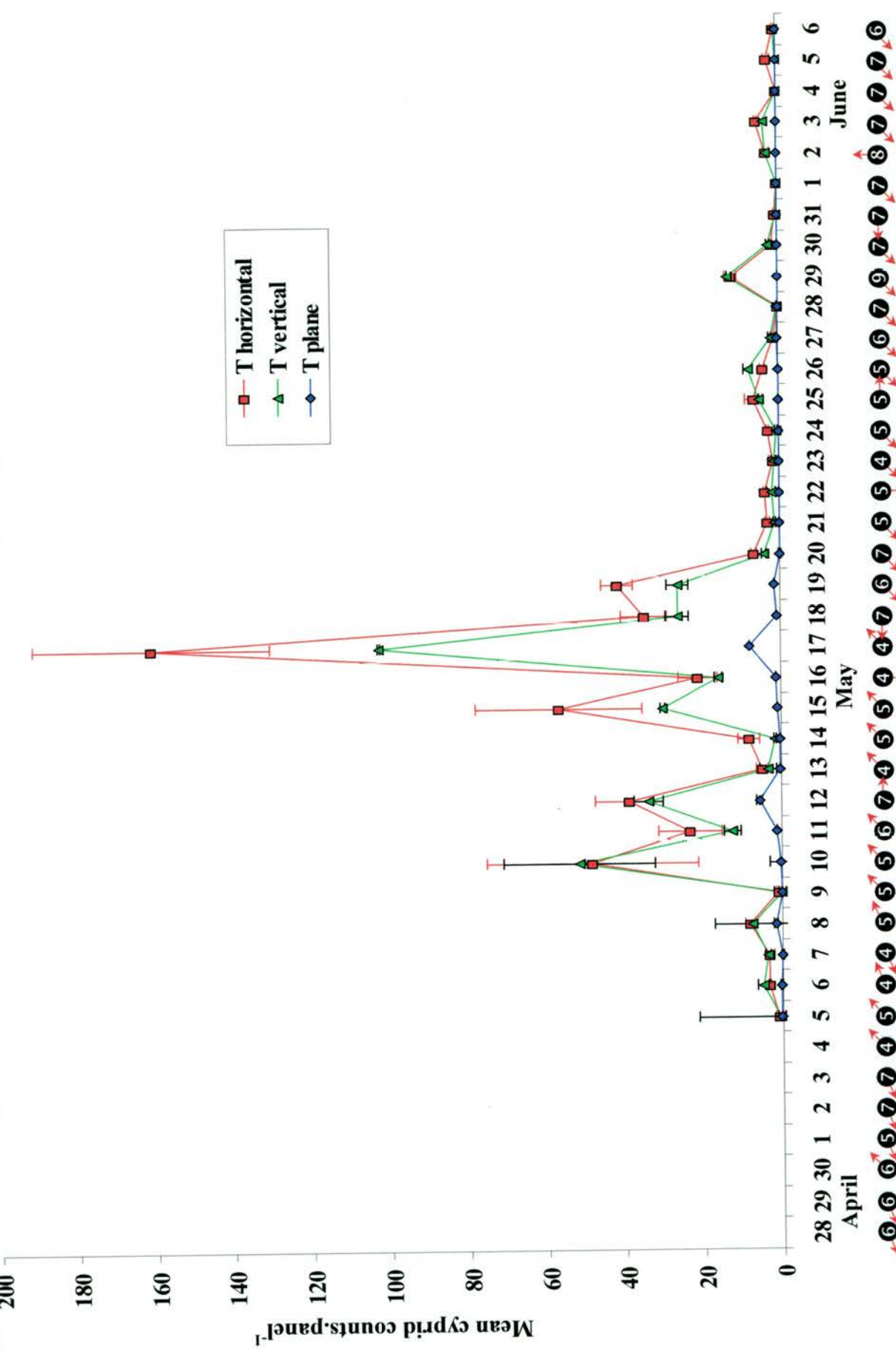


Fig. 64 – Mean daily settlement of *S. balanoides* cyprids on plane, horizontal and vertically grooved panels at Site T sampled from 5th May to 6th June 2001 (33 days). All panels painted with extract (n=3 each panel type per day). Vertical lines represent S.E.M. Wind data shown as maximum Beaufort strength and predominant direction over each daily period, calculated from 10 minute averages.

3. 2. 3. *Fife Ness, 2001*

3. 2. 3. 1. *Sites J and K*

Sites J and K were sampled daily between the 28th of April and the 6th of June (40 days) using plane sanded panels with extract and without extract (n=4 for each treatment per day), as the previous season at St Andrews had suggested that these provided a suitable surface for cyprid settlement. However as can be seen in Figs. 65 and 66, settlement was extremely poor with a maximum mean cyprid count of only ~2 cyprids and ~5 cyprids occurring on April 3rd at sites J and K respectively. Such low densities are unreliable estimators of correlations in cyprid behaviour, e.g. when compared to water flux, as indicated by captured sediment weight (Fig.65). Therefore from the 21st of May horizontal and vertical grooved panels were introduced to Site K and were used until the end of the season (Site K; duplicates of plane panels with extract, plane panels without extract, horizontally grooved panels with extract, and vertically grooved panels were deployed daily from the 21st May). These grooved panels yielded higher densities of settlers (Fig. 67), and were therefore a more reliable indicator of cyprid settlement patterns when used in data analyses. Site J was continued as before, with four panels with extract and four without, in order to prevent compounding interpretation of any influence of wind or water state.

Unlike at Site C there is no apparent one-day delay between peaks of increased sediment capture and corresponding peaks in cyprid settlement at Site K, although an increase is seen in settlement four days after the sediment peak on the 17th May and 25th May; mean cyprid counts on painted panels of 47 ± 7 and 160 ± 25 respectively (Fig. 67). Additionally as the increases in settlement densities occur after strong SW winds on the previous day (Force 7 SW 17th May, Force 9 SW 29th May), it cannot be

strongly stated that settlement was related to increased sediment weight. To further compound any correlation with wind direction, the use of the unresponsive plane panels at the beginning of the season coincided with extended periods of NE winds and as such there is little data to compare settlement densities with wind direction at Fife Ness. The plane panels performed poorly throughout the whole season (Fig. 65 and 66), therefore this latter observation of low settlement with NE winds cannot be considered a function of the wind direction itself, but rather is due to panel type. This is illustrated by the lack of any significant settlement change with wind direction throughout the season at Site J (Fig. 65), where plane panels were used for the whole season.

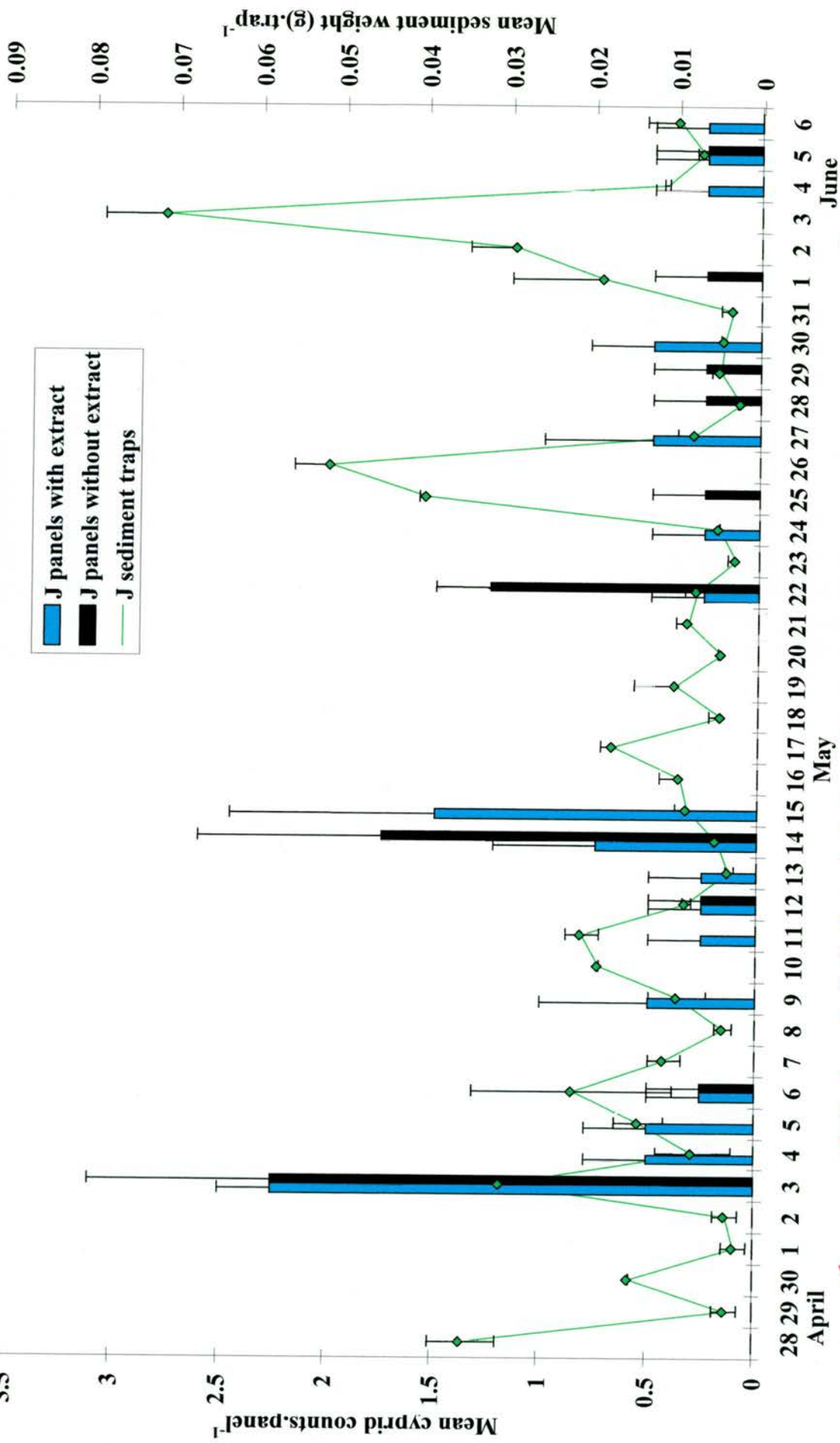


Fig. 65 – Mean daily settlement of *S. balanoides* cyprids on plane panels with captured ashed sediment weight from traps at Site J during the 2001 season. Panels; painted with extract or unpainted (n=4 each treatment each day). Sediment traps were ~ 71 cm apart at each side of the panel backplate; emptied daily (n=2 each day). Vertical lines represent S.E.M. Wind data shown as maximum Beaufort strength and predominant direction over each daily period, calculated from 10 minute averages.

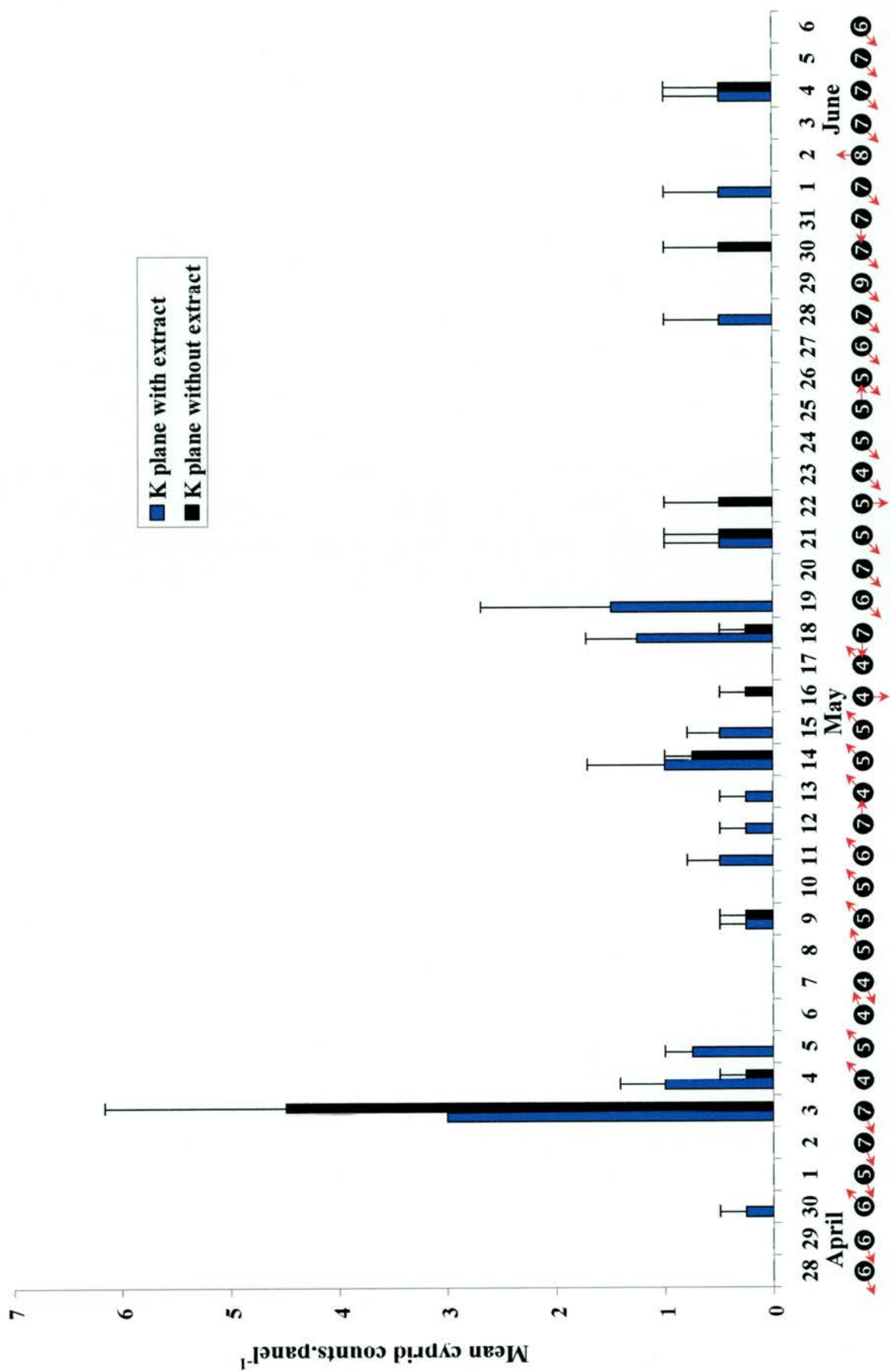


Fig. 66 – Mean daily settlement of *S. salanoides* cyprids on plane panels with and without painted extract at Site K during the 2001 season. From 28th April until the 20th May inclusive, n=4 for each panel treatment per day; from 21st May n=2 per treatment per day. Vertical lines represent S.E.M. Wind data shown as maximum Beaufort strength and predominant direction over each daily period, calculated from 10 minute averages.

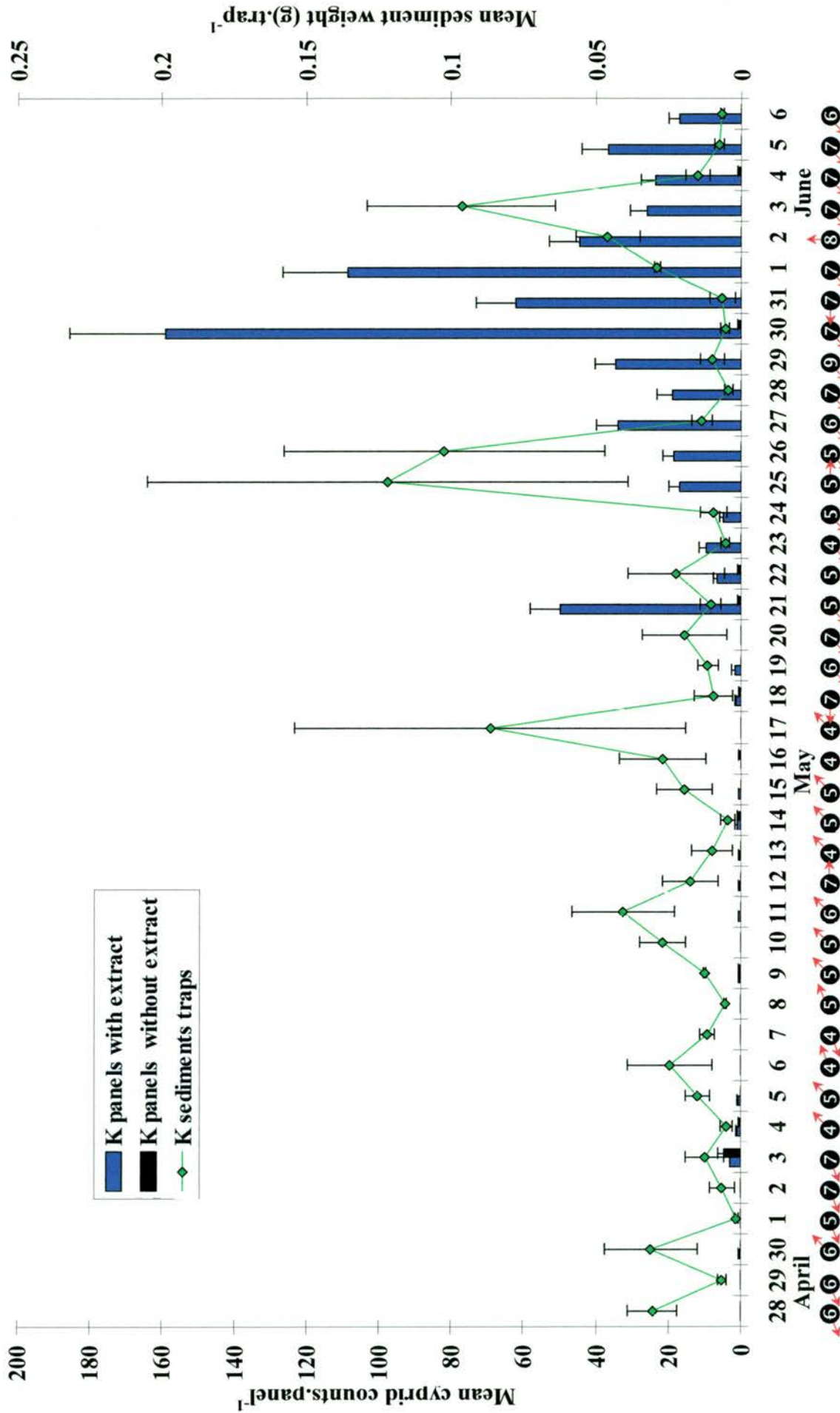


Fig. 67 – Mean daily settlement of *S. balanoides* cyprids on plane and grooved panels with captured ashed sediment weight from traps at Site K during the 2001 season. Panels; from 28th April until the 20th May inclusive, n=4 for each panel treatment per day; from 21st May bar observations n=6 for grouped panels with extract, and n=2 for panels without extract. Sediment traps were ~ 71 cm apart at each side of the panel backplate; emptied daily (n=2 each day). Vertical lines represent S.E.M. Wind data shown as maximum Beaufort strength and predominant direction over each daily period, calculated from 10 minute averages.

3. 2. 3. 2. Site K – Effects of panel type on settlement

As discussed in section 3. 2. 3. 1. panel type had an observed effect on the settlement densities of cyprids at Fife Ness and is further emphasised in Fig. 68. However unlike at Site T no clear pattern of higher settlement on either horizontally grooved or vertically grooved is apparent (Fig. 68 and 69). In Fig. 69 vertical panels yielded higher cyprid densities than horizontal grooved panels on May 30th, with mean counts of 86 ± 10 and 73 ± 15 settlers respectively, whereas on the 1st of June the reverse occurs, with mean counts of 51 ± 2 cyprids on vertical grooved panels and 58 ± 6 cyprids on horizontal grooved panels. Large observed standard errors on means of both panel types at these dates are due to low panel replication.

ANOVA tests identified that panel type and day were of significant influence to cyprid settlement, and a significant interaction also occurred (Table 9). Day was predicted to be significant due to visible differences seen in settlement throughout the season (e.g. Fig. 67). Low or persistent zero settlement on plane panels caused the observed significant interaction, therefore the ANOVA analysis was calculated again with the plane panel data omitted (Table 10).

Table 9
Settlement panels: between-treatment comparisons, Site K 2001, 17 days.

Source	<i>df</i>	SS	MS	<i>F</i>	<i>p</i>
Panel type	2	27.646	13.823	128.63	<0.001
Day	16	6.297	0.394	12.84	<0.001
Panel type x Day	32	3.439	0.107	3.51	<0.001
Error	51	1.563	0.031		
Total	101	38.945			

ANOVA for cyprid ($\log x+1$) settlement on different panel treatments (plane, horizontal and vertical grooves, all with extract, $n=2$ for each treatment per day). The factors were Panel type (fixed) and Day (random).

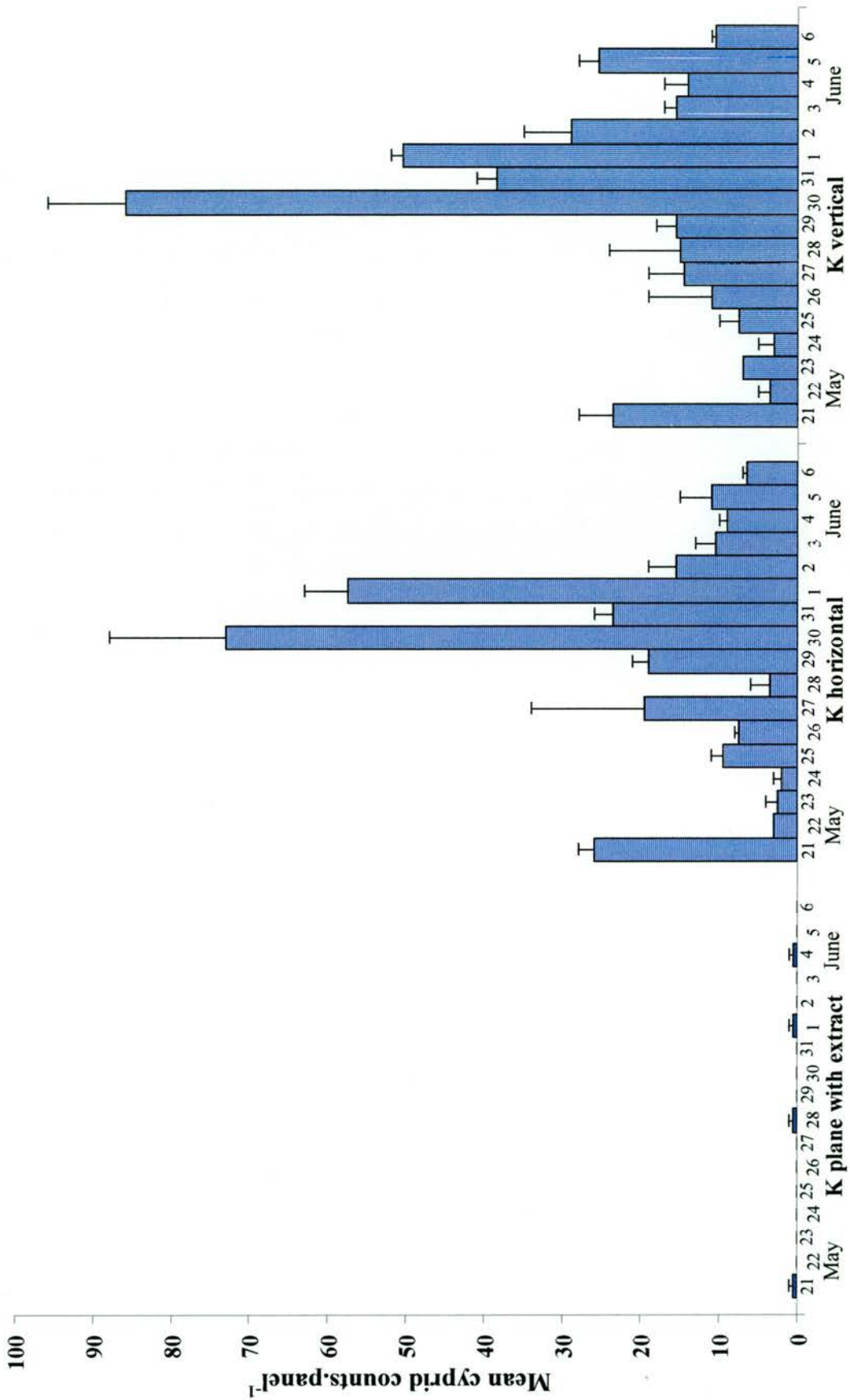


Fig. 68 – Mean daily settlement of *S. balanoides* cyprids on plane, horizontal and vertically grooved panels at Site K from 21st May to 6th June 2001 (17 days). All panels painted with extract (n=2 each panel type per day). Vertical lines represent S.E.M.

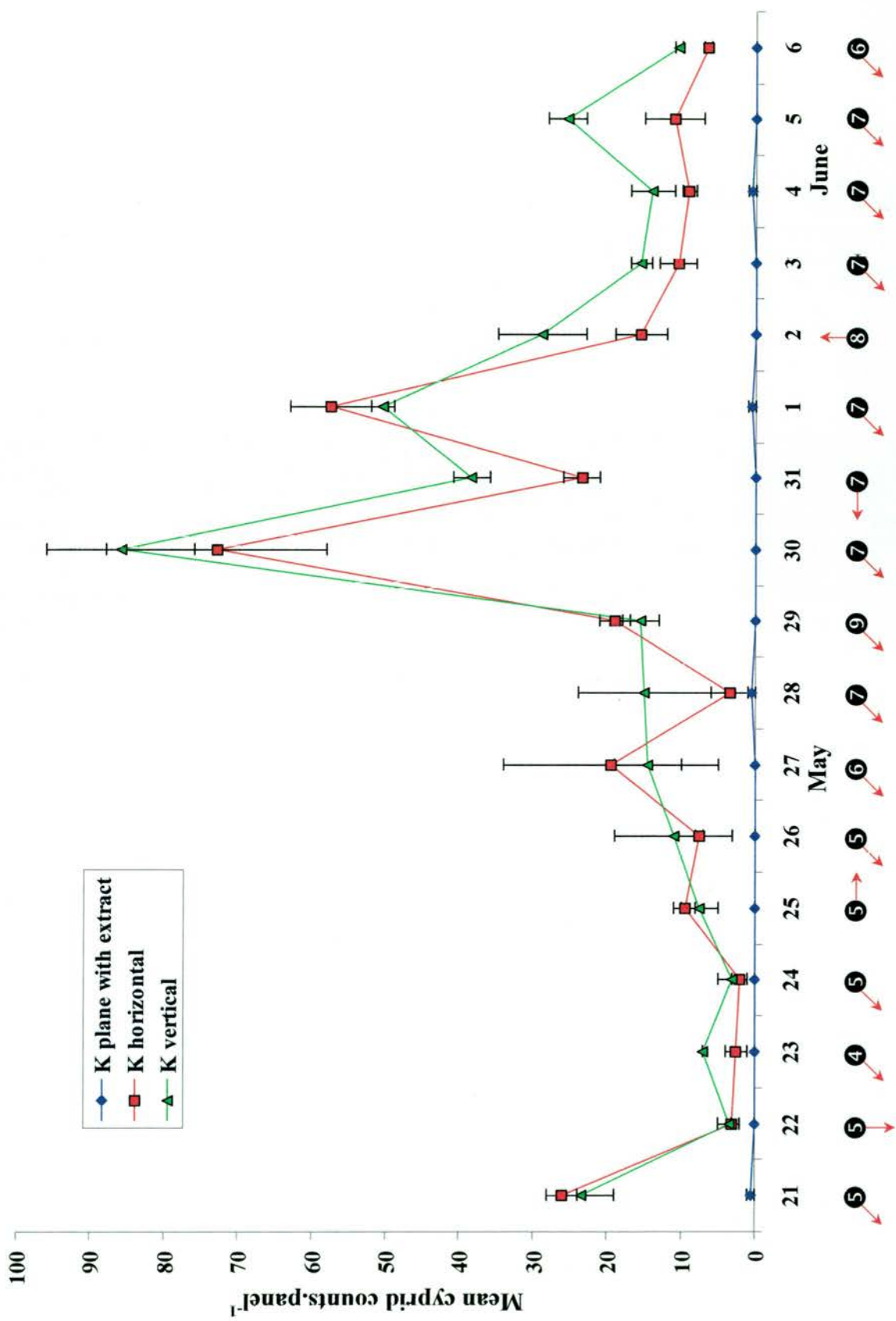


Fig. 69 – Mean daily settlement of *S. balanoides* cyprids on plane, horizontal and vertically grooved panels at Site K sampled from 21st May to 6th June 2001 (17 days). All panels painted with extract (n=2 each panel type per day). Vertical lines represent S.E.M. Wind data shown as maximum Beaufort strength and predominant direction over each daily period, calculated from 10 minute averages.

Table 10**Settlement panels: comparisons of groove orientation, Site K 2001, 17 days.**

Source	<i>df</i>	SS	MS	<i>F</i>	<i>p</i>
Groove orientation	1	0.295	0.295	8.64	0.010
Day	16	9.052	0.567	13.92	<0.001
Panel type x Day	16	0.545	0.034	0.84	0.637
Error	34	1382	0.041		
Total	67	11.274			

ANOVA for cyprid ($\log x+1$) settlement on duplicate horizontally and vertically grooved panels over 17 days. The factors were Panel type (fixed) and Day (random).

With the plane panel data omitted, horizontal and vertical panels still had significantly different settlement. Comparison of means over the sampled days revealed that settlement densities on vertical panels were greater than those on horizontal panels (22 ± 4 cyprids and 18 ± 3 cyprids respectively). Day was still found to be significant, but the lack of interaction revealed that while the settlement counts may vary, the performance of each panel type does not differ with the day sampled.

3. 2. 4. *Kingsbarns, 2001*

3. 2. 4. 1. *Sites L and M*

Sites J and K were sampled daily between the 28th April and the 6th of June (40 days) using plane sanded panels with extract and without extract (n=4 for each treatment per day), as results from the 2000 season suggested that these panels were suitable for settlement studies. However, as can be seen in Figs. 70 and 71, settlement was very low with a maximum mean cyprid count of only ~ 1 cyprid ± 0.5 occurring on both the 13th and 18th of May at Site L on extract painted panels. At the neighbouring location of Site M, settlement was also very low with a maximum mean count of ~ 6 cyprids observed on the 12th May. As with Fife Ness, these low observed counts at Kingsbarns yield little information about cyprid settlement patterns and therefore from the 21st of May horizontal and vertical grooved duplicate panels were introduced to Site M, with Site L maintaining its panel composition of four plane panels with extract and four without for the whole season. Site M was thus sampled daily with duplicates of plane panels with extract, plane panels without extract, horizontal grooved panels with extract and vertical grooved panels with extract. These grooved panels provoked a greater settlement response (Figs. 72-74), and were therefore a more reliable indicator of cyprid settlement patterns when used in data analyses.

Although no inferences can be made concerning a settlement response to any increase in captured ashed sediment weight at Site L due to low densities, a clear pattern of sediment peaks were seen with NE / N / E winds, with S / SW winds conferring little or no retained sediment. These sediment peaks occur on 30th April (NE), 4-6th May (NE), 10-11th May (NE), 14-17th May (predominantly NE), 25th May (E) with a final large peak occurring from the 2nd-3rd June with a Force 8 N gale (Fig. 70).

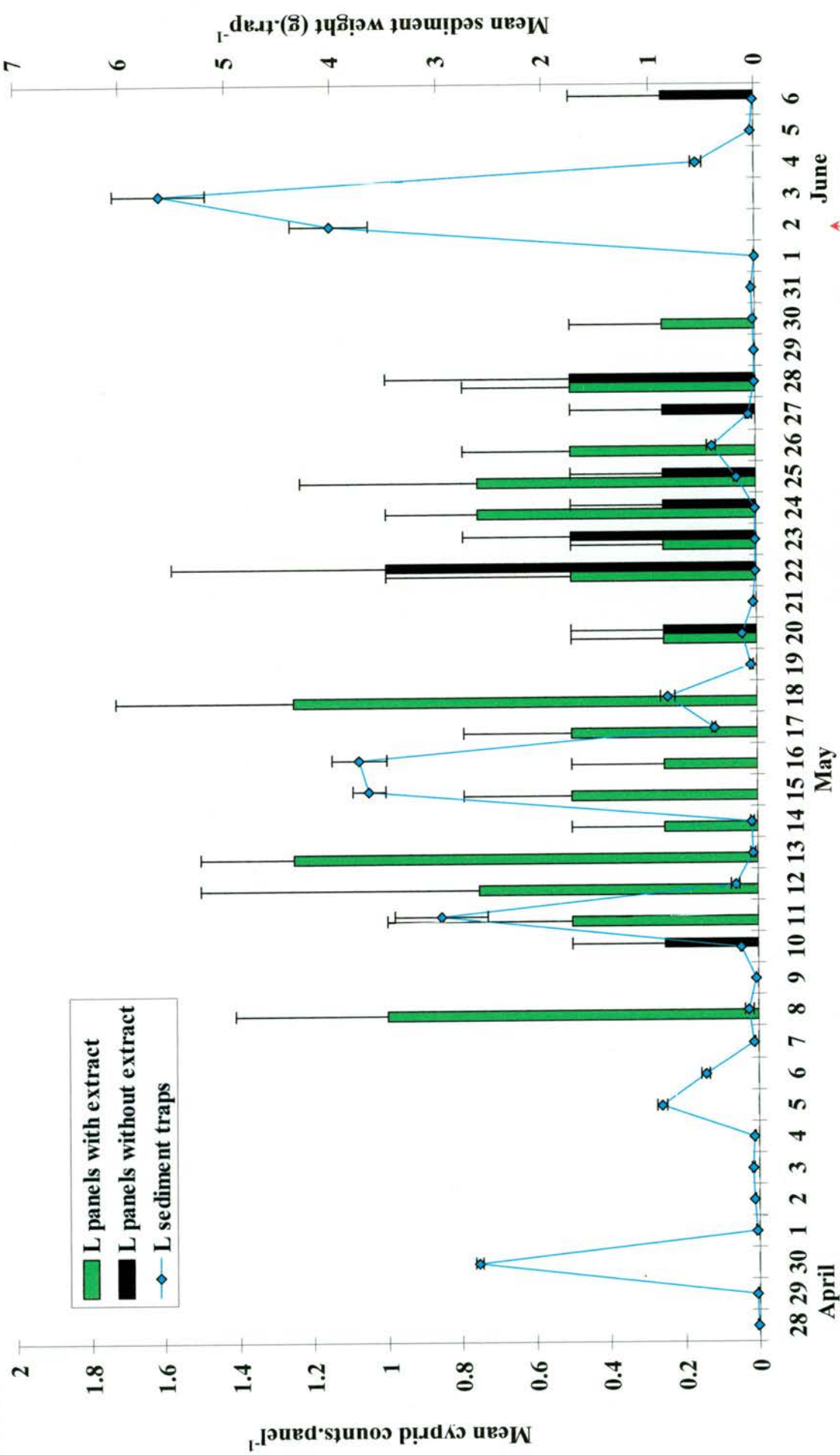


Fig. 70 – Mean daily settlement of *S. balanoides* cyprids on plane panels with captured ashed sediment weight from traps at Site L during the 2001 season. Panels; painted with extract or unpainted (n=4 each treatment each day). Sediment traps were ~71 cm apart at each side of the panel backplate; emptied daily (n=2 each day). Vertical lines represent S.E.M. Wind data shown as maximum Beaufort strength and predominant direction over each daily period, calculated from 10 minute averages.

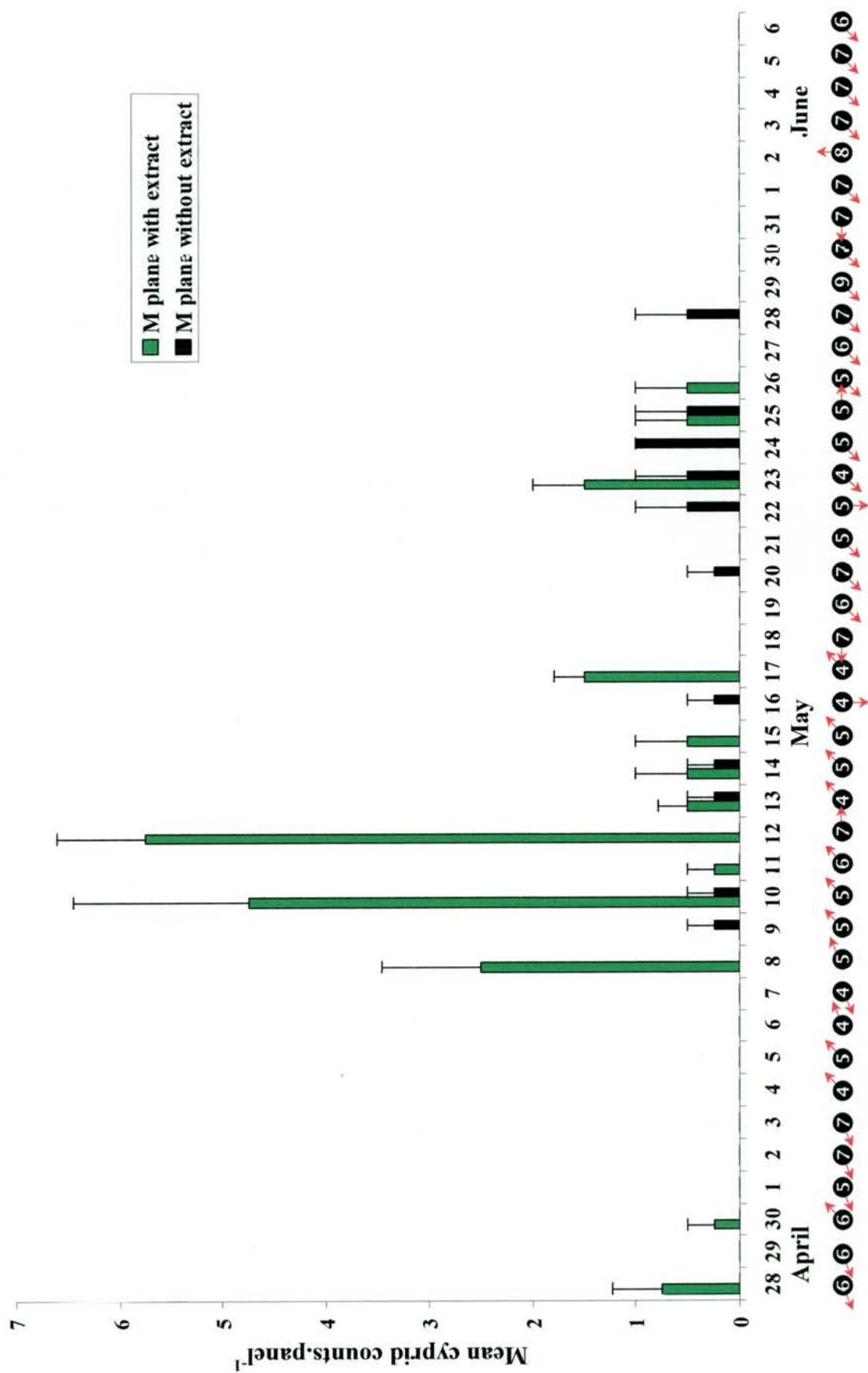


Fig. 71 – Mean daily settlement of *S. balanoides* cyprids on plane panels with and without painted extract at Site M during the 2001 season. From 28th April until the 20th May inclusive, n=4 for each panel treatment per day; from 21st May n=2 per treatment per day. Vertical lines represent S.E.M. Wind data shown as maximum Beaufort strength and predominant direction over each daily period, calculated from 10 minute averages.

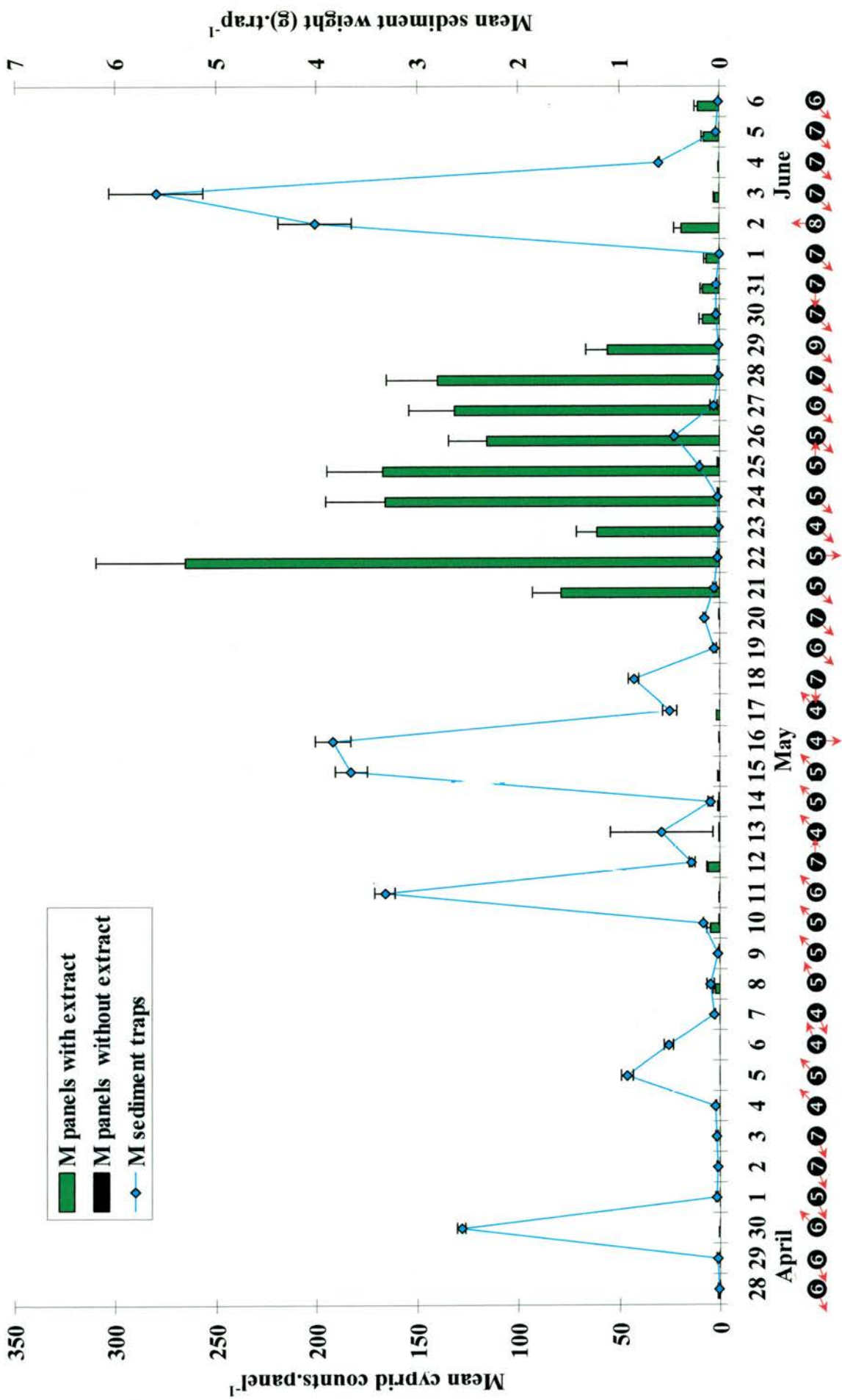


Fig. 72 – Mean daily settlement of *S. balanoides* cyprids on plane and grooved panels with extract with captured ashed sediment weight from traps at Site M during the 2001 season. Panels; from 28th April until the 20th May inclusive, n=4 for each panel treatment per day; from 21st May bar observations n=6 for grouped panels with extract, and n=2 for panels without extract. Sediment traps were ~ 71 cm apart at each side of the panel backplate; emptied daily (n=2 each day). Vertical lines represent S.E.M. Wind data shown as maximum Beaufort strength and predominant direction over each daily period, calculated from 10 minute averages.

The pattern of increases in sediment collection with NE / N / E winds is also seen with Site M (Fig.72). Settlement using grooved panels began on the 21st May, hence the large increase in settlement density seen after this period. Maximum mean settlement on panels with extract occurred on the 22nd May (255 ± 43 cyprids) with a predominantly southerly Force 5 wind and a mean ashed sediment weight of $0.026g \pm 0.005g$; this sediment weight is very low for Kingsbarns when compared to the maximum observed mean weight of $5.596g \pm 0.460g$ at this site (Force 8 N). This indicates that the larvae are settling in periods of calm water conditions. However as the period of 21st May until the end of the season on the 6th June had predominantly SW winds, any firm conclusions of settlement with wind direction and water flux cannot be made.

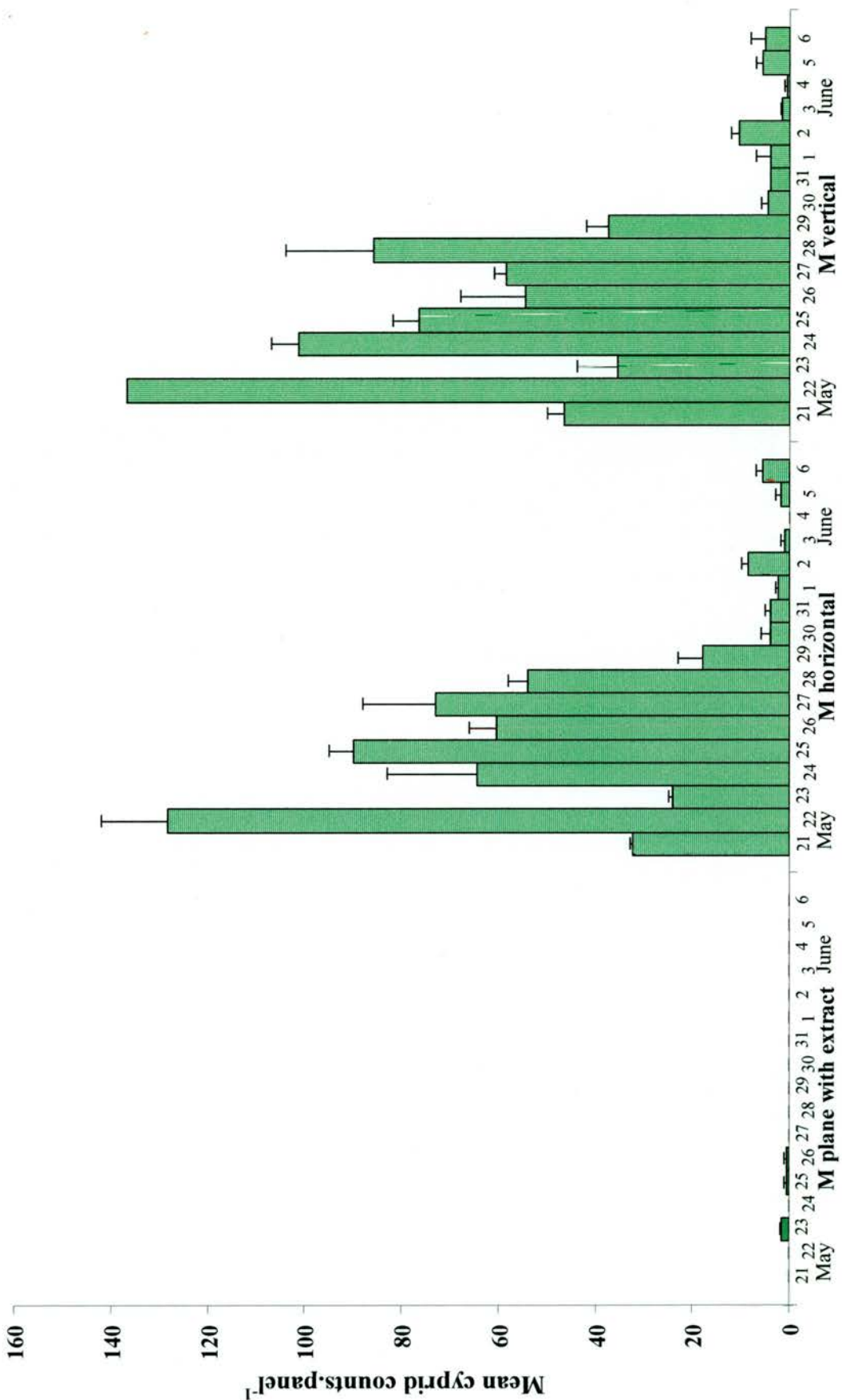


Fig. 73 – Mean daily settlement of *S. balanoides* cyprids on plane, horizontal and vertically grooved panels at Site M from 21st May to 6th June 2001 (17 days). All panels painted with extract (n=2 each panel type per day). Vertical lines represent S.E.M.

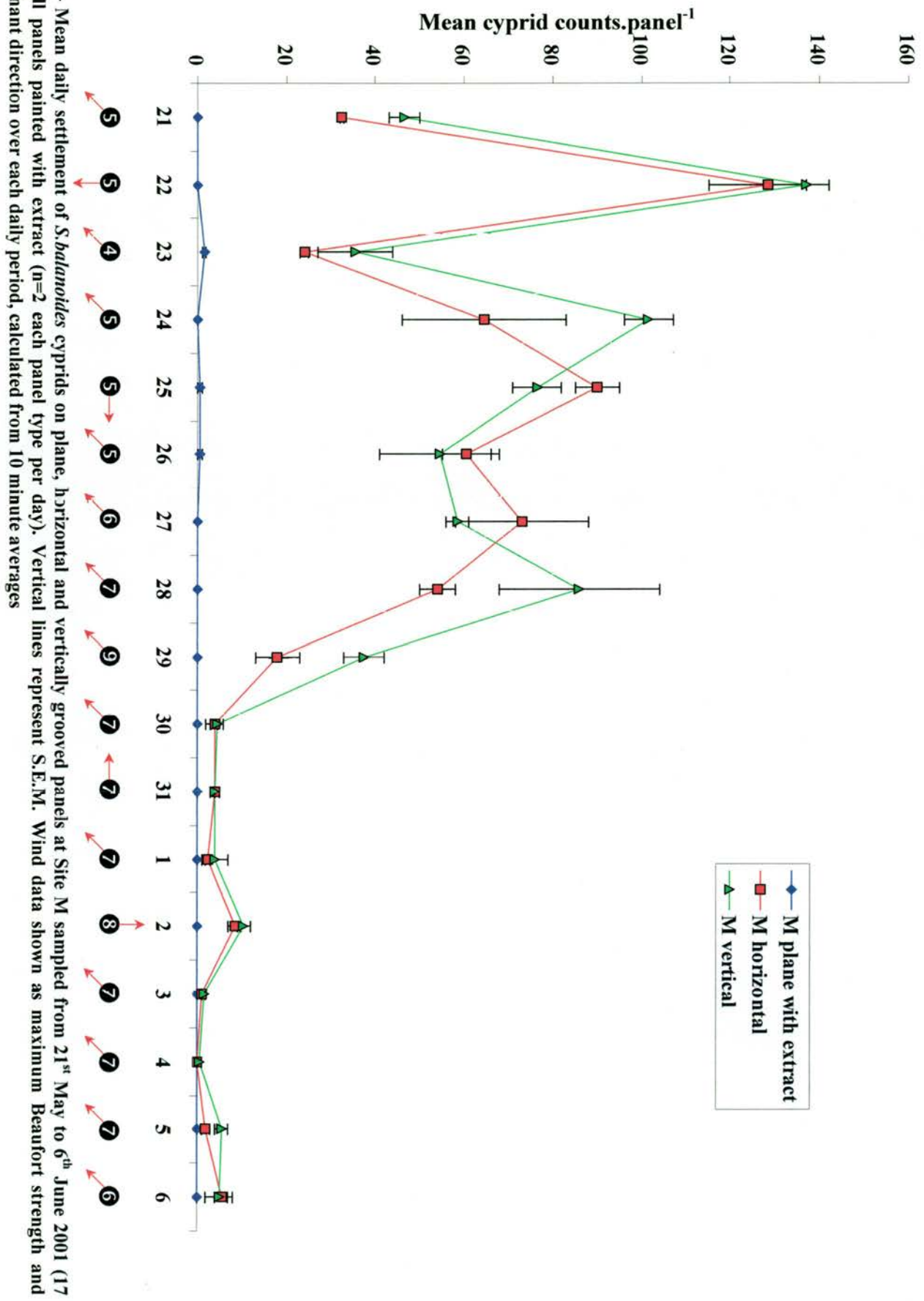


Fig. 74 – Mean daily settlement of *S. balanoides* cyprids on plane, horizontal and vertically grooved panels at Site M sampled from 21st May to 6th June 2001 (17 days). All panels painted with extract (n=2 each panel type per day). Vertical lines represent S.E.M. Wind data shown as maximum Beaufort strength and predominant direction over each daily period, calculated from 10 minute averages

3. 2. 4. 2. Site M – Effects of panel type on settlement

As mentioned in 3. 2. 4. 1. panel type had an observed effect on the settlement densities of cyprids at Kingsbarns, and is further emphasised in Fig. 73. When mean cyprid counts of daily duplicate grooved panels are plotted from the 21st May (Fig. 74) the peaks of settlement do not fully correspond, e.g. on the 24th May a peak in settlement occurs on vertical panels, but for horizontal panels an increase is seen on the following day (25th May). Pearson correlation tests found that horizontal, vertical and plane panels were not significantly temporally correlated (horizontal to vertical $r^2 = 0.02621$, $n=34$, $p = 0.3603$; plane to horizontal $r^2 = 0.05583$, $n=34$, $p = 0.1785$; plane to vertical $r^2 = 0.0666$, $n=34$, $p = 0.1405$).

ANOVA tests identified that Panel type and Day were of significant influence to cyprid densities, with a significant interaction between the two factors (Table 11). Day, as predicted, was a significant influence on settlement, as can also be seen in Figs. 73 and 74. Low or zero scores on the plane panels with extract were responsible for the significant interaction, and large contribution to the $MS_{\text{Panel type}}$, and therefore the data was re-analysed with only horizontal and vertical groove panel treatments data (Table 12).

Table 11
Settlement panels: between-treatment comparisons, Site M 2001, 17 days.

Source	<i>df</i>	SS	MS	<i>F</i>	<i>p</i>
Panel type	2	30.296	15.148	464.45	<0.001
Day	16	18.138	1.134	34.76	<0.001
Panel type x Day	32	8.481	0.265	8.13	<0.001
Error	51	1.663	0.033		
Total	101	58.578			

ANOVA for cyprid ($\log x+1$) settlement on different panel treatments (plane, horizontal and vertical grooves, all with extract, $n=2$ for each treatment per day). The factors were Panel type (fixed) and Day (random).

Table 12
Settlement panels: comparisons of groove orientation, Site M 2001, 17 days.

Source	<i>df</i>	SS	MS	<i>F</i>	<i>p</i>
Groove orientation	1	0.065	0.065	1.42	0.242
Day	16	28.827	1.614	35.24	<0.001
Panel type x Day	16	0.454	0.028	0.62	0.846
Error	34	1.557	0.045		
Total	67	27.903			

ANOVA for cyprid ($\log x+1$) settlement on duplicate horizontally and vertically grooved panels over 17 days. The factors were Panel type (fixed) and Day (random).

With the plane panel data omitted from the analysis, settlement was not found to be significantly different on horizontal and vertically grooved panels. The horizontal treatment mean was 34 ± 7 cyprids with a vertical treatment mean of 37 ± 7 cyprids, thereby demonstrating the lack of significance between the two panel types. Additionally the lack of interaction indicates that the observed cyprid response to panel type did not differ over the 17 days sampled.

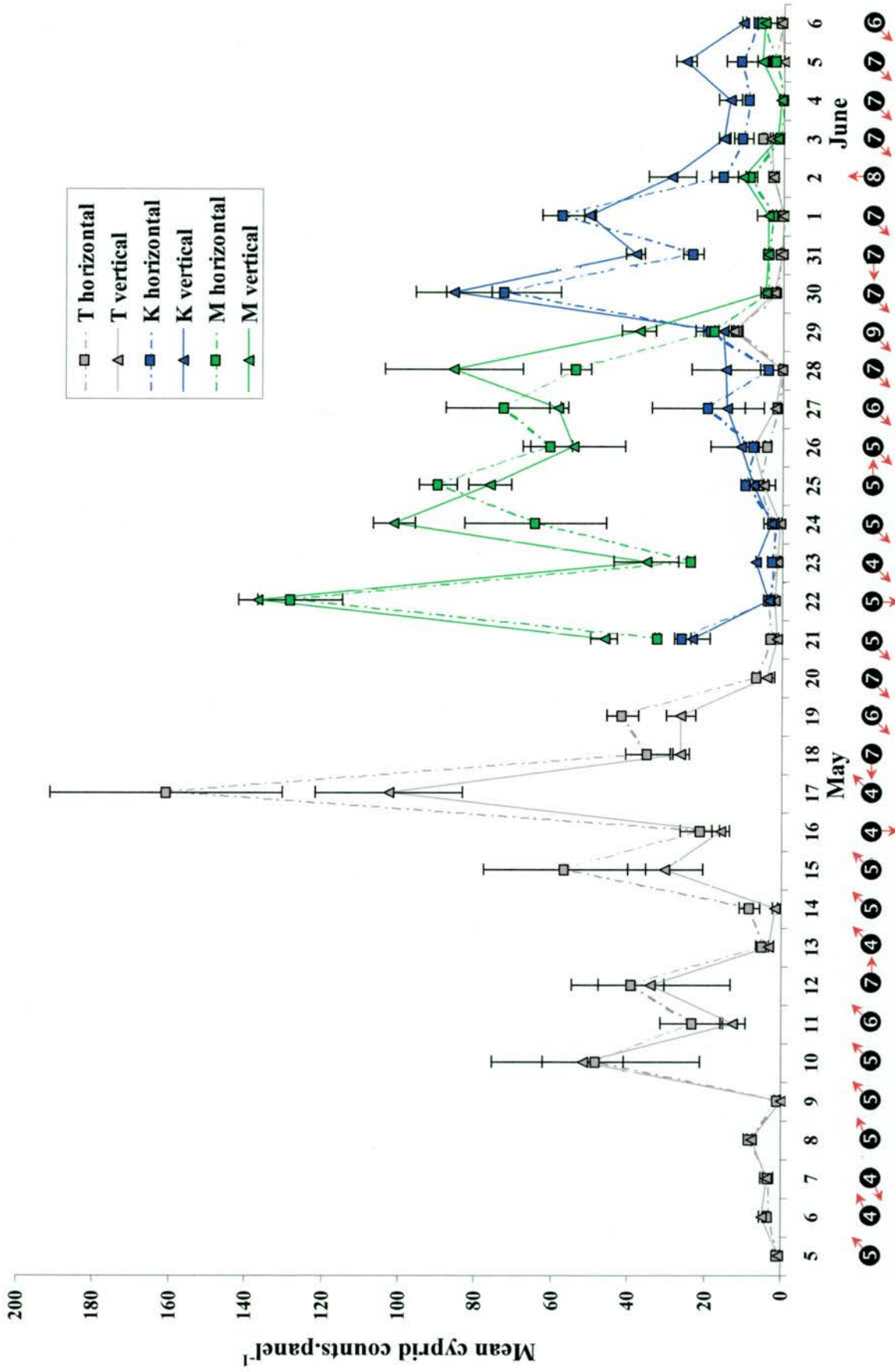


Fig. 75 – Mean daily settlement of *S. balanoides* cyprids on horizontal and vertically grooved panels at Sites K, M and T. Site T is sampled May 5th – June 6th 2001 (32 days), Sites K and M sampled from 21st May- 6th June 2001 (17 days). All panels painted with extract (n=2 each panel type per day for Sites K and M; n=3 each panel type per day for Site T). Vertical lines represent S.E.M. Wind data shown as maximum Beaufort strength and predominant direction over each daily period, calculated from 10 minute averages

3. 2. 5. Treatment comparisons of panel performance across sites, 2001

A temporal plot of cyprid settlement with the different grooved panels at each site (Fig. 75) reveals one settlement peak for each site, with an apparent temporal delay between sites moving from Site T at St Andrews to Site M at Kingsbarns and finally to Site K at Fife Ness. Mean settlement counts are seen to decrease with each successive peak, with the maximum mean settlement peak count occurring at Site T (161 ± 30 cyprids, horizontal panels, 17th May), and the minimum peak count occurring at Site K (73 ± 15 cyprids, horizontal panels, 30th May). Settlement density increases with periods of NE winds at Site T, and then decreases with the appearance of SW winds. Site M at Kingsbarns and Site K at Fife Ness both display peaks during SW winds, but the peaks do not coincide even though both have their maximum mean settlement observations in such wind conditions. Therefore this observed peak pattern may be due to larval transport down the East Fife coastline, rather than with wind direction alone. However no firm conclusions can be drawn as unfortunately the grooved panels were not sampled for the whole season at sites Fife Ness and Kingsbarns.

As horizontally and vertically grooved panels were found to have greater densities of cyprid settlers, the panels were compared across the sites. ANOVA analysis was performed on horizontal and vertical grooved panel types, across the three sites of K, M and T, for a 16-day period running from the 21st May to the 6th June (Table 13; no 4th June data was included as Site T was not sampled that day). Two replicates of the Site T triplicates were randomly selected, in order to maintain balanced sample sizes for analysis.

Table 13
Settlement panels: comparisons of panel type at Sites K, M and T 2001, 16 days.

Source	<i>df</i>	SS	MS	<i>F</i>	<i>p</i>
Panel type	1	0.011	0.011	0.11	0.763
Site	2	27.817	13.909	32.31	<0.001
Day	15	33.444	2.230	5.18	<0.001
Panel type x Site	2	0.161	0.081	3.12	0.059
Panel type x Day	15	0.739	0.049	1.90	0.065
Site x Day	30	12.916	0.431	12.85	<0.001
Panel type x Site x Day	30	0.777	0.026	0.77	0.786
Error	96	3.216	0.034		
Total	191	79.081			

ANOVA for cyprid (log $x+1$) settlement on duplicate horizontally and vertically grooved panels over 16 days. The factors were Panel type (fixed), Site (random) and Day (random).

Horizontally and vertically grooved panels were found not to have significantly different settlement densities when compared among sites ($F_{1, 2} = 0.11, p = 0.763$). Settlement was found to be significantly influenced by Site and Day over this 16 day period, as would be expected from inspection of Fig. 75. Cyprid settlement responses on the different Panel types between Sites ($F_{2, 96} = 3.12, p = 0.059$) and between Days ($F_{15, 96} = 1.90, p = 0.065$) did not show significant interactions indicating that panel performance did not alter with the sampled location or with days through the sampled season. The significant interaction of Site and Day was expected from Fig. 75, as peaks of settlement at the three sites were not temporally correlated. The non-significant interaction of all the factors ($F_{30, 96} = 0.77, p = 0.786$) reiterates that panel performance did not alter over the locations and days sampled. However whether this would be seen over a range of wind conditions over a greater temporal period, cannot be assessed as the data used for the analysis was from the latter half of the season with predominant SW winds only.

3. 2. 6. Captured sediment weight with settlement

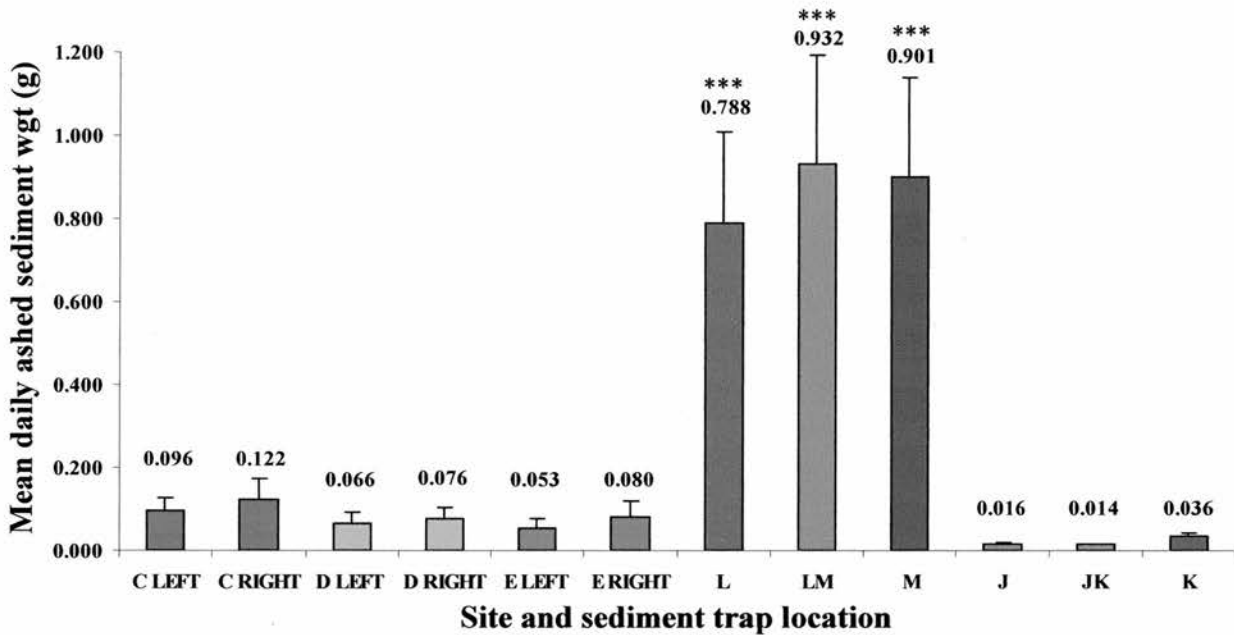


Fig. 76 –Ashed sand fractions of trapped sediment expressed as mean daily weights for all Sites ($\geq 50 \mu\text{m}$). Left and right sediment traps correspond to sediment traps located on the left and right of panel backplates in the field, $\sim 71\text{cm}$ apart. L / M and J / K were sediment traps located in the middle of two adjacent backplates, and were $\sim 71\text{cm}$ from J and K, and L and M at respective sites. From C left to K, $n = 48, 47, 45, 47, 10, 10, 44, 44, 44, 44, 44$ and 44 . Vertical bars represent the S.E.M. Stars denote groupings from Tukey-Kramer comparison test ($\alpha = 0.05$)

Captured ashed sediment weight was seen to vary (Fig. 76), with traps at Kingsbarns collecting significantly more than traps at the other sites. This is simply due to shore type, rather than any difference in trap collecting efficiency. Fife Ness has rocky flat outcrops with little sand present, while St Andrews has a fine sandy bottom with sediments at Kingsbarns being comprised of fine sand and shell fragments.

Spearman correlation analysis confirmed that no linear relationship between sediment weight and settlement on panels existed at any of the sites, indicating that increases in water flux do not provoke simultaneous settlement increases (Table 14).

Table 14**Spearman rank analysis of sediment weight with panel settlement at all sites**

Block	Panel type	r_s	n	p
C	Plane	0.1860	36	0.2773
D	Plane	0.0530	36	0.7604
J	Plane	-0.055	40	0.7632
K	Plane	-0.031	40	0.8508
K	Grooved	-0.083	17	0.7536
L	Plane	0.192	40	0.2357
M	Plane	0.216	40	0.1801
M	Grooved	-0.714	17	0.5041

Daily data collected; n = 2 sediment traps for each n=4 panel observation. Horizontal and vertical panels were pooled at Site K and Site M. Sediment weight in grams, and cyprid counts, $\alpha = 0.05$.

3. 3. *Third settlement season, 2002*

3. 3. 1. *Kinkell Braes, 2002*

3. 3. 1. 1. *Sites C left and C right.*

Adjacent mid intertidal blocks C left and C right were sampled daily with four multiple grooved panels (settlement area 48cm²) and four plane panels, both with extract, from the 20th April until the 2nd of June inclusive. Although plane panel performance was poor during the second settlement season, it was considered necessary to still use them in this final year as a comparative panel treatment through all three seasons.

Two main peaks of larval settlement are seen on panels during this season, at both C left and C right. The first peak at C left (Fig.77) occurs from the 7th to 10th of May, with a maximum mean panel density of 129 ± 13 cyprids on the multiple grooved panels and 0 on plane panels occurring on the 9th of May. At C right a mean cyprid settlement of 187 ± 21 cyprids on grooved panels, and 1 ± 0 cyprids on plane panels was observed (Fig. 78). Winds during this period start from the NE on the 7th, turning to the N for 8-9th May, and then veering to the E on the 10th May. The wind turns W on the 11th of May, and thereafter follows a four day period of southerly winds which resulted in the low observed cyprid densities. The second peak occurs after the wind changes back to the NE again on the 17th of May where it remains for a period of 3 days; the resultant peak runs from the 17th May until the 21st May, by which time the wind direction has moved to the south. In fact from the 20th May until the end of the season, wind direction is predominantly southerly in origin, and little settlement is seen on either panel type. The maximum mean settlement densities through this latter peak, is seen on the 19th of May for both Site C left and C right; 149 ± 27 and $175 \pm$

21 cyprids on grooved panels and 0 and 1 cyprid on plane panels for each site respectively (Figs. 77 and 78). Multiple grooved panels consistently yielded higher cyprid densities with counts occasionally observed as two orders of magnitude greater (19th May).

Temporal plots of C left and C right together (Fig. 79) emphasise the close correlation in settlement, with C right consistently displaying a slightly higher settlement response. Pearson correlation analysis confirmed this temporal correlation ($r = 0.9067$, $n = 176$, $p < 0.001$). ANOVA analysis of the panel types selected and the sites investigated (Table 15) revealed that grooved panels had significantly higher settlement than plane panels and that settlement did not change with site. Additionally panel performance was consistent at each site, as shown by the lack of significant interaction terms.

Table 15
Settlement panels: comparisons of panel type at Sites C left and C right, 44 days 2002.

Source	<i>df</i>	SS	MS	<i>F</i>	<i>p</i>
Panel type	1	116.305	116.305	477.64	<0.001
Site	1	0.847	0.847	3.48	0.063
Panel type x Site	1	0.604	0.604	2.48	0.116
Error	700	170.448	0.243		
Total	703	288.203			

ANOVA for cyprid ($\log x+1$) settlement on duplicate horizontally and vertically grooved panels over 16 days. The factors were Panel type (fixed), Site (random) and Day (random).

As these sites were not significantly different, they were pooled for temporal plots of settlement with trapped ashed sediment weight (Fig. 80), as only two sediment traps were sampled at St Andrews. Unlike in 2001, there was no observed ‘one day delay’ response of increased settlement after a previous increase in captured sediment the day before (Fig. 80, Fig. 58). In fact peaks of settlement occurred one to three days before the peaks of increased sediment retention. Therefore the cyprids were not settling in calmer periods after increased water flux, rather these periods of increased

settlement occurred during N / NNE winds, which indicate that wind direction rather than sea state has a greater settlement influence at this site.

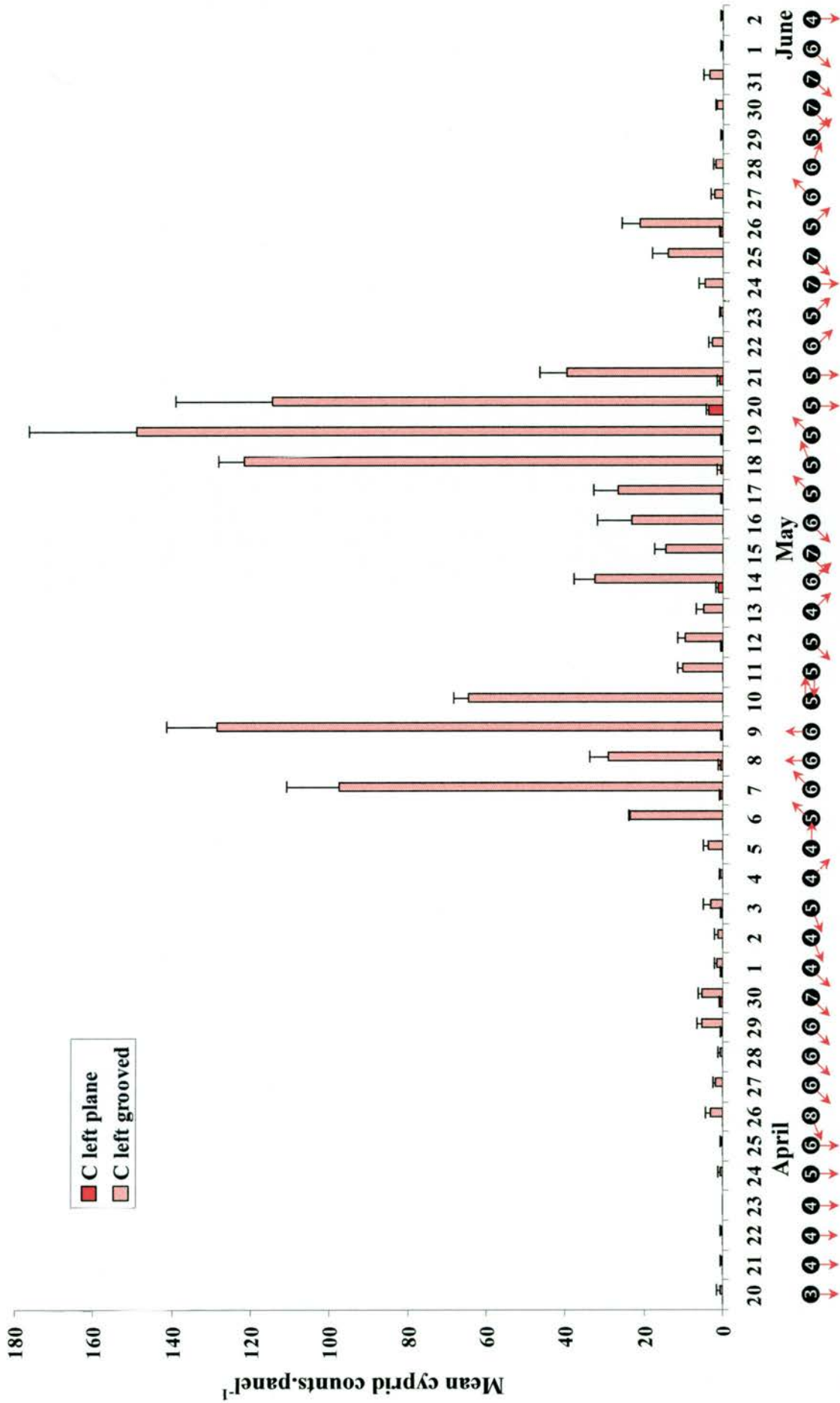


Fig. 77 – Mean daily settlement of *S. balanoides* cyprids on multiple grooved and plane panels, both with extract, at Site C left during the 2002 season. Panels; n=4 for each type, changed daily. Vertical lines represent S.E.M. Wind data shown as maximum Beaufort strength and predominant direction over each daily period, calculated from 10 minute averages.

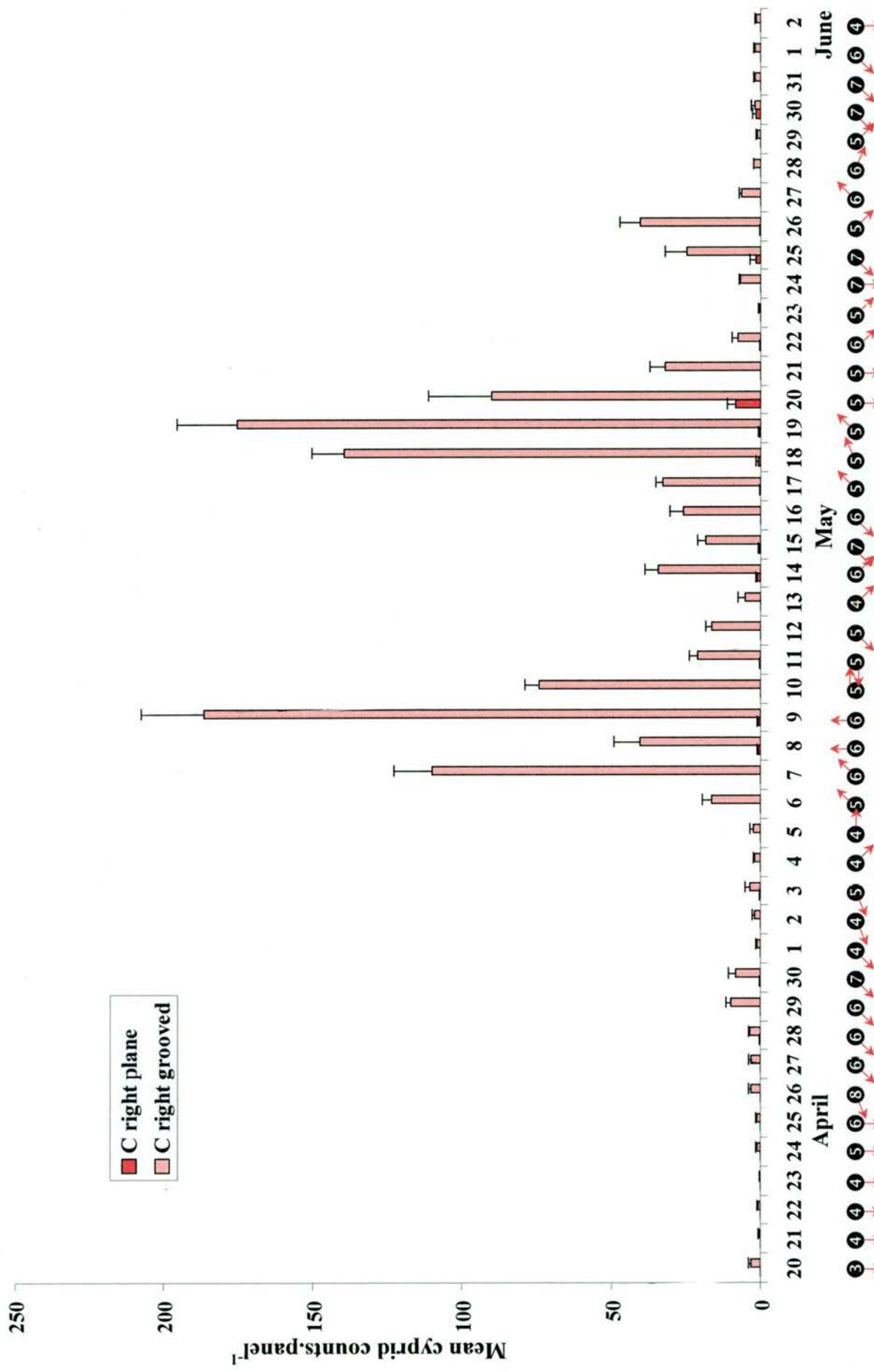


Fig. 78 – Mean daily settlement of *S. balanoides* cyprids on multiple grooved and plane panels, both with extract, at Site C right during the 2002 season. Panels: n=4 for each type, changed daily. Vertical lines represent S.E.M. Wind data shown as maximum Beaufort strength and predominant direction over each daily period, were calculated from 10 minute averages.

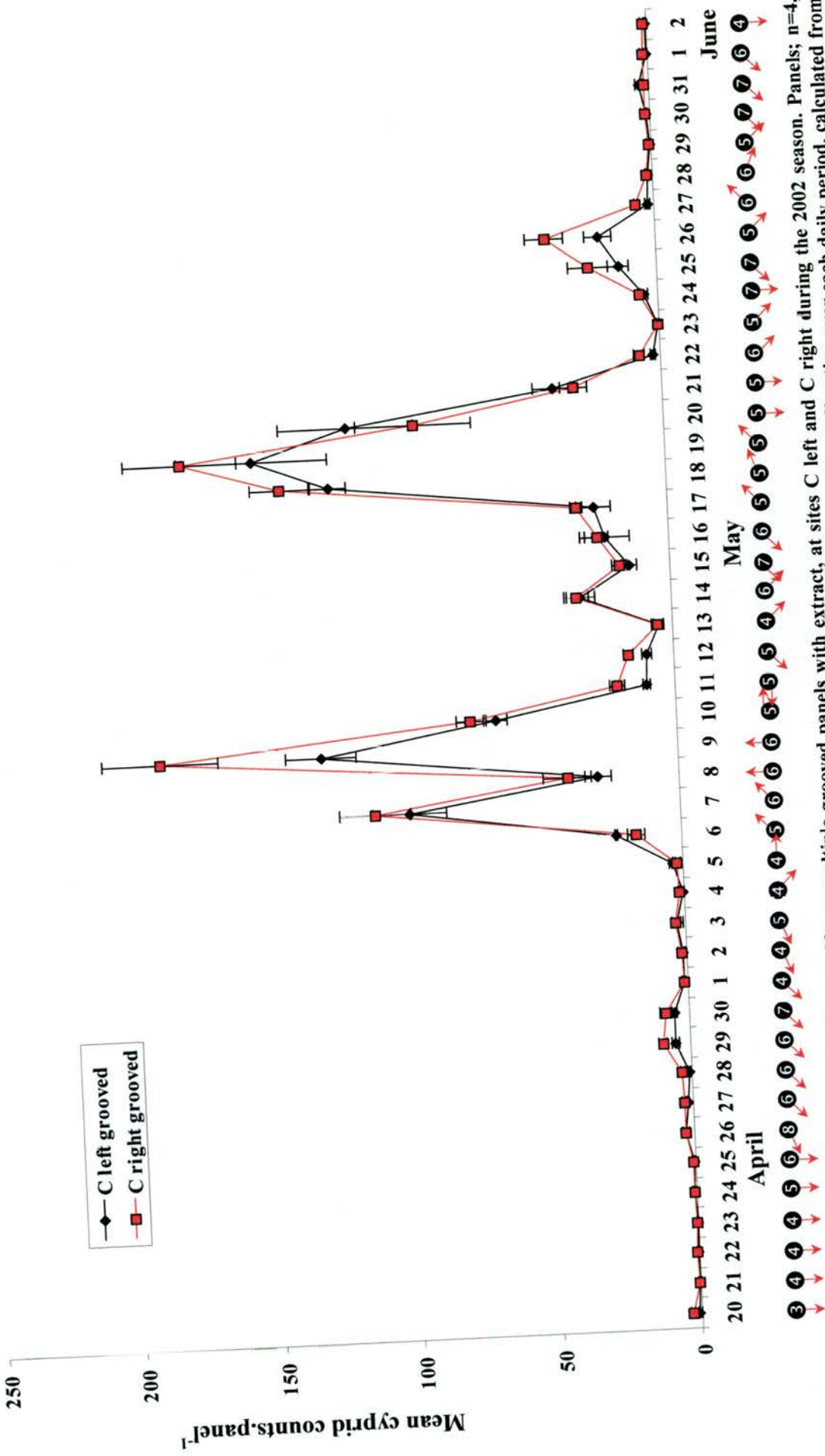


Fig. 79 – Mean daily settlement of *S. balanoides* cyprids on multiple grooved panels with extract, at sites C left and C right during the 2002 season. Panels; n=4, changed daily. Vertical lines represent S.E.M. Wind data shown as maximum Beaufort strength and predominant direction over each daily period, calculated from 10 minute averages.

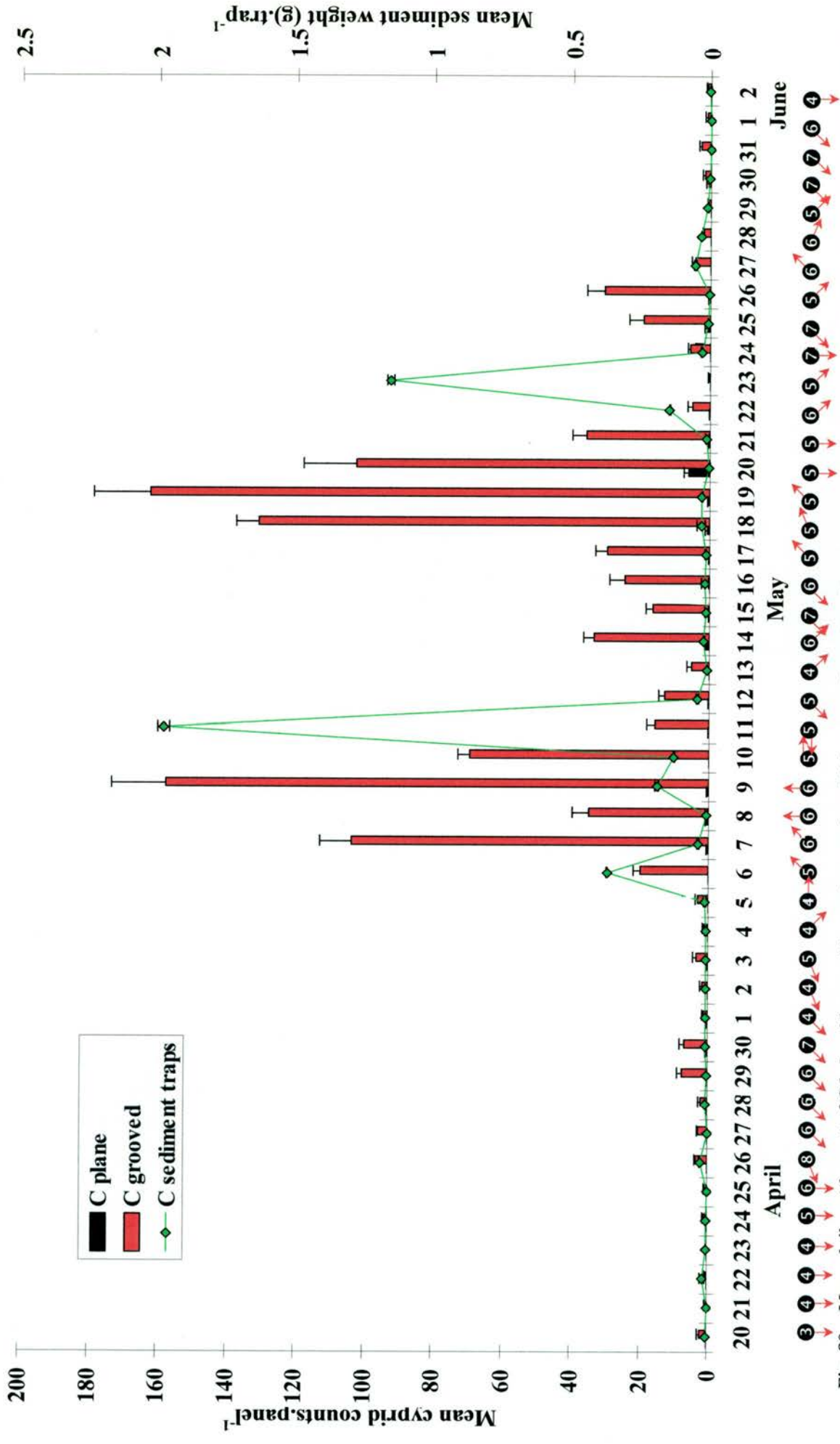


Fig. 80 – Mean daily settlement of *S.balanoides* cyprids on plane and multiple grooved panels with captured ashed sediment weight from traps at pooled sites C left and C right during the 2002 season. Panels all painted with extract; n=4 each treatment each day. Sediment traps were 9 cm apart on a backplate to the right of Site C right and were emptied daily (n=2 each day). Vertical lines represent S.E.M. Wind data shown as maximum Beaufort strength and predominant direction over each daily period, calculated from 10 minute averages.

3.3.1.2. *Site D*

Site D was sampled between 19th April and 10th May inclusive with four multiple grooved panels and four plane panels, both types painted with extract before deployment. From the 11th May until the end of the sampled season on the 2nd of June, four multiple grooved panels with extract and four multiple grooved panels without extract were deployed and changed daily (Fig. 81).

As can be observed in Fig. 81 two main settlement peaks occurred during this sampled season. Grooved panels with extract yielded higher numbers of cyprid settlers than any other panel treatment used at this site. On the 9th May mean cyprid densities were 123 ± 12 on grooved panels, compared to 0 on plane panels. On the 20th May grooved panels with extract averaged cyprid counts of 159 ± 44 compared to unpainted grooved panels with a mean of only 27 ± 7 cyprids. As for Site C left and C right, both of these observations can be related to the presence of N / NE winds at the time of the observed settlement or in the day prior. Moreover when the wind direction changes towards the south on the 20th, where it principally remains until the end of the season, settlement remains low and does not exceed 40 ± 6 cyprids on grooved panels (May 26th).

The use of multiple grooved panels with and without extract in the period 11th May – June 2nd, allows a comparison of the cyprid settlement response to the presence of conspecifics with grooves. Once grooved panels without extract replaced the plane panels with extract, settlement increased indicating the influence of groove may be more influential than the presence of conspecifics on an otherwise unfavourable surface.

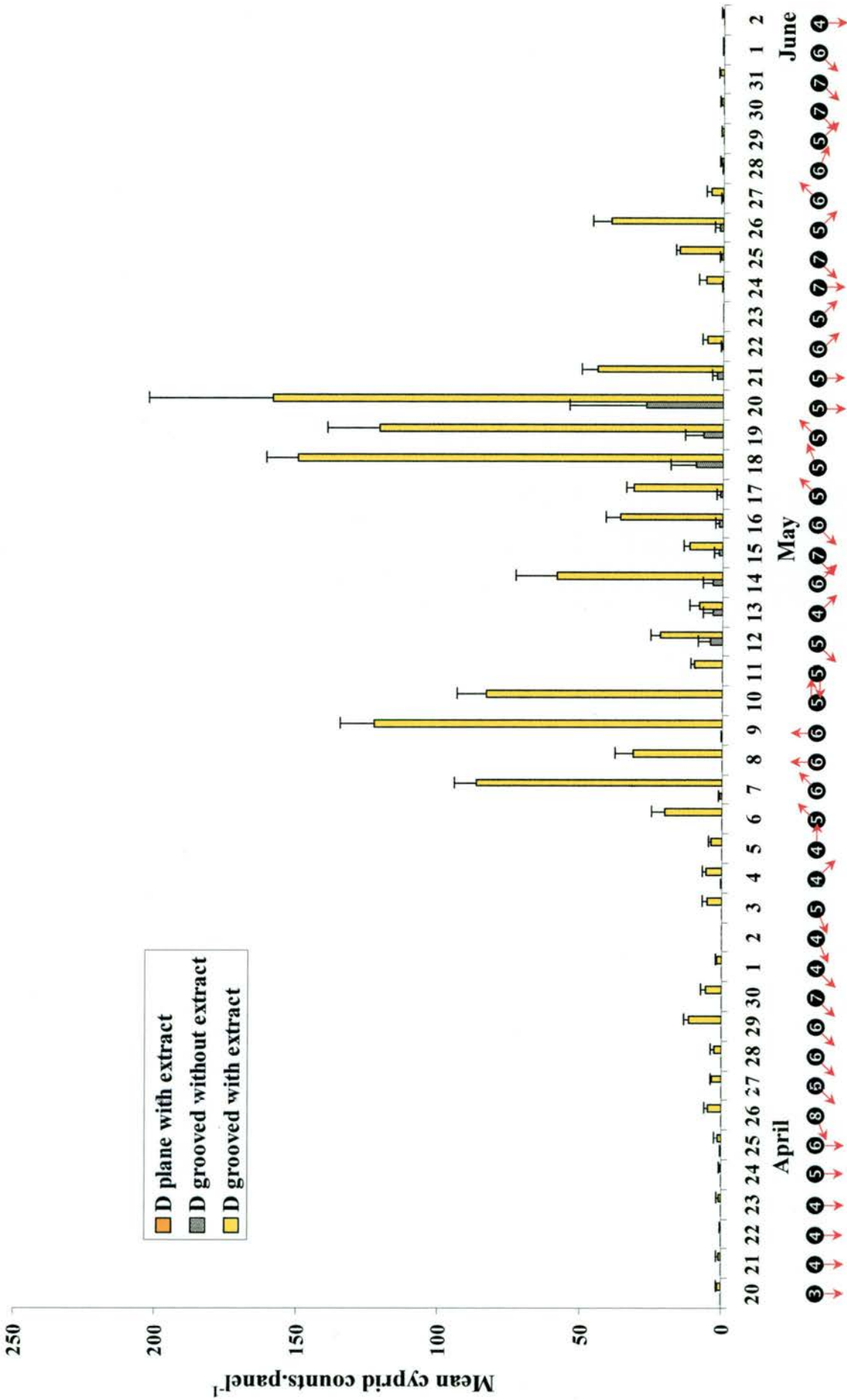


Fig. 81 – Mean daily settlement of *S. balanoides* cyprids on plane panels with extract, and multiple grooved panels with or without extract, at Site D during the 2002 season. From 19th April to 10th May four multiple grooved panels and four plane panels, both with extract were deployed. Subsequently panel composition was altered to four multiple grooved panels with extract and four multiple grooved panels without extract. Vertical lines represent S.E.M. Wind data shown as maximum Beaufort strength and pre-dominant direction over each daily period, calculated from 10 minute averages.

Table 16
Settlement panels: groove with extract comparisons, Site D 2002, 23 days.

Source	<i>df</i>	SS	MS	<i>F</i>	<i>p</i>
Extract	1	22.348	22.348	56.10	<0.001
Day	22	46.834	2.129	61.04	<0.001
Extract x Day	22	8.764	0.398	11.42	<0.001
Error	138	4.8131	0.035		
Total	183	82.759			

ANOVA for cyprid ($\log x+1$) settlement on multiple grooved panels with and without extract, n= 4 per panel treatment per day. The factors were Extract (fixed) and Day (random).

The presence or absence of painted conspecific extract on grooved panels had a significant effect on the settlement response of cyprid larvae; comparison of panel treatment means reiterated that settlement was higher on grooved panels with extract (daily mean of 32 ± 5 cyprids) than on grooved panels without extract (daily mean 3 ± 1 cyprid). Day was seen to have a significant effect on settlement again, as expected. Additionally there was a significant interaction between Extract with Day, indicating that panels were varying in performance. This was found to be caused by settlement pattern variations in grooved panels *without* extract, as those with extract behaved consistently. For example, on the 19th of May grooved panels with extract had a mean panel cyprid density of 121 ± 19 cyprids, and counts on grooved panels without extract were 7 ± 1 settlers. This is an approximate ratio of 17:1. On the 12th May mean panel cyprid counts on panels with extract were 22 ± 3 cyprids and on panels without extract the mean count was 5 ± 2 cyprids, which is an approximate ratio of 4:1.

3.3.1.3. Site T

For the first five days at Site T, four multiple grooved panels with extract, and four plane panels with extract were deployed daily. However as settlement counts on plane panels for this period was zero, four horizontally grooved panels were subsequently used. Therefore for the remaining 39 days of the 2002 settlement season, four painted multiple grooved panels and four painted horizontally grooved panels were deployed and retrieved daily at Site T at Kinkell Braes. Two main peaks of settlement occurred; the first from the 7th – 10th May (maximum mean panel count of 82 ± 8 on horizontally grooved panels, 98 ± 6 cyprids on multiple grooved panels on 9th May), and the second between the 18th and 20th May (maximum mean panel count of 30 ± 6 on horizontally grooved panels, 104 ± 17 cyprids on multiple grooved panels on 18th May). Both peaks were observed during periods of N / NE winds, see Fig. 82.

The groove area for settlement on horizontally grooved panels is 12cm^2 , whereas it is four times greater at 48cm^2 on the multiple grooved panels. Indeed multiple grooved panels were seen to have generally greater settlement counts than those of the horizontal panels. Comparison of settlement with panel type over the season was used to examine any variation in choice of panel and panel performance.

Table 17
Settlement panels: grooved panel comparisons, Site T 2002, 39 days.

Source	<i>df</i>	SS	MS	<i>F</i>	<i>p</i>
Panel type	1	1.613	1.613	32.08	<0.001
Day	38	97.266	2.560	60.55	<0.001
Panel type x Day	38	1.911	0.050	1.19	0.219
Error	234	9.892	0.042		
Total	311	110.682			

ANOVA for cyprid ($\log x+1$) settlement on multiple grooved panels and horizontally grooved panels with extract, $n= 4$ per panel treatment per day. The factors were Extract (fixed) and Day (random).

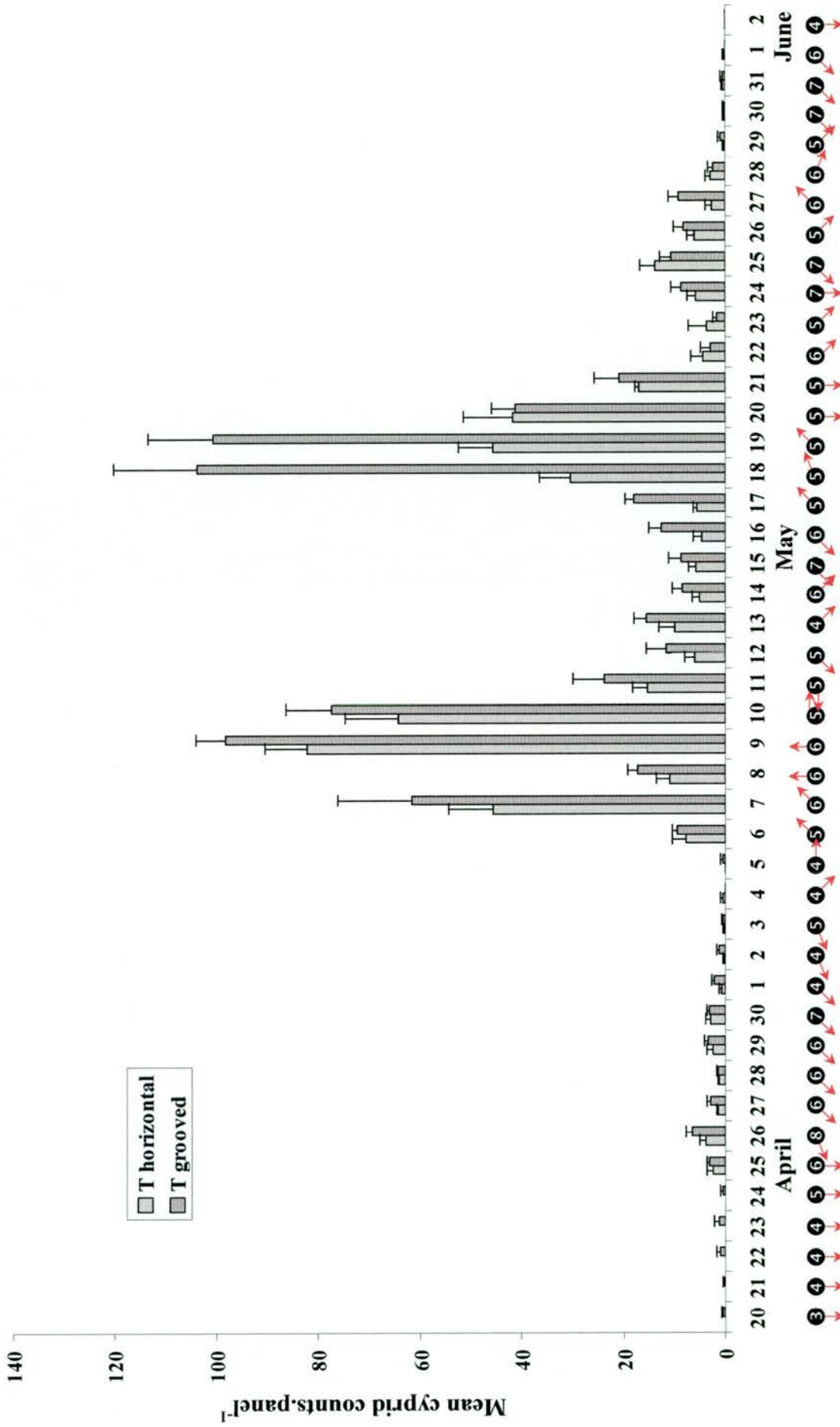


Fig. 82 – Mean daily settlement of *S. balanoides* cyprids on horizontal and multiple grooved panels with extract, at Site T during the 2002 season. n=4 for each panel type per day; vertical lines represent S.E.M. Wind data shown as maximum Beaufort strength and predominant direction over each daily period, calculated from 10 minute averages.

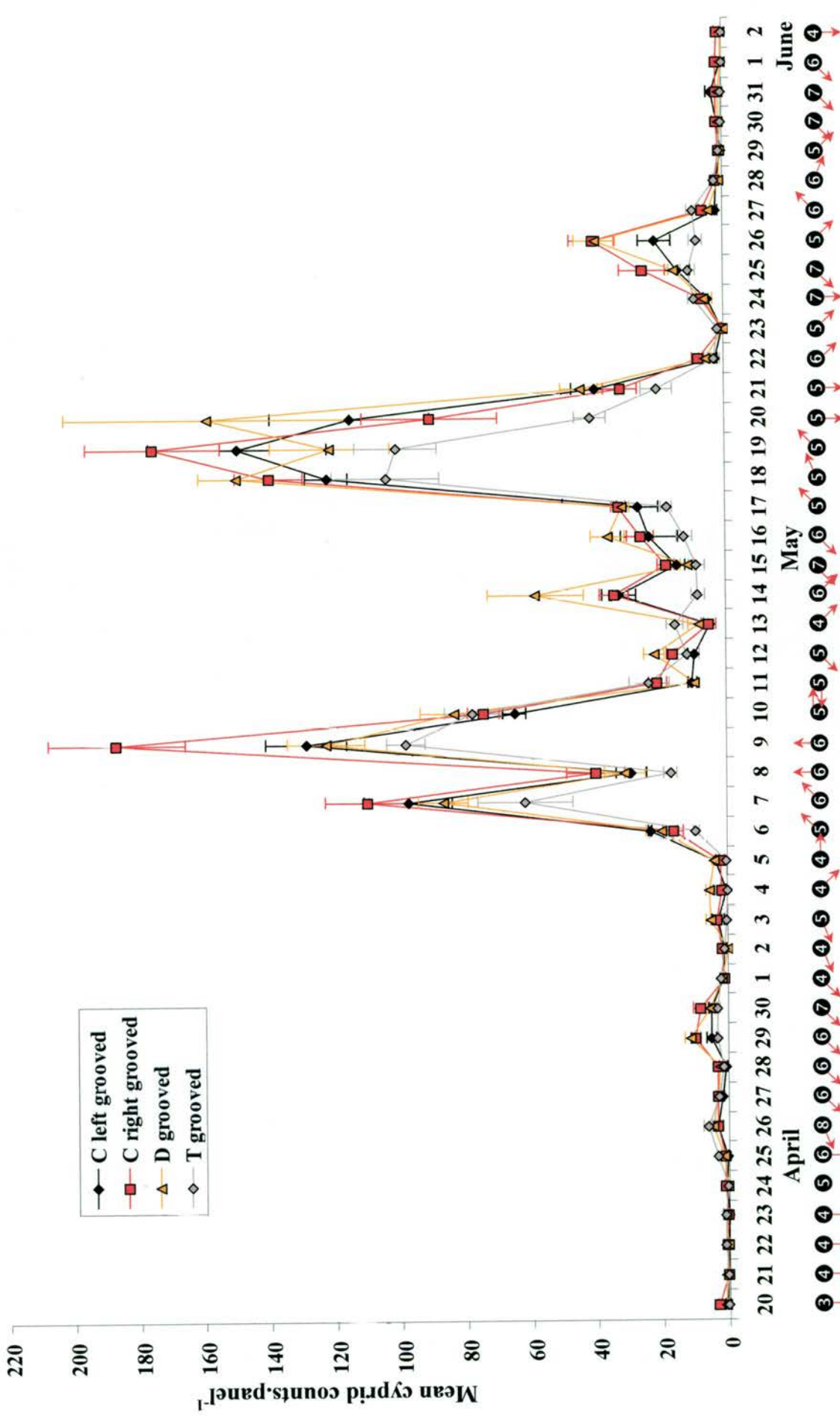


Fig. 83 – Mean daily settlement of *S. balanoides* cyprids on multiple grooved panels with extract, at all the Kinkell Braes sites during the 2002 season. n=4 for each site per day; vertical lines represent S.E.M. Wind data shown as maximum Beaufort strength and predominant direction over each daily period, calculated from 10 minute averages.

ANOVA analysis confirmed that panel type was indeed of significant influence to cyprid settlement densities (Table 17, $F_{1, 234} = 32.08$, $p < 0.001$), with comparison of daily means over the season corroborating that 48cm² groove area multiple grooved panels had consistently higher settlement counts (18 ± 2 cyprids) than the 12cm² groove area horizontally grooved panels (12 ± 2 cyprids). Once again Day was a significant influence of settlement. No interaction occurred between Panel type and Day ($F_{38, 234} = 1.19$, $p = 0.219$, therefore horizontal and multiple grooved panels performed similarly over the season.

3. 3. 1. 4. Multiple grooved panel performance with Kinkell Braes sites

ANOVA tests of comparisons of $\log x+1$ cyprid settlement counts with sites C left, C right, D and T over 44 days (April 20th to June 2nd) showed significant Site, Day and interaction effects (Table 18). Day was expected to be a significant effect, but the presence of a significant effect of Site dictated further analysis. From Fig. 83 Site T has consistently lower settlement counts across the season, due to its locale 30m apart from sites C left, C right and D. Additionally Site T faces north, whereas the other sites are immediately adjacent to one another and face southeast. Comparison of the site means illustrates that Site T has much lower settlement than that of the other sites; C left 22 ± 3 cyprids, C right 26 ± 4 , D 25 ± 3 and T 16 ± 2 . Hence Site T data was omitted and the analysis performed again (Table 19).

Table 18**Settlement panels: between-site comparisons, Sites C left, C right, D and T 2002, 44 days.**

Source	<i>df</i>	SS	MS	<i>F</i>	<i>p</i>
Site	3	3.220	1.073	10.46	<0.001
Day	43	276.327	6.427	62.60	<0.001
Site x Day	129	13.243	0.103	2.68	<0.001
Error	528	20.203	0.038		
Total	703	312.993			

ANOVA for cyprid ($\log x+1$) settlement on multiple grooved panels with extract, $n=4$ per panel treatment per day. The factors were Site (random) and Day (random).

Following the omission of panel data for Site T, Site is no longer a significant effect (Table 19), confirming that sites C left, C right and D all have similar settlement means, and that Site T was responsible for the previous observed significant result. There still remains a significant interaction between Site and Day, which on further examination was due to the varied performance of panels at Site D. Site D is also located in the upper intertidal region of the shore, therefore such variation could be linked to cyprid fitness.

Table 19**Settlement panels: between-site comparisons, Sites C left, C right, D 2002, 44 days.**

Source	<i>df</i>	SS	MS	<i>F</i>	<i>p</i>
Site	2	1785.6	892.8	2.39	0.098
Day	43	890018.6	20698.1	55.33	<0.001
Site x Day	86	32173.4	374.1	1.75	<0.001
Error	396	84718.7	213.9		
Total	527	10086963.3			

ANOVA for cyprid ($\log x+1$) settlement on multiple grooved panels with extract, $n=4$ per panel treatment per day. The factors were Site (random) and Day (random).

3. 3. 2. Fife Ness, 2002

3. 3. 2. 1. Sites J / K and Alpha

Sites J / K and Alpha were sampled between the 19th of April and the 2nd of June inclusive, providing 44 days of data on cyprid settlement relationships. Four multiple grooved panels with extract and four plane panels with extract were deployed and retrieved daily.

Conversely to the Kinkell Braes sites, Fife Ness was found to show increases in settlement with southerly winds, and decreases with northerly winds (Fig. 84). For example, on the 8th – 9th May Force 6 N winds occur which results in a mean settlement peak count of 129 ± 13 cyprids at Site C left on multiple grooved panels (Fig. 77), whereas at Site J / K only 9 ± 1 cyprid are recorded. Again at Site J / K from the 21st May to the 25th May another increase in cyprid density is seen (16 ± 5 cyprids grooved panels) during a 7-day period of southwesterly winds, although settlement at Site C left was 3 ± 1 cyprids. When comparing the maximum observed mean settlement for the season at each site (149 ± 27 cyprids at Site C left, 37 ± 8 cyprids), Site C left was found to have approximately four times greater cyprid densities than at Site J / K. Plane panels are once more shown to perform poorly throughout the season.

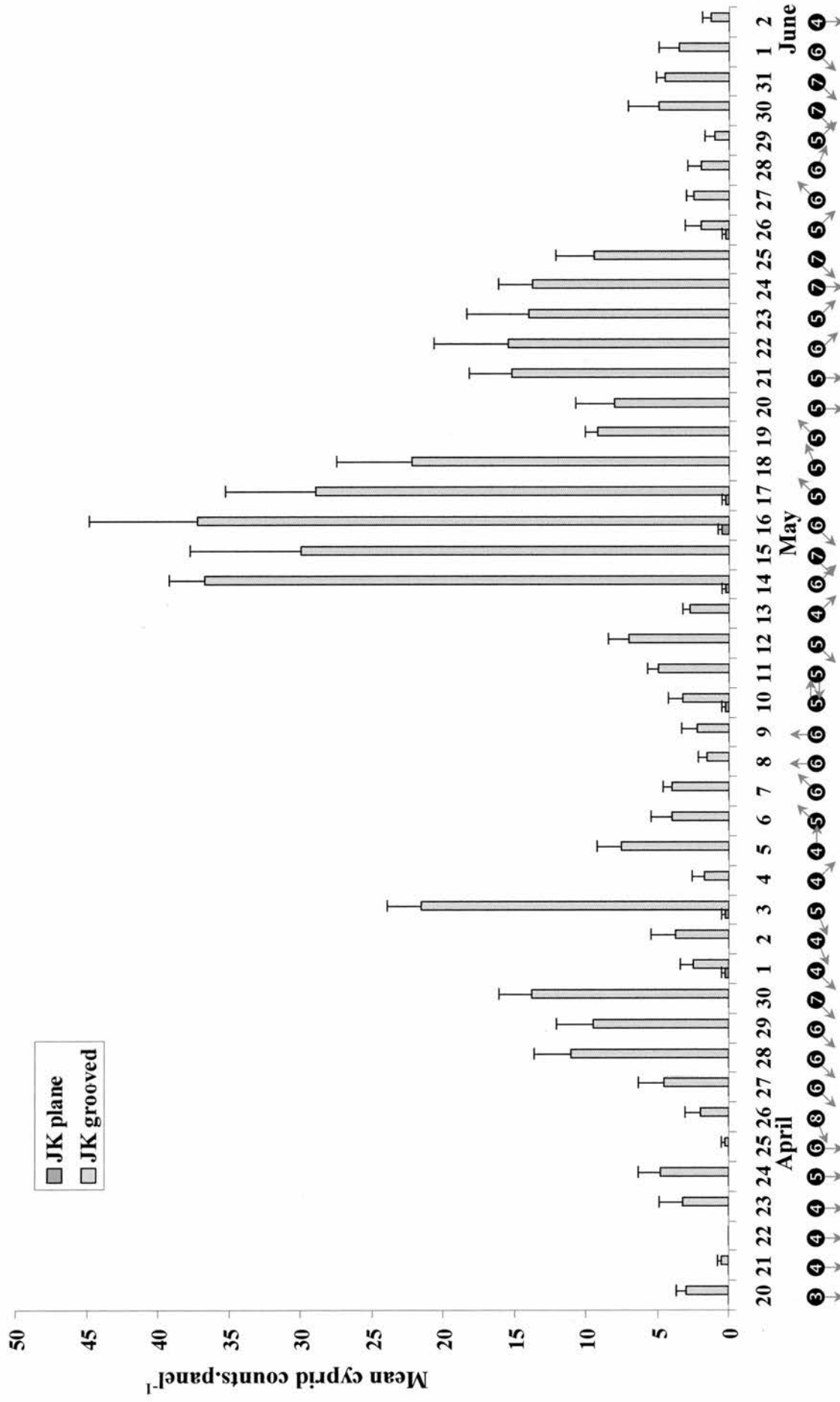


Fig. 84 – Mean daily settlement of *S. balanoides* cyprids on multiple grooved and plane panels, both with extract, at Site J / K during the 2002 season. Panels, n=4 for each type, changed daily. Vertical lines represent S.E.M. Wind data shown as maximum Beaufort strength and predominant direction over each daily period, calculated from 10 minute averages.

Site Alpha was located adjacent to Site J / K, ~50cm back towards the shore, and followed the same settlement rises and dips (Fig. 85). Therefore four peaks were seen, all corresponding to periods of SE / SW winds. Peak 1 occurs between the 26th – 3rd May, with a mean maximum cyprid count of 29 ± 8 cyprids on the multiple grooved panels. Peak 2 occurs between the 10-13th May, with a maximum mean cyprid count of 18 ± 1 cyprid with grooved panels on the 12th May. The third, and greatest peak, occurs from the 14th – 19th May, with a mean maximum count of 53 ± 4 cyprids per grooved panel. The fourth and final peak runs from the 21st to the 26th May, with a mean maximum of 21 ± 5 cyprids on the 21st May with grooved panels (0 cyprids on plane panels).

When plotted together, the correlation between the peaks is seen, with Site Alpha showing a minor increased settlement over Site J / K (Fig. 86). When pooled and temporally plotted with mean ashed sediment weights, a large amount of sharp sediment peaks are seen (Fig. 87). However trapped sediment weight was very low at this location, and sediment weights vary sharply during periods of the same SW winds (28th April – 2nd May). The final settlement peak on panels, from the 21st to the 25th, does coincide with an increase in trapped sediment weight ($0.035\text{g} \pm 0.003\text{g}$), but no consistent pattern is seen.

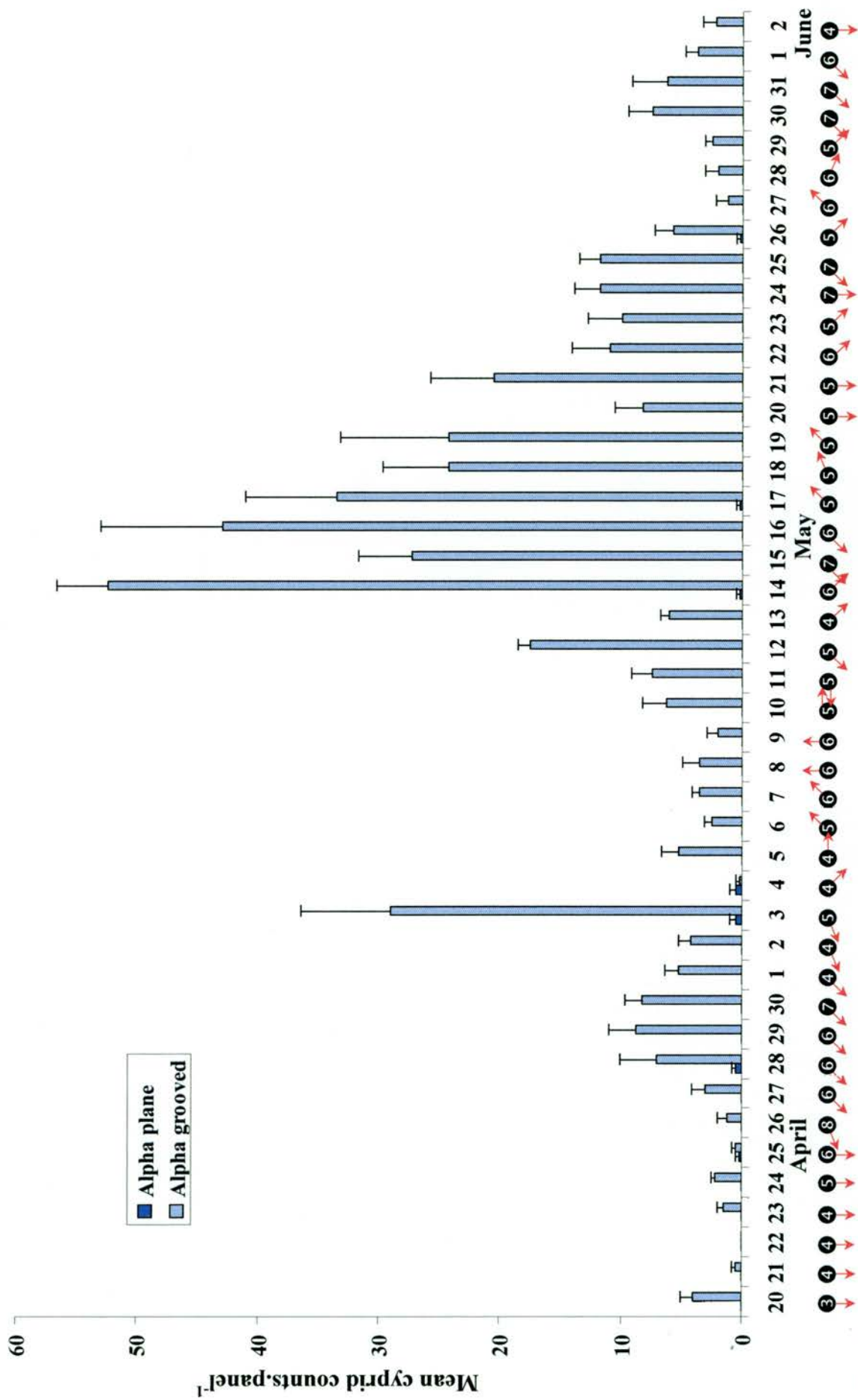


Fig. 85 – Mean daily settlement of *S. balanoides* cyprids on multiple grooved and plane panels, both with extract, at Site Alpha during the 2002 season. Panels; n=4 for each type, changed daily. Vertical lines represent S.E.M. Wind data shown as maximum Beaufort strength and predominant direction over each daily period, calculated from 10 minute averages.

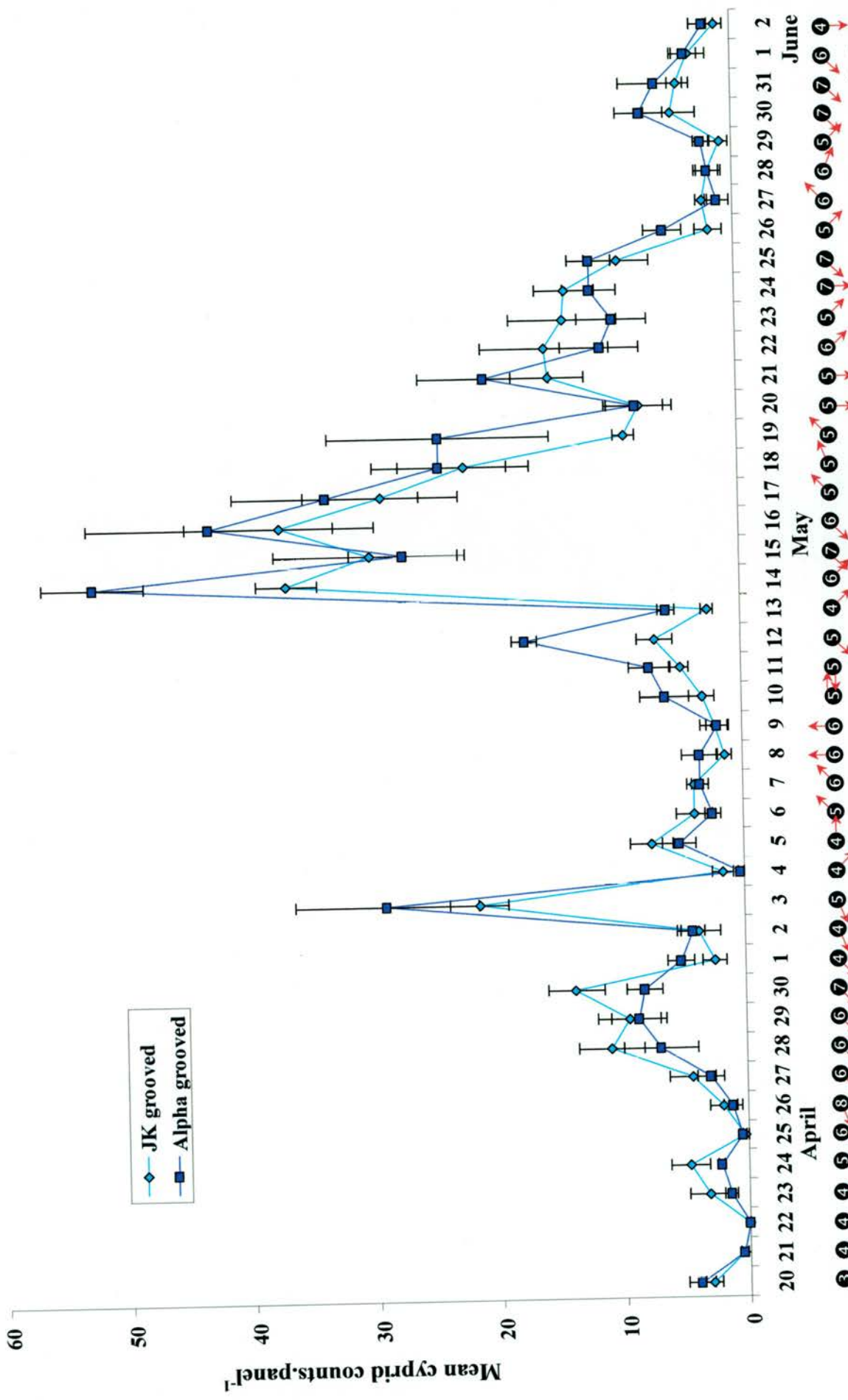


Fig. 86 – Mean daily settlement of *S. balanoides* cyprids on multiple panels with extract, at Site J / K and Alpha during the 2002 season. Panels; n=4 daily for each site. Vertical lines represent S.E.M. Wind data shown as maximum Beaufort strength and predominant direction over each daily period, calculated from 10 minute averages.

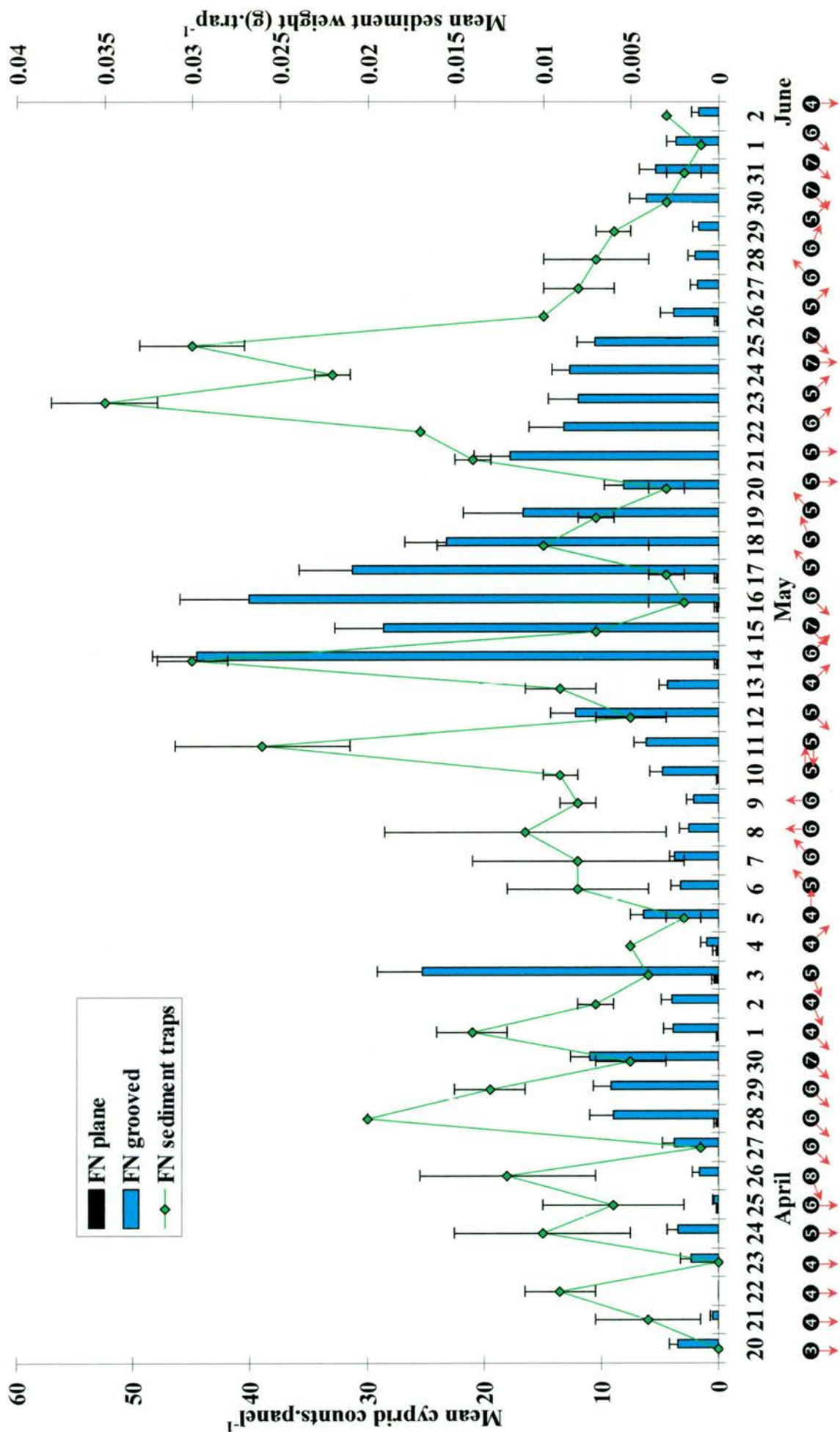


Fig. 87 – Mean daily settlement of *S. balanoides* cyprids on plane and multiple grooved panels with captured ashed sediment weight from traps at pooled sites J / K and Alpha during the 2002 season. Panels all painted with extract; n=4 each treatment each day. Sediment traps were 9 cm apart on a backplate to the left of J / K (Fig. 42) and were emptied daily (n=2 each day). Vertical lines represent S.E.M. Wind data shown as maximum Beaufort strength and predominant direction over each daily period, calculated from 10 minute averages.

3.3.2.2. Panel treatment comparisons at Fife Ness

Plane panels with extract yet again exhibit very low settlement densities (Fig. 87), and unsurprisingly were statistically significantly different (Table 20). Settlement at sites J / K and Alpha did not vary ($F_{1, 528} = 2.98, p = 0.092$), and both panel types showed similar settlement performance over each site ($F_{1, 528} = 1.76, p = 0.191$). No significant interaction occurred between Site and Day ($p = 0.676$), and with all three factors ($p = 0.157$), indicating that panel settlement at the sites was temporally correlated (see also Fig. 86). However, a significant interaction did occur between Panel type and Day, suggesting that panel performance varied daily. This was attributable to the extremely poor settlement on the plane panels, which showed no / little variance over the whole season. Therefore the analysis proceeded without the inclusion of the plane panel data (Table 21).

Table 20
Settlement panels: comparisons of panel type at Sites J / K, and Alpha 2002, 44 days.

Source	<i>df</i>	SS	MS	<i>F</i>	<i>p</i>
Panel type	1	102.664	102.664	154.19	<0.001
Site	1	0.078	0.078	2.98	0.092
Day	43	30.145	0.701	26.79	<0.001
Panel type x Site	1	0.064	0.064	1.76	0.191
Panel type x Day	43	27.444	0.638	17.63	<0.001
Site x Day	43	1.125	0.026	0.89	0.676
Panel type x Site x Day	43	1.557	0.036	1.23	0.157
Error	528	15.557	0.030		
Total	703	178.633			

ANOVA for cyprid ($\log x+1$) settlement on plane and multiple grooved panels, both with extract, $n=4$ per treatment per day. The factors were Panel type (fixed), Site (random) and Day (random).

With the omission of the plane panel data, no significant difference was found in settlement at the two sites ($F_{1, 264} = 2.41, p = 0.128$) as before. However there is now no significant interaction, confirming that the multiple grooved panels performed consistently throughout the season ($F_{43, 264} = 2.41, p = 0.348$, Table 21).

Table 21**Settlement panels: between-site comparisons at Sites J / K, and Alpha 2002, 44 days.**

Source	<i>df</i>	SS	MS	<i>F</i>	<i>p</i>
Site	1	0.141	0.141	2.41	0.128
Day	43	57.300	1.333	24.51	<0.001
Site x Day	43	2.53	0.059	1.08	0.348
Error	264	14.355	0.054		
Total	351	74.321			

ANOVA for cyprid ($\log x+1$) settlement on multiple grooved panels, with extract, n=4 per day. The factors were Site (random) and Day (random).

3. 3. 3. Kingsbarns, 2002

3. 3. 3. 1. Sites L / M and Beta

Sites L / M and Beta were sampled daily using four multiple grooved panels and four plane panels, both types painted with extract. Unfortunately due to vandalism daily data was not obtained for the whole settlement season. Therefore 36 days of observations were recorded at this site, with data unavailable for the days of 21st, 23rd, 25th, 26th, 30th and 31st May, and the 1st – 2nd June.

During the previous settlement season peaks in settlement appeared correlated to SW winds (Fig. 72), but as mentioned no firm conclusion could be drawn due to the use of uninformative plane panels at the beginning of the season. During the 2002 season, two main peaks are seen and a daily peak also occurs on the 12th May at both sites (Fig. 88 and 89). Both of the main peaks occur during periods of predominantly N / NE winds, with the single peak on the 12th taking place during SW winds. The first main peak occurs from the 6th to the 10th May at both sites, with maximum mean cyprid counts of 95 ± 4 and 162 ± 24 on the multiple grooved panels at Site L / M and Beta respectively. Plane panel counts for this day are 0 at Site L / M and 1 ± 0 at Site Beta. The second main peak ran from the 15th to the 19th May, with a maximum average cyprid count on grooved panels of 170 ± 17 cyprids at Site L / M on the 18th May, and 247 ± 64 on the 16th of May at Site Beta. Cyprid densities on grooved panels for the single day peak on the 12th May were 126 ± 16 at Site L / M, and 162 ± 24 cyprids at Site Beta.

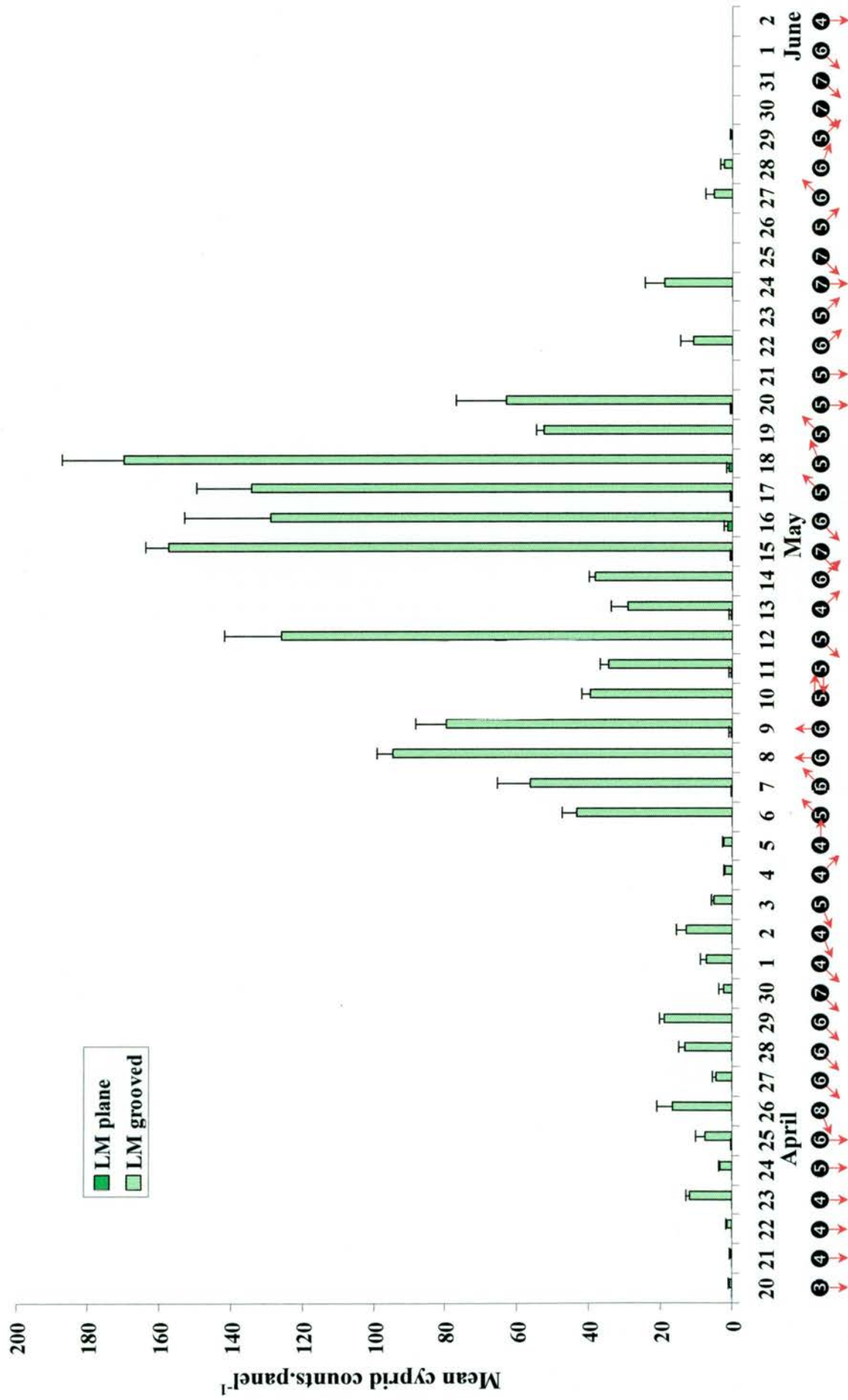


Fig. 88 – Mean daily settlement of *S. balanoides* cyprids on multiple grooved and plane panels, both with extract, at Site L / M during the 2002 season. Panels; n=4 for each type, changed daily. Vertical lines represent S.E.M. Wind data shown as maximum Beaufort strength and predominant direction over each daily period, calculated from 10 minute averages.

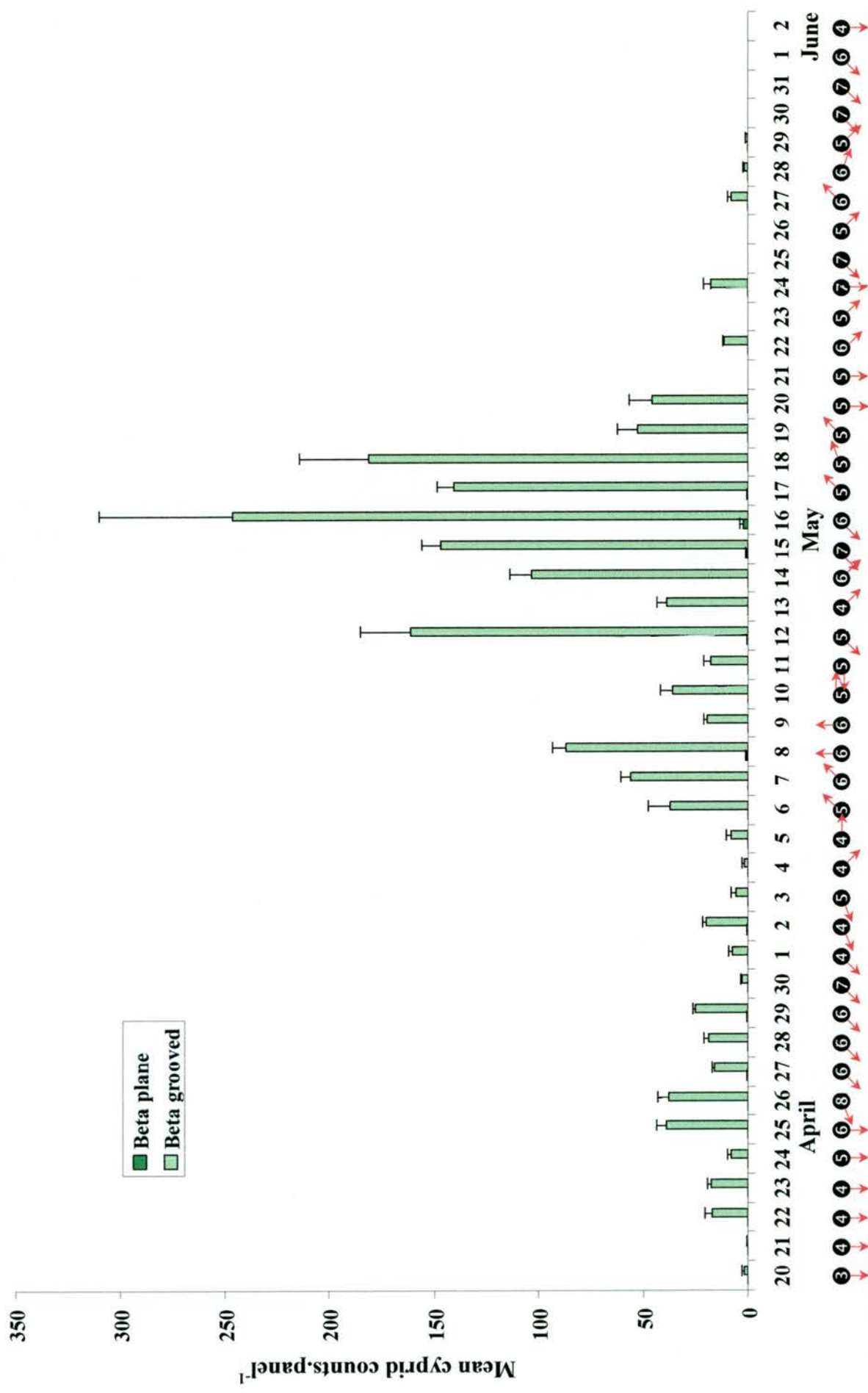


Fig. 89 – Mean daily settlement of *S. balanoides* cyprids on multiple grooved and plane panels, both with extract, at Site Beta during the 2002 season. Panels; n=4 for each type, changed daily. Vertical lines represent S.E.M. Wind data shown as maximum Beaufort strength and predominant direction over each daily period, calculated from 10 minute averages.

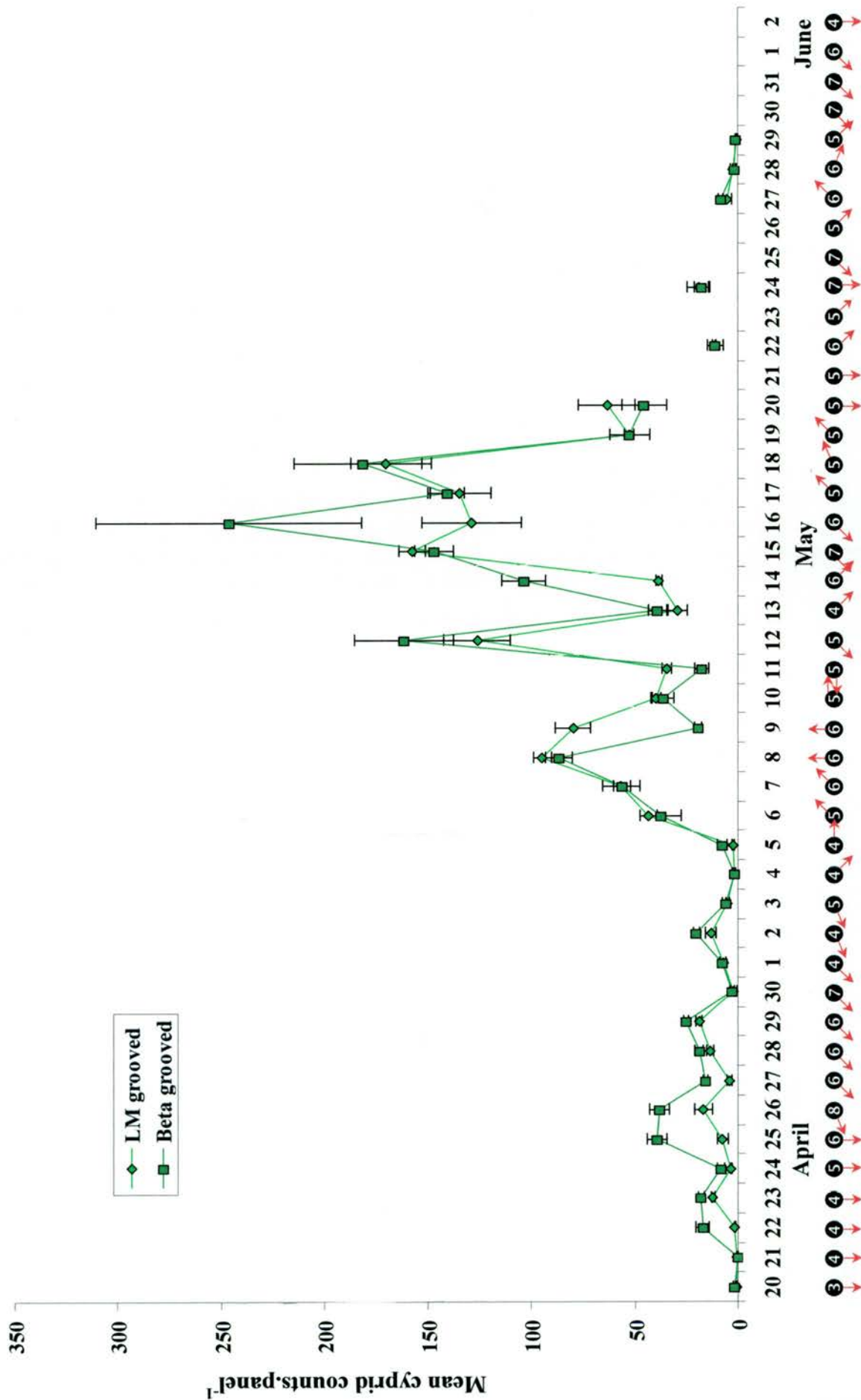


Fig. 90 – Mean daily settlement of *S. balanoides* cyprids on multiple panels with extract, at Site L / M and Beta during the 2002 season. Panels; n=4 daily for each site. Vertical lines represent S.E.M. Wind data shown as maximum Beaufort strength and predominant direction over each daily period, calculated from 10 minute averages. Broken lines indicate missing observations, due to vandalism.

Plots of both sites show that although the sites generally follow the same settlement pattern there are differences in settlement densities between the two sites, with Site Beta recording greater cyprid counts (Fig. 90).

Increased trapped sediment weight is found with N / NE winds at Kingsbarns in 2002 (Fig. 91), as also occurred during the 2001 season (Fig. 72). As in the previous season, larval settlement densities increased with decreased trapped sediment weight, indicating an inverse relationship (Fig. 91). For example on the 8th May mean ashed sediment weight was $0.173\text{g} \pm 0.004\text{g}$ and mean cyprid settlement on grooved panels was 91 ± 4 cyprids. Additionally on the 11th May mean ashed sediment weight was $13.797\text{g} \pm 0.201\text{g}$ and mean cyprid settlement on grooved panels was 26 ± 4 cyprids. Again on the 15th May mean ashed sediment weight was $0.112\text{g} \pm 0.019\text{g}$ and mean cyprid settlement on grooved panels was 152 ± 6 cyprids. Whilst there appears a visual inverse correlation between settlement on grooved panels and the captured sediment weight, Spearman rank correlation analysis shown to be not significant ($r_s = 0.256$, $n = 36$, $p = 0.1312$), which may be attributed to the missing data through vandalism incidents. Spearman rank correlation found that unsurprisingly there was no correlation between the plane panels and sediment weights ($r_s = 0.014$, $n = 36$, $p = 0.9344$).

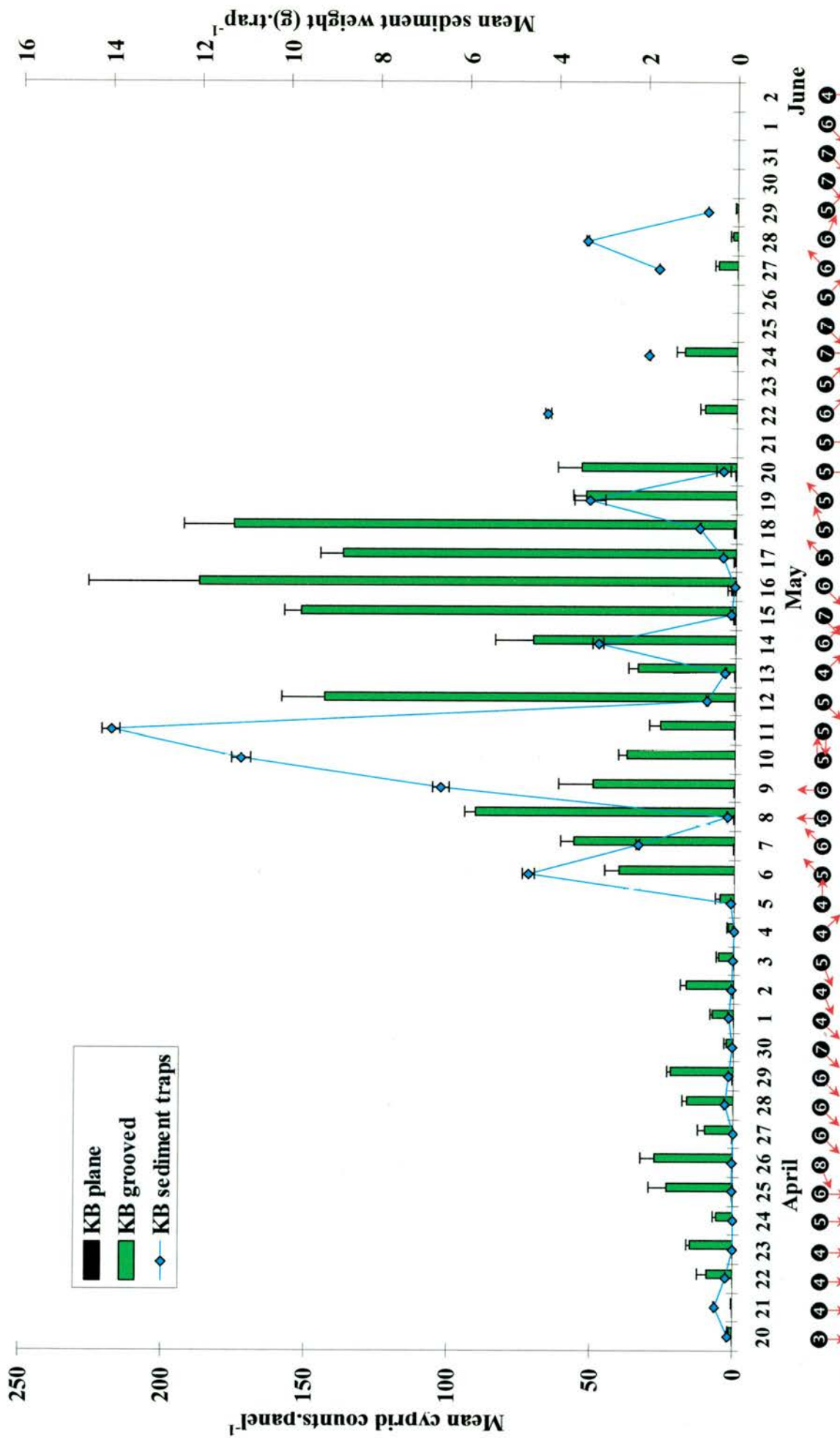


Fig. 91 – Mean daily settlement of *S.balanoides* cyprids on plane and multiple grooved panels with captured ashed sediment weight from traps at pooled sites L/M and Beta during the 2002 season. Panels all painted with extract; n=4 each treatment each day. Sediment traps were 9 cm apart on a backplate to the left of L/M (Fig. 36) and were emptied daily (n=2 each day). Vertical lines represent S.E.M. Wind data shown as maximum Beaufort strength and predominant direction over each daily period, calculated from 10 minute averages.

3. 3. 3. 2. Panel treatment comparisons at Kingsbarns

Plane panels with extract yet again exhibit very low settlement densities (Fig. 91) and unsurprisingly were statistically different to grooved panels (Table 22). Settlement with Site was also found to be of significance, as settlement at Site Beta was greater. The sampled day throughout the season produced a significant variance, as expected. Panel type with Site was also seen to be significantly different as shown by the interaction in Table 22, indicating that panel performance varied with site. ANOVA interaction plots revealed that at Site Beta grooved panels had higher cyprid settlers than at Site L / M (46 ± 5 cyprids and 39 ± 4 cyprids respectively), whereas plane panels showed poorer settlement at Site Beta than at Site L / M (0.17 ± 0.05 cyprids and 0.15 ± 0.6 cyprids). The Panel type and Day interaction was caused by plane panels consistently showing low settlement, with the significant Site and Day interaction by the offset peaks as seen in Fig. 90.

Table 22
Settlement panels: comparisons of panel type at Sites L / M, and Beta 2002, 36 days.

Source	<i>df</i>	SS	MS	<i>F</i>	<i>p</i>
Panel type	1	213.086	213.086	117.43	<0.001
Site	1	0.447	0.447	5.34	0.027
Day	35	60.513	1.729	20.66	<0.001
Panel type x Site	1	0.575	0.575	8.50	0.006
Panel type x Day	35	45.763	1.308	19.34	<0.001
Site x Day	35	2.929	0.084	3.95	<0.001
Panel type x Site x Day	35	2.367	0.068	3.19	<0.001
Error	432	9.159	0.021		
Total	575				

ANOVA for cyprid ($\log x+1$) settlement on plane and multiple grooved panels, both with extract, $n=4$ per treatment per day. The factors were Panel type (fixed), Site (random) and Day (random).

Further ANOVA tests for grooved panels only confirmed that Site was still a significant factor ($F_{1, 216} = 7.28, p = 0.011$), as was Day ($F_{35, 216} = 21.48, p < 0.001$). A

significant interaction of Site and Day also remained, indicating that settlement on grooved panels was different at each site each day.

3. 3. 4. *Between-site groove treatment comparisons*

3. 3. 4. 1. *Settlement with grooved panels between sites*

During the 2001 season an apparent temporal delay occurred between sites, moving from Site T in St Andrews to Site M at Kingsbarns and then to Site K at Fife Ness (Fig. 75). However unlike the previous season two main settlement peaks are seen in 2002 (Fig. 92). Examination of the maximum mean grooved panel counts of each peak at the three sites, indicates that there is a temporal delay in settlement beginning in Fife Ness and ending in St Andrews for each peak. For example the first peak is seen at Fife Ness on the 3rd of May, followed by the peak at Kingsbarns on the 8th May and then on the 9th of May at St Andrews. This first observation at Fife Ness occurs after 14 days of southerly winds, which reached a maximum strength of Force 8 on the 26th April. The second peak is at its maximum on the 14th May at Fife Ness, the 16th of May at Kingsbarns and the 19th May at St Andrews (Fig. 92).

Cyprid settlement counts ($\log x + 1$) on grooved panels were compared over the eight sites of C left, C right, D, T, J / K, Alpha, L / M and Beta over the 2002 settlement season. As eight days of data had been lost at Kingsbarns due to vandalism, the 36 remaining days were used for analysis and in order to maintain balanced tests only the corresponding day data from the other sites was used. Therefore each site data consisted of four grooved panel observations per day over the 36-day period (144 replicates). The daily data included comes from 20th April to 20th May, 22nd - 24th May, and 27th -29th May

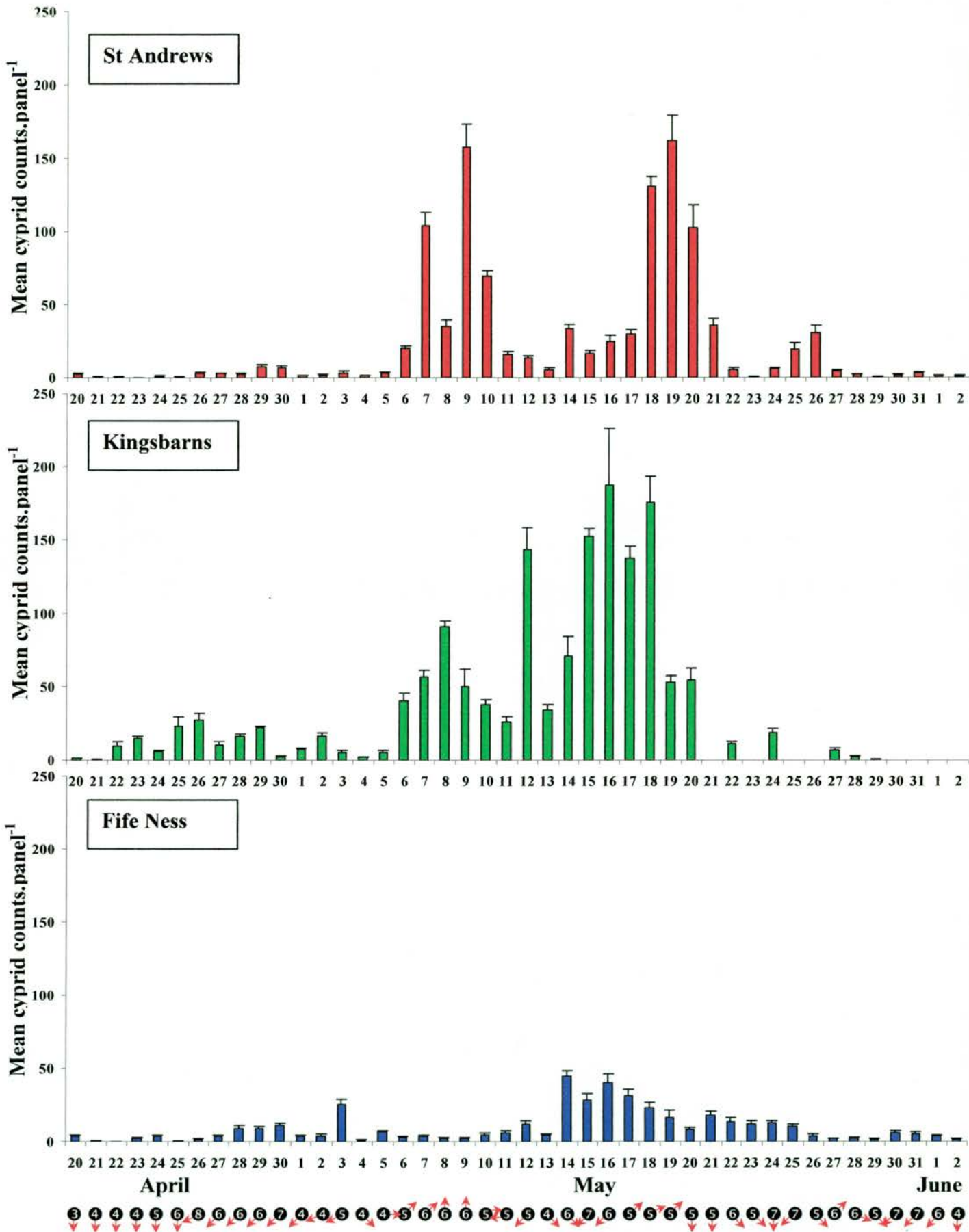


Fig. 92 – Mean daily settlement of *S.balanoides* cyprids on multiple grooved panels at St Andrews (C left, C right pooled), Kingsbarns (L / M and Beta pooled) and Fife Ness (J / K and Alpha pooled). Panels; n= 4 per site per day and all painted with extract. Vertical lines represent S.E.M. Wind data shown as maximum Beaufort strength and predominant direction over each daily period, calculated from 10 minute averages.

Table 23**Settlement panels: between-site comparison on grooved panels, all sites 2002, 36 days.**

Source	<i>df</i>	SS	MS	<i>F</i>	<i>p</i>
Site	7	31.684	4.5262	8.42	<0.001
Day	35	273.467	7.813	14.53	<0.001
Site x Day	245	131.714	0.538	13.84	<0.001
Error	864	33.568	0.039		
Total	1151	470.432			

ANOVA for cyprid ($\log x + 1$) settlement on multiple grooved panels with extract, $n=4$ per treatment per day. The factors were Site (random) and Day (random).

ANOVA of $\log x + 1$ cyprid counts on multiple grooved panels across the sites showed significant variation in both factors as well as a significant interaction term (Table 23). Daily variations were to be expected, and analysis of means using Tukey-Kramer tests found that Sites L / M and Beta at Kingsbarns had significantly higher settlement means than the other sites. Therefore the analysis proceeded again without data from Kingsbarns, and Site was considered not significant ($F_{5, 648} = 2.16, p = 0.060$). The interaction was still significant, as larval peaks did not temporally coincide.

3.3.4.2. Larval settlement behaviour within grooves on panels

Throughout the settlement season detailed spatial data was collected of cyprid settlement location upon each deployed panel, and this included the position of cyprids within each groove on the panel. This positional data was used to investigate whether cyprids were preferentially selecting the upper or lower part of each of the 12 grooves on each panel; the terms upper and lower refer to the milled edge of the groove on panels as horizontally deployed in the field. Additionally data on cyprid settlement was collated to investigate settlement on top or bottom halves of the panel, i.e. from the screw-hole to the top edge of the panel for top half counts, and from the screw-hole to the bottom edge of the panel for bottom half counts. Again this reference to ‘top’ and ‘bottom’ sections of the panel refers to their orientation in the field.

GLM nested analysis was used to investigate the spatial pattern of settlement of the cyprids within grooves, with top and bottom halves of the panel and with large spatial variations (i.e. Site). In this analysis all factors are considered fixed.

Table 24
Settlement panels: upper/lower groove, half, and site comparisons 2002, 36 days.

Source	<i>df</i>	Adj SS	Adj MS	<i>F</i>	<i>p</i>
Groove	1	20.978	20.978	87.60	<0.001
Half (Groove)	2	1.530	0.765	3.19	0.041
Panel (Half (Groove))	12	0.833	0.069	0.29	0.991
Site (Panel (Half (Groove)))	112	109.955	0.982	4.10	<0.001
Error	4480	1072.787	0.240		
Total	4607				

GLM for cyprid ($\log x+1$) settlement on multiple grooved panels with extract, $n=4$ per treatment per day, per site. The factors were Groove, Half, Panel and Site (all fixed).

The settlement on upper and lower grooves was found to be significantly different, $F_{1,4480} = 87.60, p < 0.001$ (Table 24). The large MS calculated value indicates that the effect of upper and lower groove produces the most variation in the cyprid counts.

Grooves nested within Panel Half was also found to be significant, indicating that there is variation in settlement on the top and bottom halves of the panels. The high p value of Grooves and Panel Half with Panel ($F_{12, 4480} = 0.29, p = 0.991$) indicates that the settlement panels are acting as true replicates with very little variation of settlement in upper and lower grooves and halves within daily replicates. The significant influence of Site upon settlement is seen, with $F_{112, 4480} = 4.10, p < 0.001$, marking the variation in settlement in the panel grooves with top and bottom sections of the panel.

Interaction bar plots (Fig. 93a) were used as a preliminary indicator of the main effects, before proceeding to unplanned multiple comparison tests. Upper grooves within the bottom half of the panel have a higher mean (3.07 ± 0.04 cyprids) than in the upper grooves on the top halves of the panels (2.68 ± 0.04 , Fig. 93a (i)), which produced the significant analysis result ($F_{2, 4480} = 3.19, p = 0.041$). Therefore S-N-K analysis of grooves within panel halves was used to determine the main effect (Table 25). For Q critical values $\alpha = 0.01$, to prevent any excessive Type I errors. Through this analysis it was determined that the upper and lower groove was the main effect influencing cyprid spatial settlement on the panels.

Table 25
Settlement panels: upper/lower groove within half comparisons 2002, 36 days.

Rank Order	1	2	3	4	g	Q	D = Q x S. E.
Rank Name	LB	LT	UT	UB			
Rank Mean	0.440	0.467	0.566	0.610			
Comparisons	⁴⁻¹ 0.170*				4	4.497	0.117
	³⁻¹ 0.126*	⁴⁻² 0.143*			3	4.200	0.1092
	²⁻¹ 0.027	³⁻² 0.099*	⁴⁻³ 0.044		2	3.707	0.0962

S-N-K analysis using with Q values are with g and 4604 df, $\alpha = 0.01$. Significant differences are shown by asterisks. U = upper groove, L = lower groove, T = top panel half, B = bottom panel half. S.E. = $\sqrt{(MS_{within}/n)} = \sqrt{(0.7651/1152)} = 0.026$

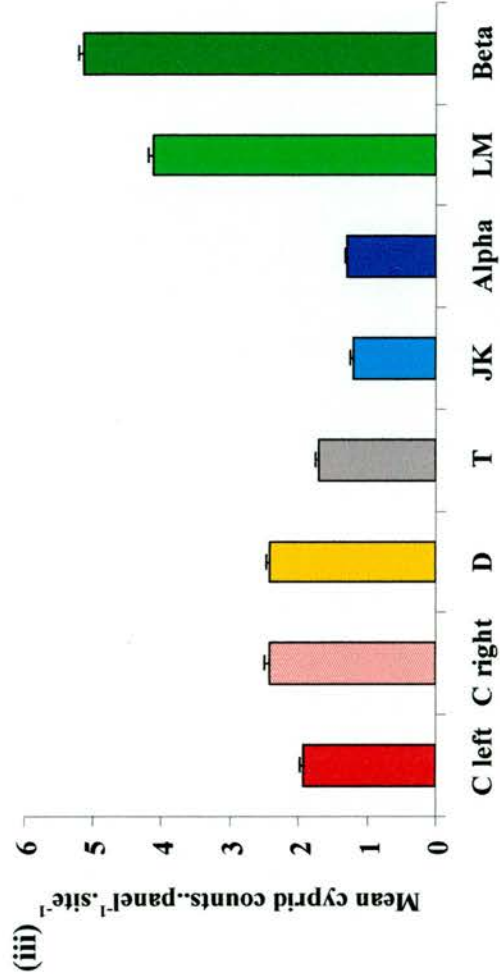
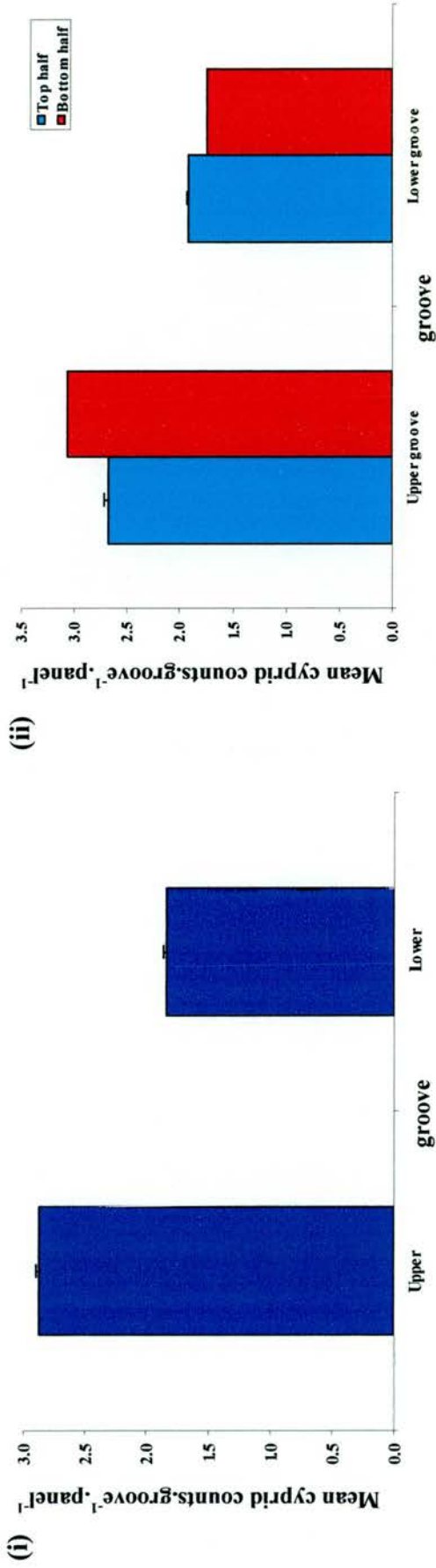


Fig. 93a – Interaction bar plots of treatment means for (i) grooves within panels, (ii) panel halves within panels and (iii) sites

Further investigation was warranted for the significant effect of grooves and panel halves within Site, to examine if the small-scale spatial settlement among panels differed at a larger scale. As panels themselves were replicates and not influential in the pattern of spatial settlement ($F_{12, 4480} = 0.29, p = 0.991$, Table 24), they were not included as a factor in the following comparison of grooves with panel halves with sites. This was confirmed by re-analysis of the GLM nested model without the inclusion of the panel replicate data; all significance differences were maintained. This altered the MS_{Residual} for the three nested factors of Site (Panel (Half (Groove))) from 0.2395 to 0.2357. Tukey HSD comparisons were then performed, with Q values at $\alpha = 0.01$.

Although the GLM model showed a significant difference in cyprid settlement within panels with sites, the Tukey HSD test revealed that there was no clear correlation of settlement on upper / lower grooves, within top and bottom panel halves, within sites (Appendix 13). This was caused by means for certain treatments overlapping the two means for the highest and lowest site groups; i.e. Kingsbarns sites and Fife Ness sites were considerably different, but due to the varied results of comparisons using the St Andrews sites no distinctive relationships can be observed. Consequently the results were not interpretable for comparisons of groove and panel section over the sites although the H_0 of no variation has been rejected, and therefore a further unplanned multiple comparison test was performed for the groove and half variances within sites (Fig. 93b). A Tukey-Kramer comparison test was then used; the groupings are shown on Fig. 93b for panel treatment within site.

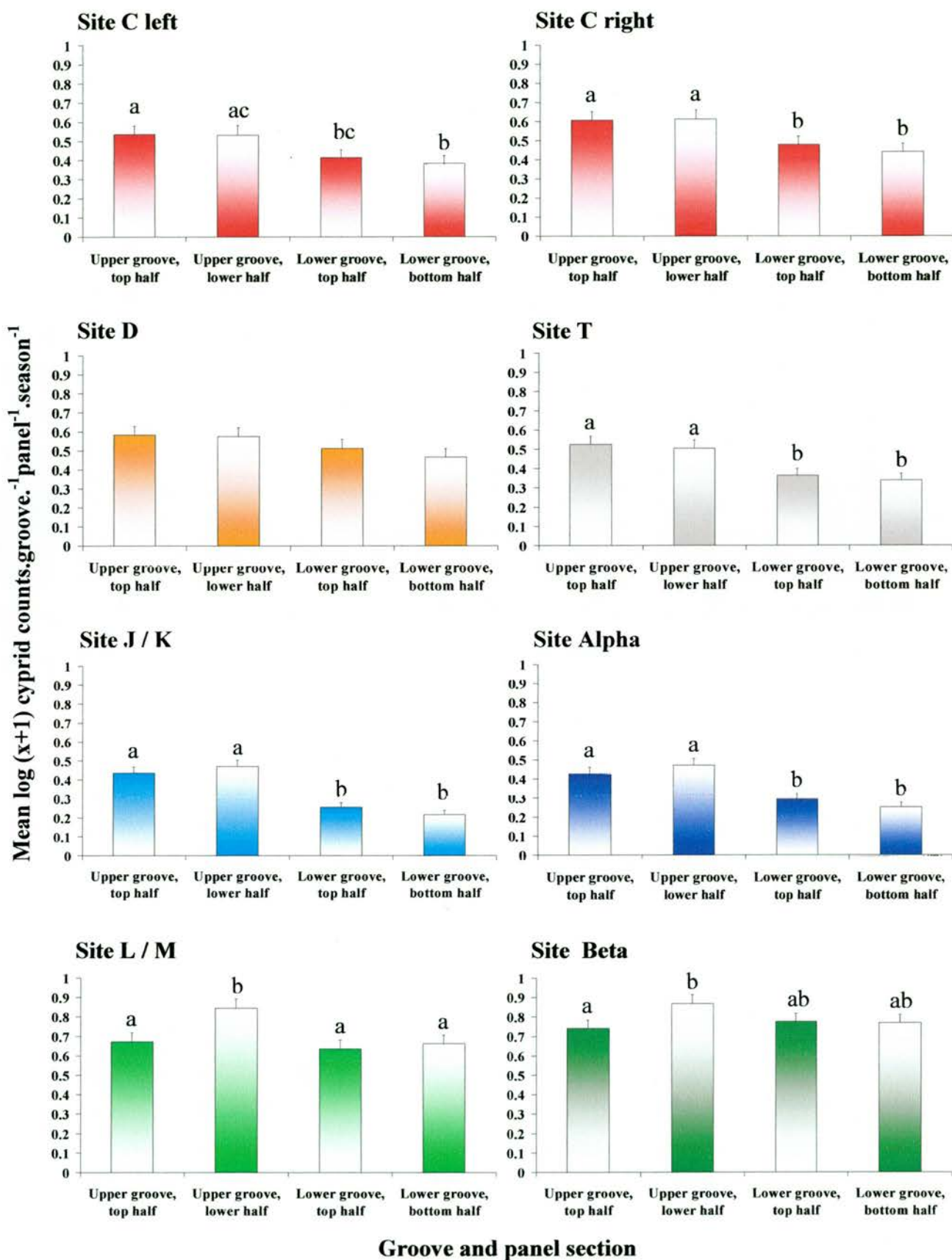


Fig. 93b – Comparison of groove and panel half with observed log $x+1$ cyprid counts within each site. Each bar represents $n=144$ observations, with each site data representing 144 panels. Vertical lines are S.E.M. Letters denote Tukey-Kramer groupings following GLM unplanned comparisons.

The Tukey-Kramer groupings, as shown on Fig. 93b, indicate that the general pattern is that groove is the main effect rather than panel half; this occurs at Sites C left, C right, T, J / K and Alpha. This groove main effect confirms the analysis of the S-N-K test. However this does not occur at Kingsbarns, where upper grooves on the lower half have significantly higher settlement than the other treatments. Additionally no significant difference is seen with upper grooves on the top half and both lower groove treatments at Site L / M, which may be a result of larval interaction, such as spacing themselves from each other at higher densities. This pattern is similar at Site Beta with larvae preferentially settling on upper grooves in the lower half. This Site therefore explains the variation in mildly significant settlement seen on top and bottom halves of the panel ($F_{2, 4480} = 3.19, p = 0.041$, Table 24, Fig. 93b). Unlike any of the other locations panels at Site D were found to show no effect of groove or panel section on settlement (Fig. 93b). As this site is located in the upper intertidal region of the shore, it suggests that larvae settling here are less selective. Additionally this lack of pattern of settlement with treatment at this site can explain the lack of cohesive patterns found in the Tukey HSD test (Appendix 13).

3.3.5. Larval traps

3.3.5.1. Larval trap performance within sites

At Site T, Site J / K and Site L / M four larval traps were attached to backplates and remained *in situ* for the settlement season (Fig. 31). These were emptied daily and larval counts were made of the collected samples back in the laboratory. 4M Urea was used as a larval fixative, with the addition of 1ppt Bromophenol Blue dye, which enabled the spectrophotometric percentage of urea retention to be calculated (Section 2.3.). Stock solutions were used to calculate standard curves, Appendix 10, and the resulting regression lines were used for the calculation of urea retention. Two trap leaks occurred during the season (Trap 2 St Andrews 15th May, Trap 4 Kingsbarns 22nd May), and missing values were substituted by the mean of the other traps. Additionally at the beginning of the season at Kingsbarns (20th – 21st April) Trap 3 leaked for two consecutive days (Fig. 95), producing trap urea percentages of 22% and 9% respectively. These were found to have a significant influence in analysis and therefore, as their values could be explained, the mean of the other traps for that day was substituted.

Temporal plots of mean cyprid counts with percentage urea retention were used to visually examine any apparent coinciding peaks of supply with urea retention, which would suggest variability in trap performance. However the high peak of trapped larvae (55 ± 3 cyprids) on the 20th May at St Andrews (Fig. 94) does not show a corresponding higher peak in percentage urea retention ($79.8 \% \pm 1.1\%$), indicating that the efficiency of the traps is not being compromised by any loss of urea through wave action. A Spearman rank correlation test found no significant correlation between the factors ($r_s = 0.09448$, $n = 50$, $p = 0.0720$) confirming there is no temporal correlation between the trap counts and percentage retention. Additionally the

standard errors of the traps are consistent throughout the season at St Andrews demonstrating that although there is variability among the traps, they are collectively performing to the same standard each day over the season.

The Kingsbarns traps also do not show any temporal correlation between an increase in urea retention and an increase in trapped cyprids, again suggesting the traps are performing similarly across the season ($r_s = -0.09445$, $n = 36$, $p = 0.5836$). Large standard errors and decreased mean percent urea retention are seen on the 20th and 21st May as Trap 4 was faulty and was replaced after panel collection on the 21st May (Fig. 95). A peak of trapped cyprid counts is also seen on the 20th May as at St Andrews, with a mean count of 44 ± 1 cyprids and a corresponding urea retention of $62.3\% \pm 0.98$. Unfortunately, following this period, data is missing due to the vandalism incidents and therefore any observations after the 21st May provide only partial information.

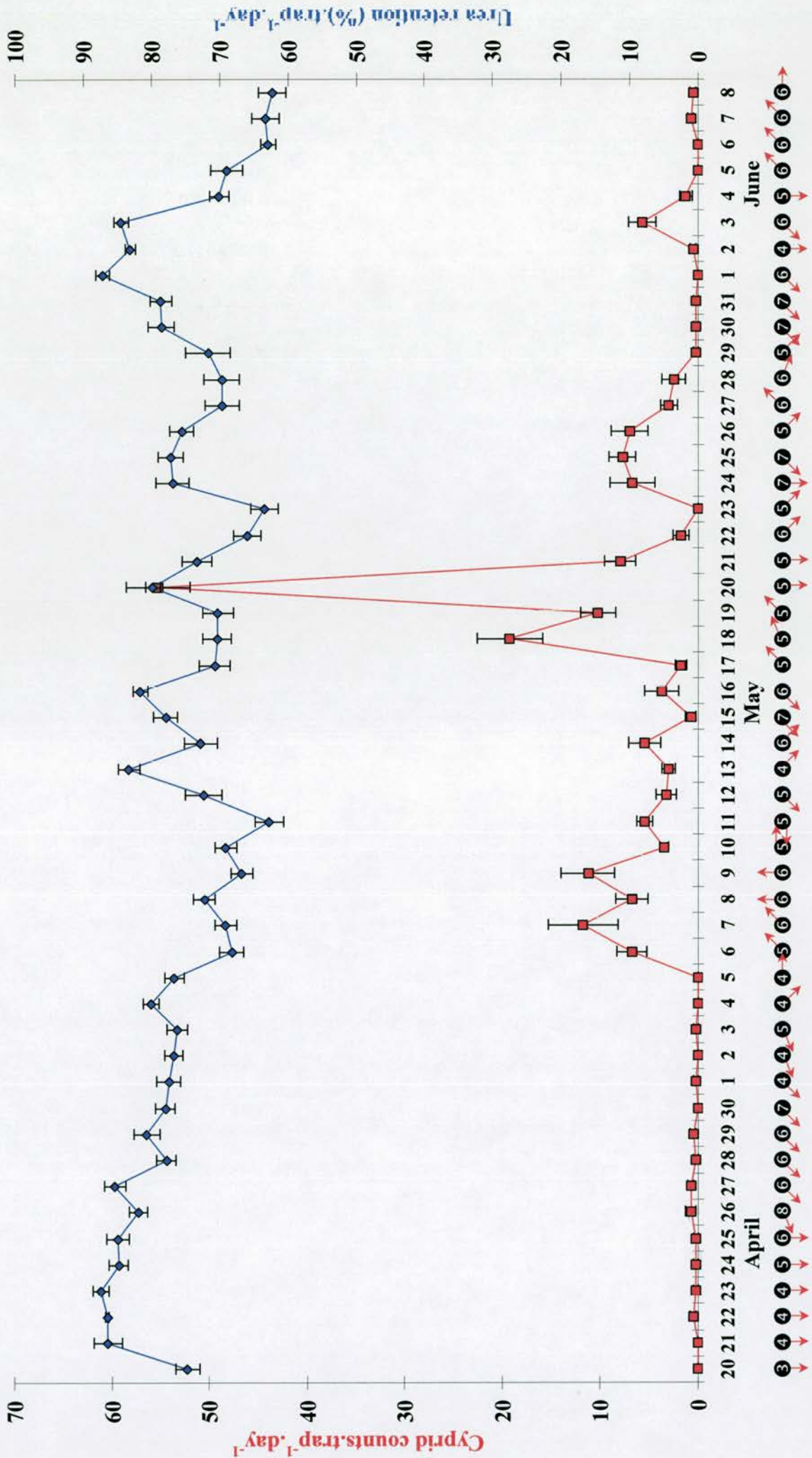


Fig. 94 - Daily trapped larval counts with urea retention (%) sampled daily at St Andrews from the 20th April until the 8th June inclusive (50 days). Each data point represents the mean of four larval traps, with S.E.M. as vertical lines. Wind data shown as maximum Beaufort strength and predominant direction over each daily period, calculated from 10 minute averages.

At Fife Ness a full season of observations over 50 days was collected, and an incidence of supply and urea retention increase occurs on 23rd-27th April, the 2-6th May and from the 30th May to the 2nd of June. However Spearman correlation analysis found that the cyprid trap counts and the percentage retention in the traps were not quite temporally correlated with $p = 0.072$ ($r_s = -0.2566$, $n=50$). Captured larval counts were lower at this site with a maximum of 35 ± 10 cyprids and urea retention of $62.2\% \pm 2.3$ (Fig. 96); for St Andrews the maximum mean larval count per trap was 55 ± 3 cyprids, and 44 ± 1 cyprid at Kingsbarns.

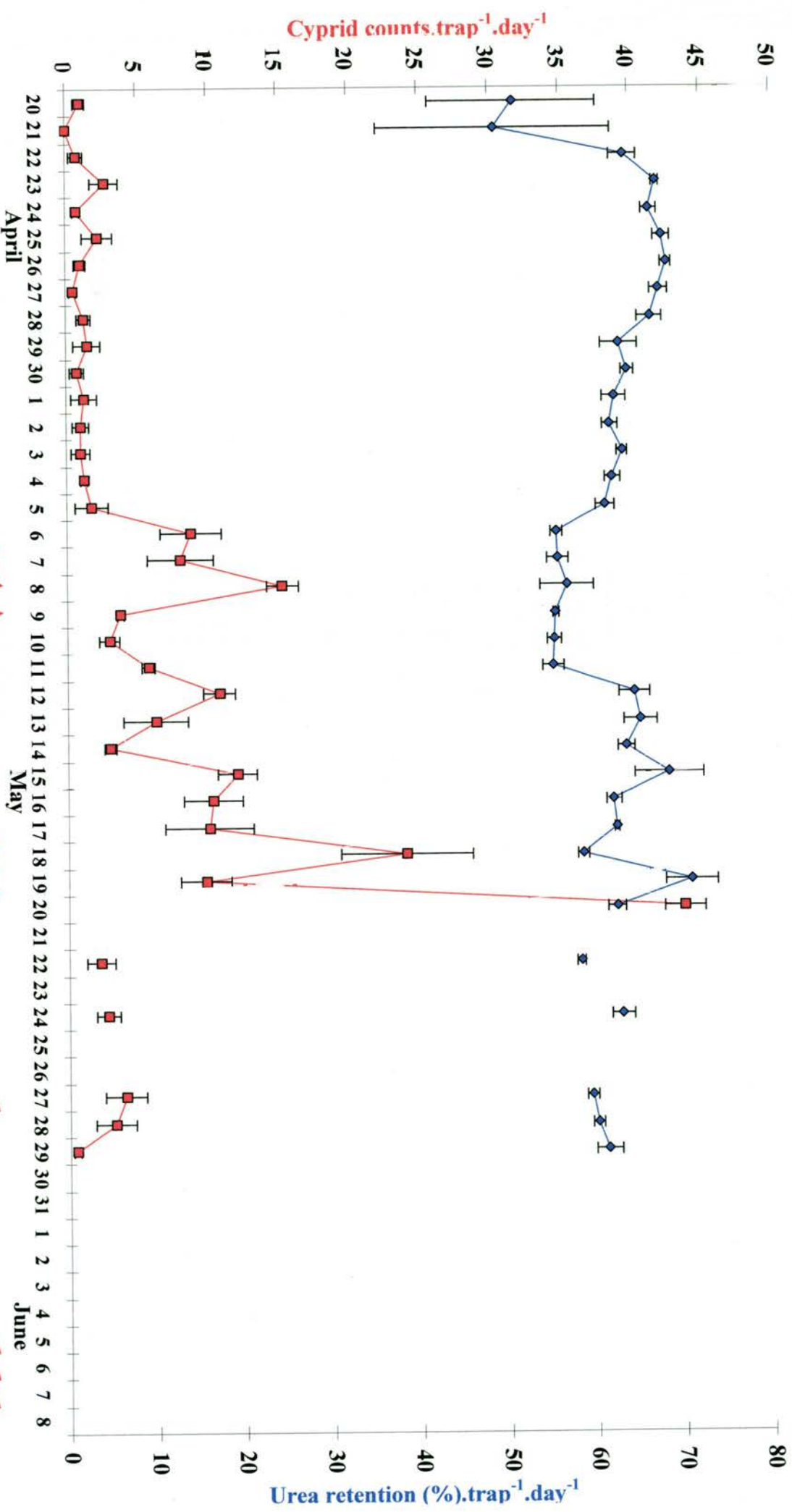


Fig. 95 - Daily trapped larval counts with urea retention (%) sampled daily at Kingsbarns from the 20th April until the 8th June inclusive (50 days). Broken lines indicate missing data due to vandalism; 36 days sampled over season. Each data point represents the mean of four larval traps, with S.E.M. as vertical lines. Wind data shown as maximum Beaufort strength and predominant direction over each daily period, calculated from 10 minute averages.

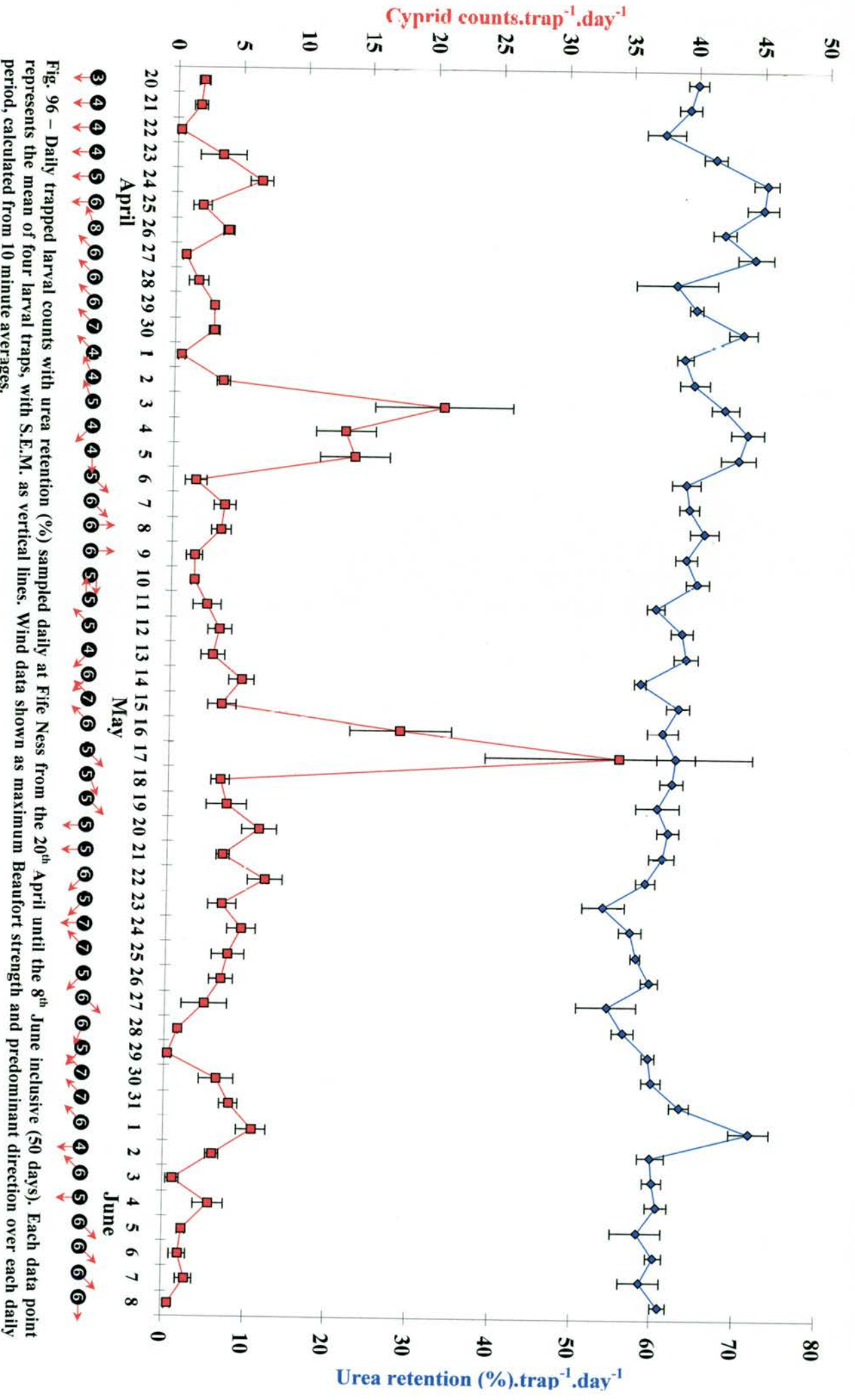


Fig. 96 – Daily trapped larval counts with urea retention (%) sampled daily at Fife Ness from the 20th April until the 8th June inclusive (50 days). Each data point represents the mean of four larval traps, with S.E.M. as vertical lines. Wind data shown as maximum Beaufort strength and predominant direction over each daily period, calculated from 10 minute averages.

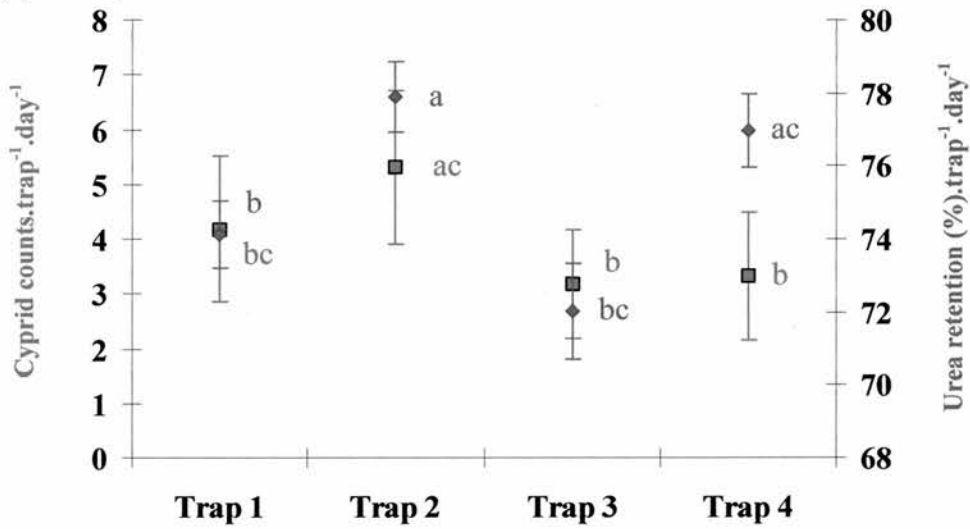
As consistent standard errors had been observed with mean urea percentage retention per day, it was implied that the larval traps each had different efficiencies, although their efficiency level remained constant over the season. Plots of each trap position with mean cyprid counts per trap per day and percentage urea retention per trap per day show that the traps are indeed performing differently.

At Site T at Kinkell Braes in St Andrews, Trap 4 had lower larval counts even though urea retention was 77% (Fig. 97a). Also Traps 1 and 2 were located on the left hand side of the backplate and have higher mean trapped cyprid counts of 4 and 5 cyprids respectively than Traps 3 and 4 located on the right side with 3 cyprids each (Fig. 31). Therefore although the urea retention was 5% different between Traps 3 and 4, the larval counts were still the same, thus small-scale hydrodynamic effects between the left and right side of the backplate were influencing the percentage of urea retention but not to a degree that larval capture was affected.

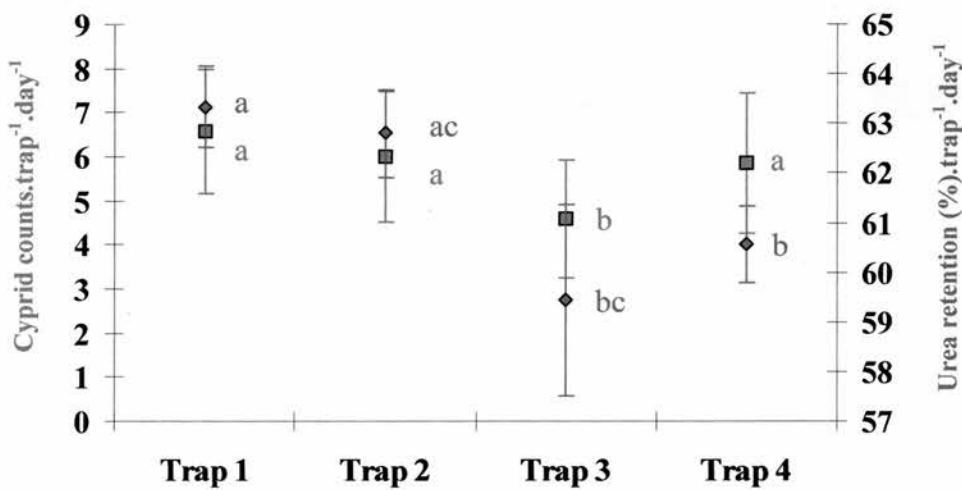
At Kingsbarns (Fig. 97b) the left and right traps had captured mean larval counts of 6.5 and 6.0 cyprids at Traps 1 and 2, with similar levels of urea retention (~63%). Traps 3 and 4 located on the right side of the backplate have lower urea retention percentages (59.5 and 60.5% respectively), but the cyprid counts were 5.5 cyprids for Trap 3 and 6.0 cyprids for Trap 4. This was found to be a significant difference indicating that Trap 3 performs less efficiently than the other traps. Additionally the large standard errors seen ($\pm 2\%$ retention) indicate that the trap performance varies during the season.

At Fife Ness (Fig. 97c) trapped larval counts and percentage retention were similar in Traps 1-3. Trap 4 however, showed lower urea retention efficiency with a mean of 4% less than its neighbouring Trap 3. Trap 4 was located next to a high flat rock, almost in a corner (Fig. 41), and therefore it is likely that local eddies are responsible for the decrease in retention. This decrease in the amount of urea fixative in the traps was correlated with a decrease in trapped larvae, but this observation may also be linked to local hydrodynamics rather than poor trap efficiency.

(a) Site T, Kinkell Braes



(b) Site L / M, Kingsbarns



(c) Site J / K, Fife Ness

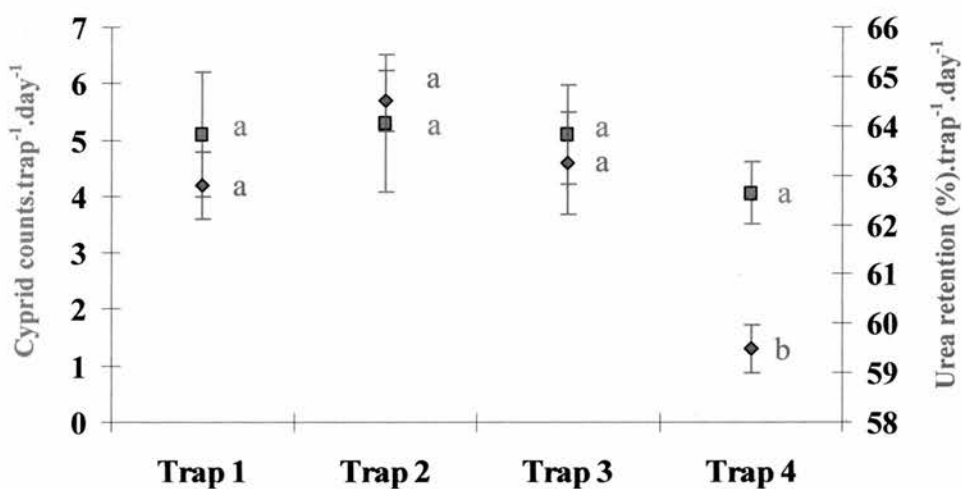


Fig. 97 – Positional effects of percentage urea retention and larval trap capture for replicate traps at each site for the 2002 season. Traps; n=4, collected and refilled daily. For (a) Traps 1, 3 and 4 n=50, Trap 2 n= 49 due to trap leakage, (b) Traps 1, 2 and 3 n=36, Trap 4 n = 35, (c) n= 50 for all Traps. Letters denote Tukey groupings following GLM analysis (Tables 26-28).

3. 3. 5. 2. Analysis of larval trap performance

3. 3. 5. 2. 1. Site T, Kinkell Braes 2002

GLM analysis was performed on arcsine transformed percentage urea retention data and $\log x + 1$ trapped cyprid counts, to assess the positional effects upon the trap capabilities. Trap performance varied with day, as would be expected with changing weather conditions. Trap slot position on the backplate at Site T was found to be highly significant, with both urea retention and trapped larval counts (Table 26a, 26b). Analysis proceeded to Tukey's unplanned multiple comparison tests (Fig. 97). Trap 2 showed the greatest performance efficiency as shown by the highest percentage urea retention and larvae trapped.

Table 26

Larval traps: positional effects on trap performance at Site T, as denoted by (a) urea retention and (b) trapped larval counts.

(a) Urea retention

Source	<i>df</i>	Adj SS	Adj MS	<i>F</i>	<i>p</i>
Trap	3	0.238	0.079	59.00	<0.001
Day	49	2.421	0.049	36.81	<0.001
Error	147	0.197	0.001		
Total	199	2.856			

GLM analysis for urea retention (arcsine percent) sampled daily for 50 days. Factors were Trap (fixed) and Day (random).

(b) Trapped larval counts

Source	<i>df</i>	Adj SS	Adj MS	<i>F</i>	<i>p</i>
Trap	3	0.494	0.165	5.92	<0.001
Day	49	35.309	0.721	25.90	<0.001
Error	147	4.089	0.028		
Total	199				

GLM analysis for trapped cyprid larval counts ($\log x + 1$) over 50 tides. Factors were Trap (fixed) and Day (random).

3.3.5.2.2. Site L / M, Kingsbarns 2002

Trap location on the backplate at the Kingsbarns site was also found to have a highly significant influence on the densities of larvae caught and the percent of urea retained. Large error bars are seen with Trap 3, indicating variability of trap performance during the season. The low retained urea percentage at this trap ($59.5\% \pm 4$) and its corresponding Tukey grouping difference confirm that this trap was less efficient at catching the larvae, due to a greater degree of 'washout'.

Table 27

Larval traps: positional effects on trap performance at Site L / M, as denoted by (a) urea retention and (b) trapped larval counts.

(a) Urea retention

Source	<i>df</i>	Adj SS	Adj MS	<i>F</i>	<i>p</i>
Trap	3	0.030	0.010	10.99	<0.001
Day	35	0.374	0.010	11.58	<0.001
Error	105	0.097	0.001		
Total	143				

GLM analysis for urea retention (arcsine percent) sampled daily for 36 days. Factors were Trap (fixed) and Day (random).

(b) Trapped larval counts

Source	<i>df</i>	Adj SS	Adj MS	<i>F</i>	<i>p</i>
Trap	3	0.055	0.018	4.03	0.009
Day	35	0.537	0.015	3.39	<0.001
Error	103	0.474	0.005		
Total	143				

GLM analysis for trapped cyprid larval counts ($\log x + 1$) over 36 days. Factors were Trap (fixed) and Day (random).

3.3.5.2.3. Site J / K, Fife Ness 2002

At Fife Ness a significant effect of Day was seen as expected, due to variations caused by weather conditions rather than trap inefficiency. Trap position was also found to be of significance for urea % retention (Table 28a), and Tukey groupings indicate that Trap 4 is responsible; this affect is due to the local hydrodynamics within the rock corner as mentioned previously (Fig. 41). However GLM analysis of the larval density counts reveals that this decrease in urea retention does not correspond to a decrease in larval efficiency (Fig. 97c, Table 28b), therefore the traps could withstand a 40% washout without larval collection being affected.

Table 28

Larval traps: positional effects on trap performance at Site J / K, as denoted by (a) urea retention and (b) trapped larval counts.

(a) Urea retention

Source	<i>df</i>	Adj SS	Adj MS	<i>F</i>	<i>p</i>
Trap	3	0.116	0.039	26.72	<0.001
Day	49	0.671	0.014	9.45	<0.001
Error	147	0.213	0.001		
Total	199				

GLM analysis for urea retention (arcsine percent) sampled daily for 50 days. Factors were Trap (fixed) and Day (random).

(b) Trapped larval counts

Source	<i>df</i>	Adj SS	Adj MS	<i>F</i>	<i>p</i>
Trap	3	0.146	0.049	1.18	0.318
Day	49	18.469	0.377	9.17	<0.001
Error	147	6.041	0.041		
Total	199				

GLM analysis for trapped cyprid larval counts ($\log x + 1$) over 50 days. Factors were Trap (fixed) and Day (random).

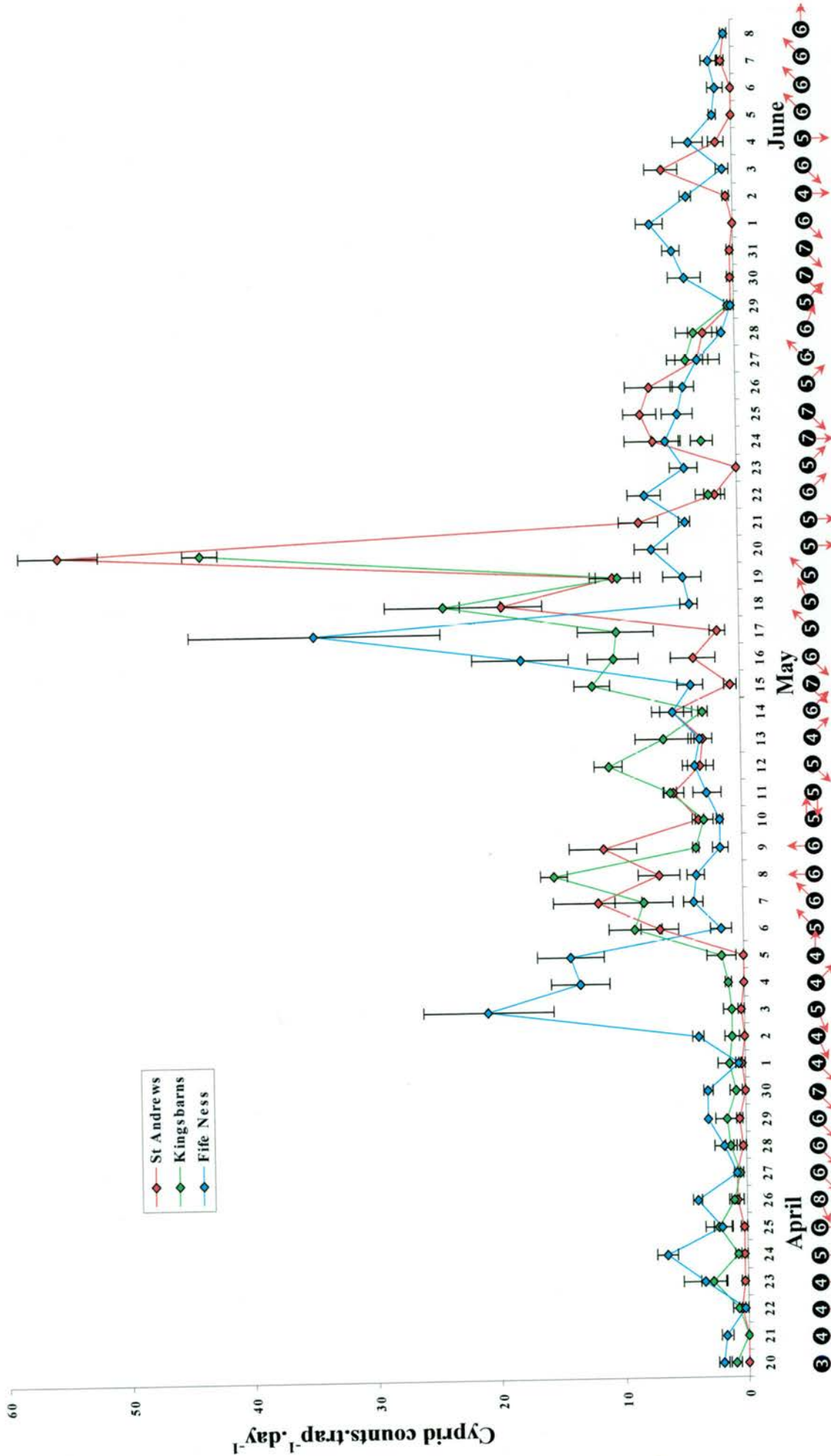


Fig. 98 – Mean daily trapped larval counts sampled daily at St Andrews, Kingsbarns and Fife Ness from the 20th April until the 8th June inclusive (n=50 days for Fife Ness and St Andrews, n=36 days for Kingsbarns). Each data point represents the mean of four larval traps, with S.E.M. as vertical lines. Wind data shown as maximum Beaufort strength and predominant direction over each daily period, calculated from 10 minute averages.

3. 3. 5. 3. Larval trap performance between sites

Larval trap percentage urea retention data and captured larval counts were then used to assess the performance of the traps with Site. Balanced ANOVAs for 36 days of observations were used (Tables 29a and 29b). Day was expected to be of significance, due to temporal variations in larval supply at such large spatial scales (Tables 29a and 29b, Fig. 98). Unplanned Tukey multiple comparison analysis of the highly significant Site effect with urea retention (Table 29) revealed that St Andrews had significantly higher percentage urea retention ($77.9\% \pm 0.8$) than Fife Ness ($63.3\% \pm 0.5$) and Kingsbarns ($63.0\% \pm 0.4$).

Table 29

(a) Larval traps: between-site comparisons, Sites T, K and M over 36 days

Source	<i>df</i>	SS	MS	<i>F</i>	<i>p</i>
Site	2	3.461	1.731	138.61	<0.001
Day	35	0.477	0.042	3.38	<0.001
Site x Day	70	0.874	0.012	5.74	<0.001
Error	324	0.705	0.002		
Total	431	6.517			

ANOVA for urea retention (arcsine percent) from n=4 traps sampled daily at each site, over 36 days. Factors were Site (random) and Day (random).

(b) Larval traps: between-site comparisons, Sites T, K and M over 36 days

Source	<i>df</i>	SS	MS	<i>F</i>	<i>p</i>
Site	2	3.177	1.588	4.06	0.021
Day	35	37.639	1.075	2.75	<0.001
Site x Day	70	27.355	0.390	10.03	<0.001
Error	324	12.627	0.039		
Total	431	80.798			

ANOVA for trapped cyprid counts ($\log x + 1$) from n=4 traps sampled daily at each site, over 36 days. Factors were Site (random) and Day (random).

When trapped cyprid counts are compared across the sites, an increase in probability is seen ($F_{2,324} = 4.06$, $p = 0.021$) for Site variations, although the treatment remains significant (Table 29). Variations in daily observations were seen to be significant once more. A significant interaction between Site and Day remained; Tukey unplanned comparisons revealed that the St Andrews site was responsible for this significance with a lower daily cyprid mean cyprid catch (1.57 ± 0.08 cyprids) than the other sites at Fife Ness (3.12 ± 0.06 cyprids) and Kingsbarns (2.93 ± 1.32 cyprids). As the urea percentage was the greatest at St Andrews, this suggests that the larval traps can operate in a range of environments with a decrease in urea retention to ~63% showing no adverse effect on capture capabilities.

3. 3. 5. 4. Larval trap performance with water flux

Plots were used to investigate any relationship between the water flux (sediment weight as index of wave crash) and percentage urea retention in traps. As would be expected the percentage urea retention is high in low wave conditions. However the curve appears to have an inverse 1st order polynomial distribution, although this cannot be firmly stated due to a lack of observed sediment weight during the section from 0.2 g upwards (Fig. 99). The maximum mean sediment ashed weight (1.987g) occurs on the 11th May during a Force 5 W wind. However on the three days prior to this recorded weight ran a four day period of N / NE Force 5 / 6 winds. The next maximum observed sediment weight is seen at 1.159g, corresponding to a period of Force 5 SE winds. Regression analysis confirms that although the two variables may not have an obvious linear relationship, they are significantly related (regression equation $y = 76.868 - 11.733x$; $r = 0.5883$, $p < 0.001$).

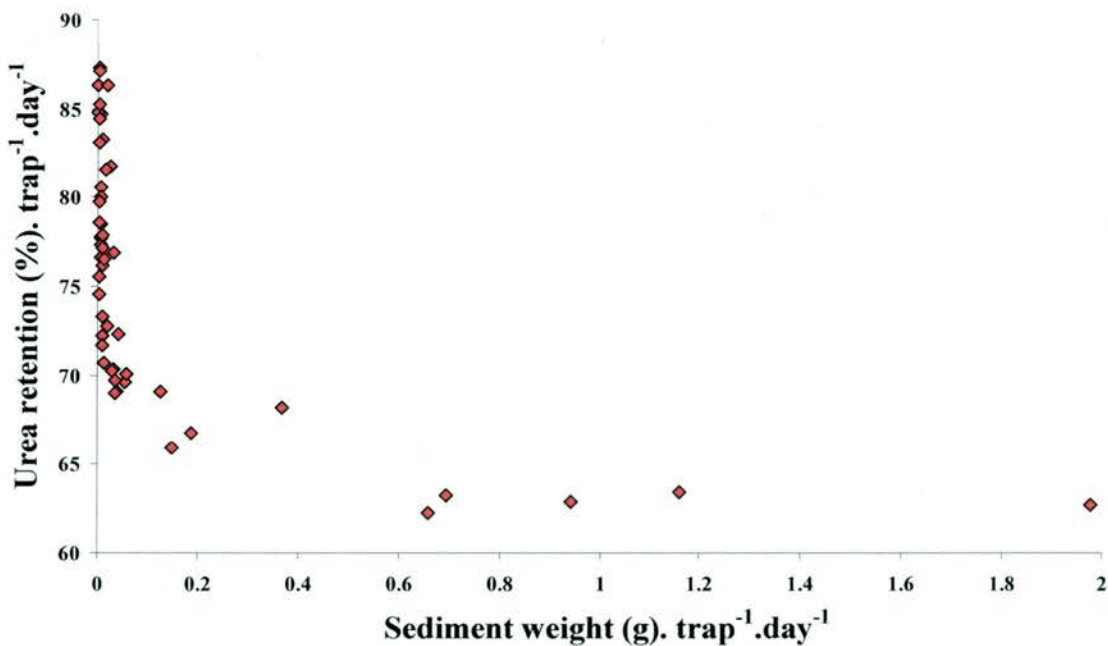


Fig. 99 – Scatter plot of mean percent urea retention for larval traps against captured ashed sand sediment weight (g) at St Andrews. Sediment traps n=2, larval traps n=4 sampled daily over 50 days.

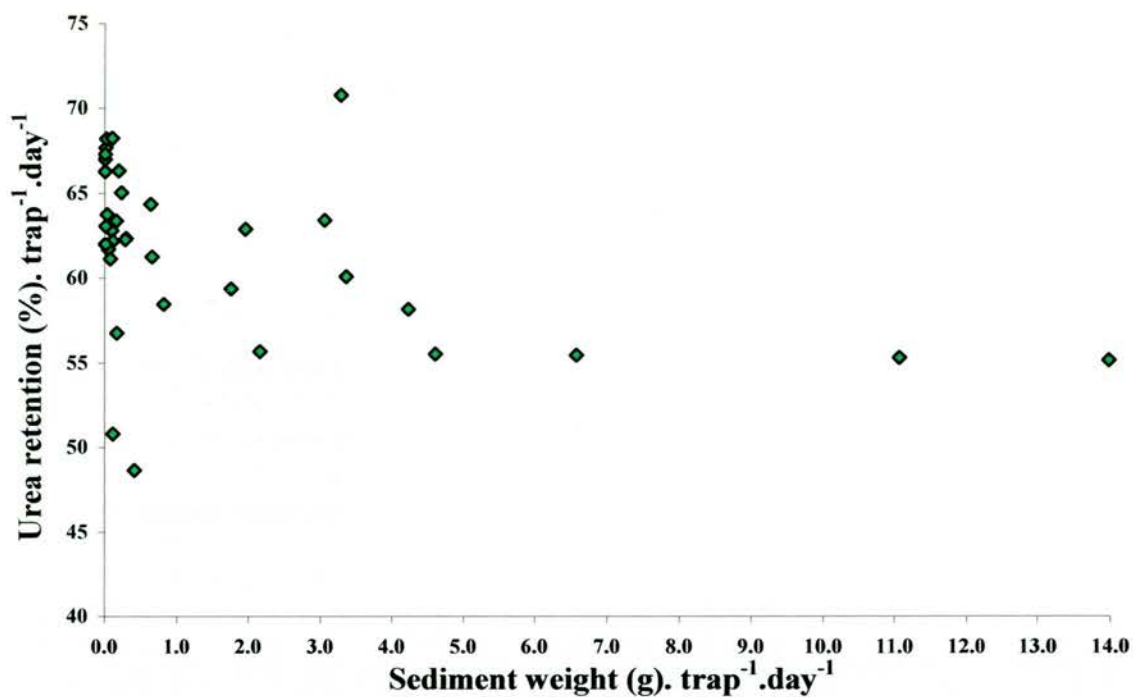


Fig. 100 – Scatter plot of mean percent urea retention for larval traps against captured ashed sand sediment weight (g) at Kingsbarns. Sediment traps n=2, larval traps n=4 sampled daily over 36 days.

Kingsbarns also showed no clear linear relationship; for example at 3g trapped weight there is over 10% urea retention difference. As at St Andrews, large collections of sediment weight occurred infrequently, with many of the studied days coinciding with days of little wave crash. The maximum recorded sediment weight was 13.797g occurring on the 11th May during a Force 5 SW, corresponding to the same large value also seen at Site T. The regression equation for a linear fitted line is $y = 62.6329 - 0.659834x$, $r = 0.412$, $p = 0.013$.

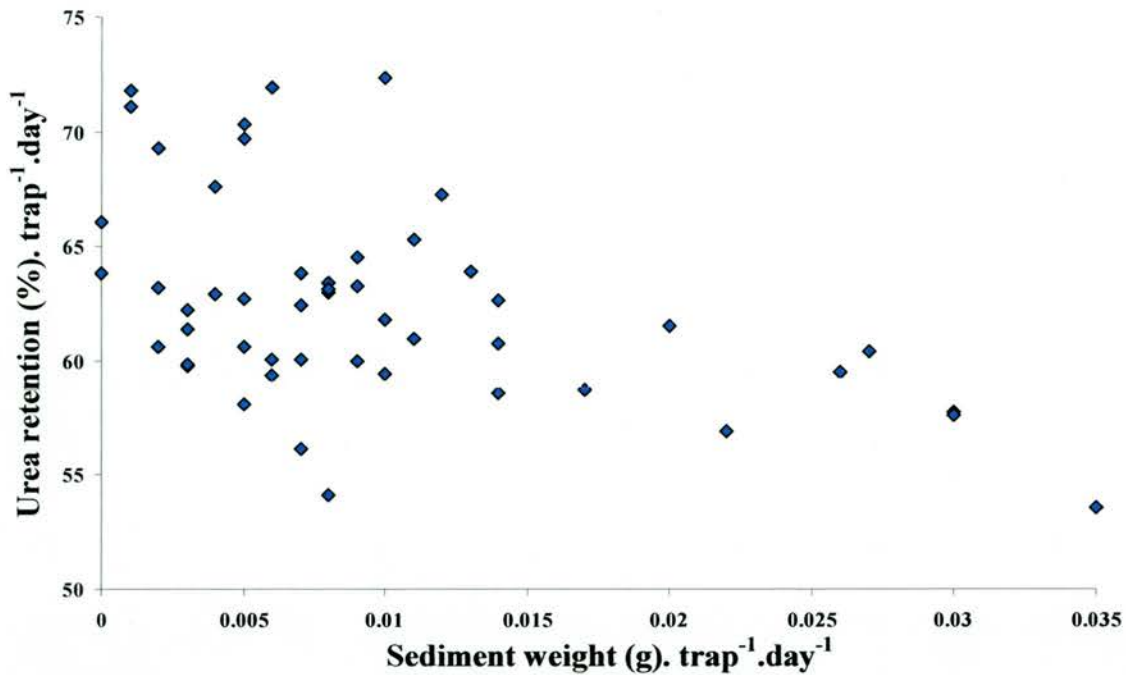


Fig. 101 – Scatter plot of mean percent urea retention for larval traps against captured ashed sand sediment weight (g) at Fife Ness. Sediment traps n=2, larval traps n=4 sampled daily over 50 days.

Percentage urea retention was also correlated significantly at Site J / K, even though points were scattered (regression line equation is $y = 65.027 - 260.114 x$, $r = 9.482$, $p < 0.001$). Unlike Kingsbarns and St Andrews, the maximum mean ashed sediment weight was related to a period of southerly winds on the 23rd May (0.035g, see Fig. 101).

3. 3. 6. Supply and settlement relationships

3. 3. 6. 1. Larval supply and settlement on artificial substrata

The relationship between cyprid supply and settlement on multiple grooved panels was plotted in Fig. 102 and when examined per site the strength of the relationship varied. Linear regression analysis found that the St Andrews site (r^2 value of 0.7392) had the largest correlation coefficient of $r = 0.860$, indicating a strong supply to settlement relationship. At Kingsbarns $r = 0.836$ with r^2 of 0.6997, therefore showing a slightly weaker linear relationship between larval supply and settlement. At Fife Ness the correlation is further decreased as only 35% of the variation in the panel counts could be explained by linear regression with larval trap densities ($r^2 = 0.3477$, $r = 0.590$). However the decrease was not sufficient to alter the significance of the correlation as all relationship lines were statistically significant with $p < 0.001$

At each site one value was found to have a large influence on the regression line (as shown on the chart), which corresponded to an increased supply to settlement ratio. This increased capture observation occurred on the 20th May at both St Andrews and Kingsbarns, while the corresponding settlement peak had already been seen on the 18th / 19th of May at St Andrews (Fig. 82) and the 18th of May at Kingsbarns (Fig. 90). The influential observation at Fife Ness occurred on the 17th of May, while panel densities had previously peaked on the 14th-16th May (Fig. 86). Such observations are interesting in themselves as they suggest that larvae are not 'desperate' to settle, and therefore cannot be omitted from the regression analysis. ANCOVA analysis revealed that while the relationship may vary slightly in linearity with site, it does not vary significantly ($p > 0.05$ for all comparisons). Therefore the fluctuations in linearity of

sites caused by particular hydrodynamics or orientation, does not affect the larval supply and settlement relationship.

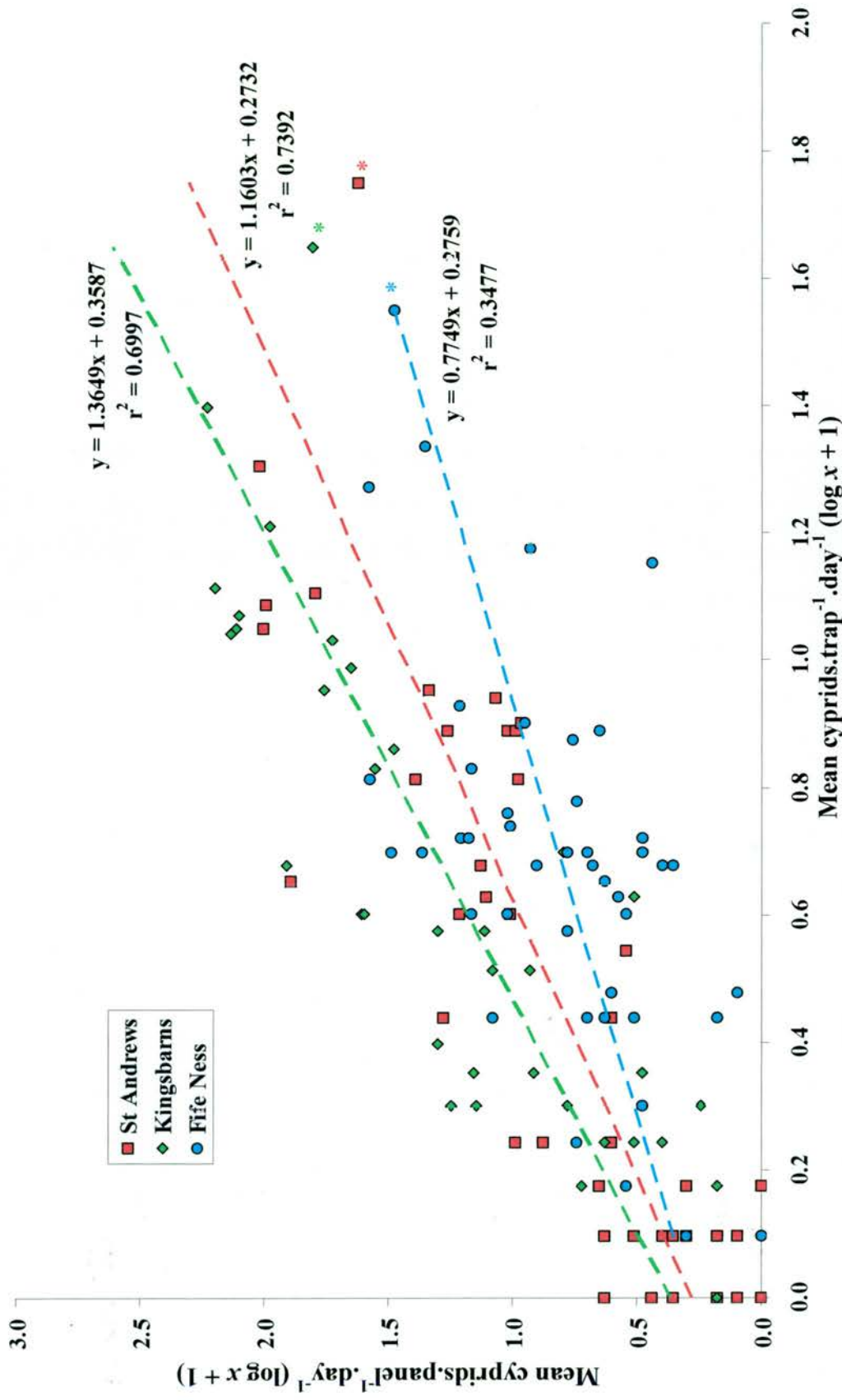


Fig. 102 - Scatter plots of $\log x + 1$ mean daily settlement densities per multiple grooved panel (groove area 48cm^2 , plane area 56cm^2) at Sites T, J / K and L / M in relation to larval supply. Panels; mean of $n=4$ daily deployed, with extract. Traps; mean of $n=4$ emptied daily, located on the backplate in the field. Days; $n=44$ for Sites T and J / K, $n=36$ for Site L / M. Regression equations included on plot, with $r = 0.860$, $p < 0.001$ for St Andrews; $r = 0.836$, $p < 0.001$ for Kingsbarns; $r = 0.590$, $p < 0.001$ for Fife Ness. Asterisks denote observations that greatly influenced the regression analysis.

3. 3. 6. 2. *Supply and settlement on natural substrata.*

Triplicate 5 x 5cm quadrats of rock at each site were counted and cleared daily to examine cyprid settlement on natural substrata. Settlement varied with quadrat, due to topological differences, but performed similarly over days.

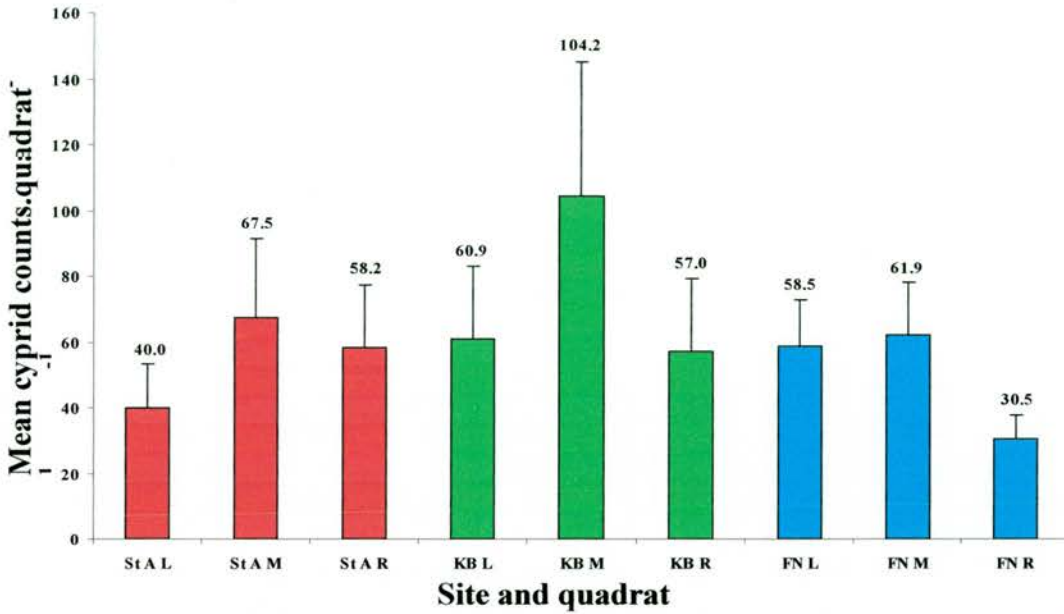


Fig. 103 -Mean daily settlement on 25cm² triplicate clearance quadrats at each site in 2002. Numbers denote mean values, with letters indicating site and position (left, middle and right) St Andrews quadrats sampled 16th May-6th June (22 days); Kingsbarns sampled 15th May to 8th June, minus vandalism dates (23 days); Fife Ness sampled 15th May to 8th June (25 days).

These cyprid quadrat clearances were located on the left, middle and right sides of the backpanel and the mean daily densities were compared to the trapped larvae to examine larval supply and settlement relationships on natural substrata (Fig. 104). As seen in Fig. 103, the quadrat located on the right of Site J / K at Fife Ness has considerably lower settlement than the other two quadrats at this site, which further supports the theory of localised hydrodynamic effects at this position affecting the performance of larval Trap 4 (Fig. 97c).

Strong correlations are seen between trapped cyprids and cleared quadrats at St Andrews and Fife Ness, with 85% and 75% of the respective variation in the explained by variations in the supply of larvae. However, the relationship at

Kingsbarns is less pronounced ($r = 0.582$, $r^2 = 0.339$). This cannot be firmly concluded as a significant deviation from the larval supply and settlement patterns seen at the other sites; the vandalism incidents detailed the loss of larval trap observations, and although subsequent clearances were still maintained until the 8th of June, no further traps were deployed after the 30th May.

ANCOVA comparisons of the supply / settlement relationship with site resulted in a significant deviation of Kingsbarns from the other two sites, which themselves were not significantly different ($t = -0.214$, $df = 43$, $p > 0.05$). However future samples of quadrats and traps would need to be attained for the true pattern of this relationship to be assessed.

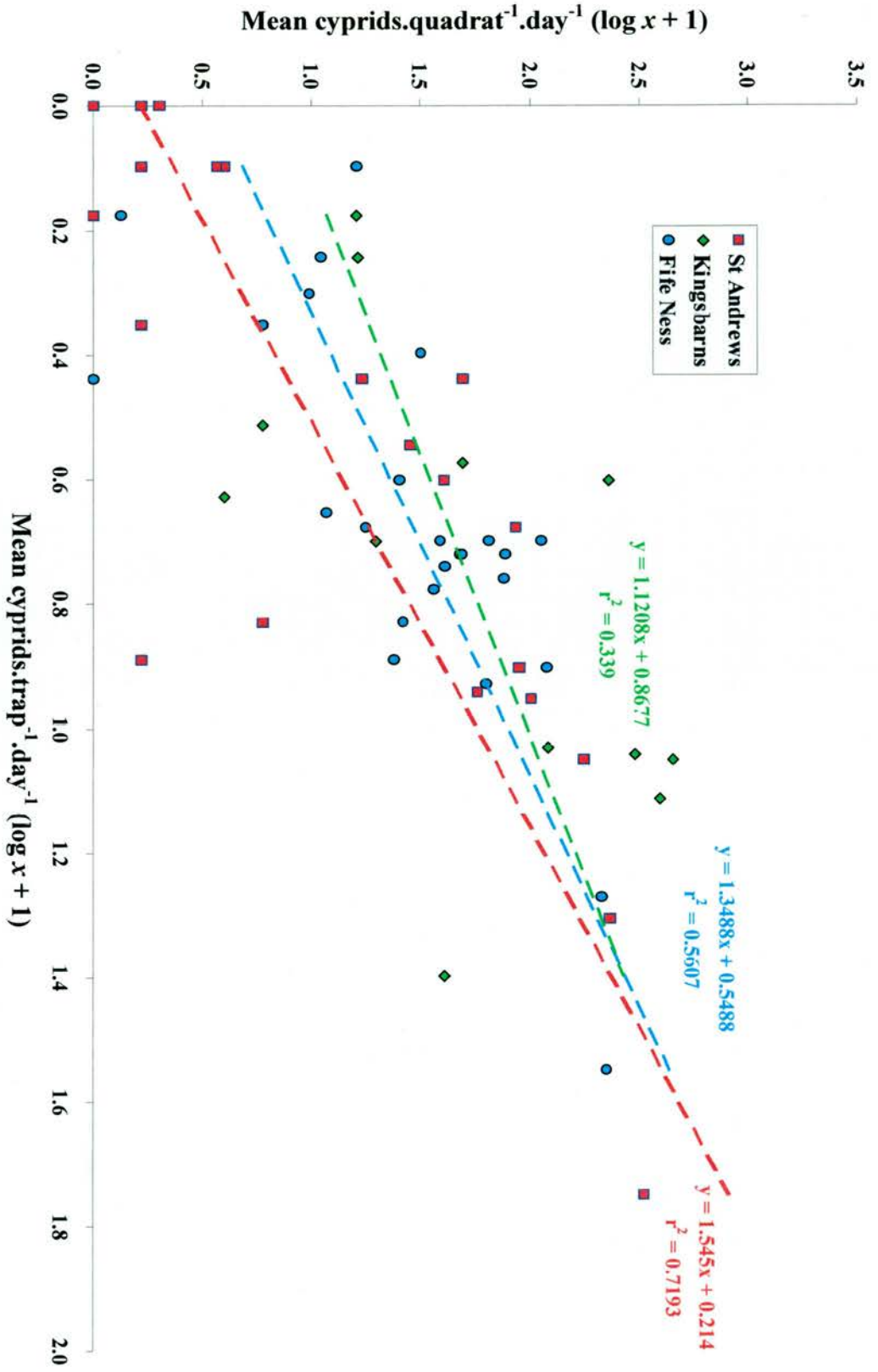


Fig. 104 – Scatter plot of $\log x + 1$ mean daily settlement densities on cleared 25cm² quadrats at Sites T, J / K and L / M in relation to larval supply. Traps: mean of $n=4$ deployed daily. Quadrats: mean of $n=3$ cleared, located by the backpack in the field. Days: $n=22$ for Site T, $n=12$ for Site L / M, $n=25$ for J / K. Regression equations included on plot, with $r = 0.848, p < 0.001$ for St Andrews; $r = 0.582, p < 0.001$ for Kingsbarns; $r = 0.749, p < 0.001$ for Fife Ness.

3.3.7. Larval settlement on natural and artificial substrata

Data collected of cyprid densities on grooved panels and on the cleared quadrats were converted into cyprids.cm², transformed ($\log x + 1$) and then plotted to compare settlement densities on natural and artificial substrata (Fig. 105). Regression analysis found that all sites were highly correlated with correlation coefficients of 0.796, 0.949 and 0.847 for Site T at St Andrews, Site L / M at Kingsbarns and Site J / K at Fife Ness respectively ($p < 0.001$ for all sites). Additionally the regression indicates that rocks are much preferred for settlement by cyprids than panels; for every 10 cyprids settling on the rocks 0.3 cyprids, 0.5 cyprids and 1.1 cyprids would settle on grooved panels at Fife Ness, St Andrews and Kingsbarns respectively. However the strong correlation coefficients indicate that panels performed consistently throughout the season. ANCOVA tests of the settlement relationship between sites found that none were significant ($p > 0.05$ for all sites).

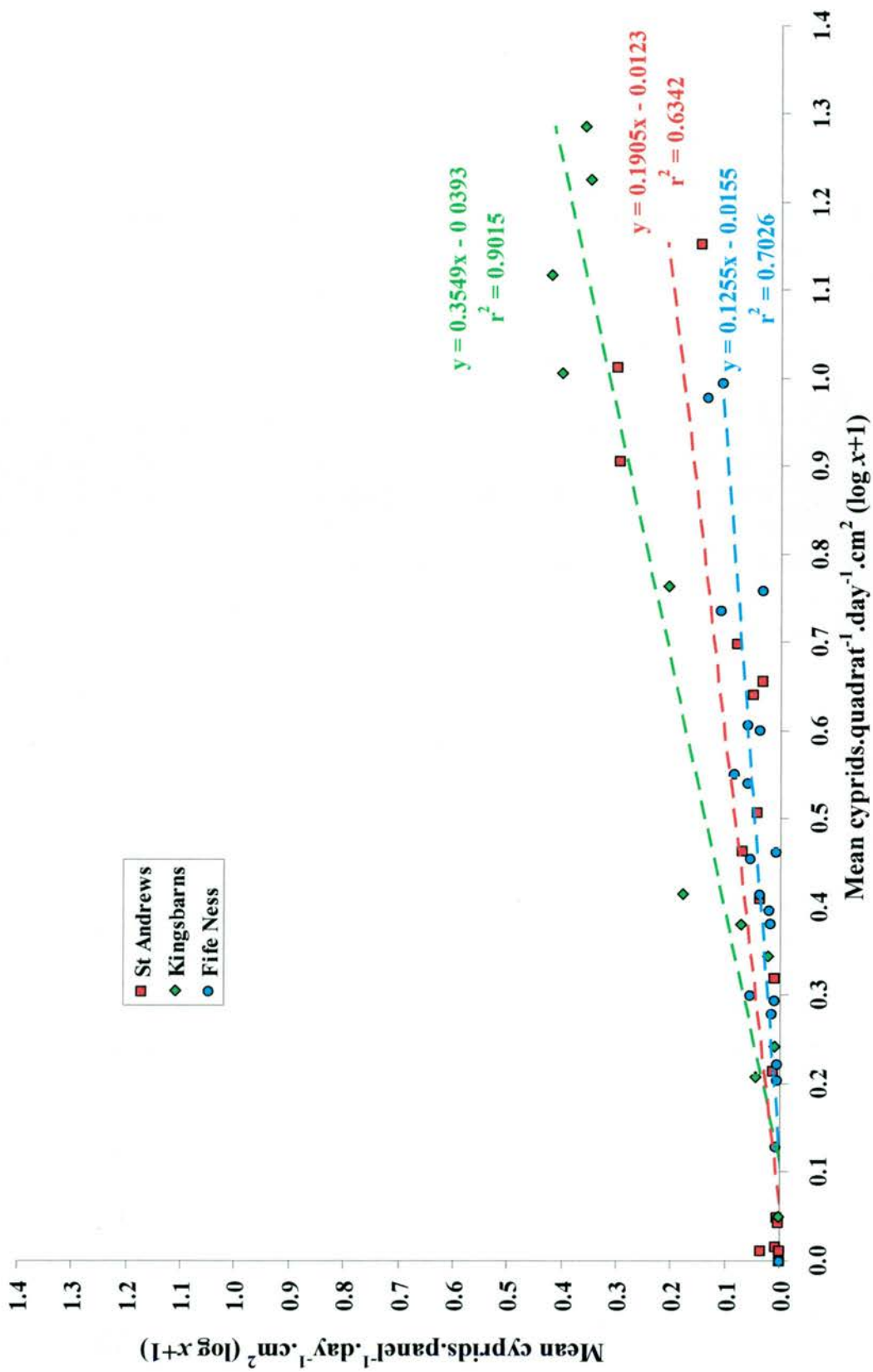


Fig. 105 – Scatter plots of $\log x + 1$ mean daily settlement densities on cleared quadrats per cm^2 and grooved panels per cm^2 at Sites T, J / K and L / M in relation to larval supply. Triplicate quadrats sampled daily and cleared, located by the backplate in the field. Days; n=19 for Site T and J / K, n=10 for Site L / M. Regression equations included on plot, with $r = 0.796$, $p < 0.001$ for St Andrews; $r = 0.949$, $p < 0.001$ for Kingsbarns; $r = 0.847$, $p < 0.001$ for Fife Ness.

3.3.8. Larval supply relationships of *S. balanoides* and *Balanus crenatus*

During the 2002 season *Balanus crenatus* larvae were also captured in the larval traps at the three sites. Therefore this data was temporally plotted with *S. balanoides* larval trap counts to ascertain if the supply occurred spontaneously in these two species (Figs. 106 – 108). *B. crenatus* supply was seen to occur exclusively with winds from the SW / S / SE, with very little to zero cyprids captured during periods of other wind directions (Fig.106). Additionally, apart from a small peak correlation between the 24th - 27th May, supply was not correlated. Indeed the relationship was almost mutually exclusive. Spearman correlation analysis found that the relationship was not quite significant ($r_s = 0.1295$, $n = 200$, $p = 0.0676$). Further years of settlement data may prove the exclusivity of this relationship. The peaks in larval densities of *B. crenatus* also occurred only in periods of low water movement, as shown by low weights of ashed sediments (Fig. 80). The maximum mean of 28 ± 1 *B. crenatus* cyprids across the four traps occurred with a SW wind and low captured sediment weight on the 25th May.

Unfortunately trapped densities of *B. crenatus* were very poor at both Fife Ness and Kingsbarns (Fig. 107, 108). Maximum mean cyprid densities at Fife Ness were 35 ± 10 *S. balanoides* larvae (16th May) with only 6 ± 2 *B. crenatus* larvae on the 25th May. No correlation could be seen with water movement (Figs. 87 and 107). Supply of *B. crenatus* larvae was seen to increase during periods of SW / S / SE winds at Kingsbarns, but not above a 3 cyprid average. The maximum observed supply of *B. crenatus* larvae occurred on the 15th May (3 ± 1) during a period of SW Force 6/7 winds but with very low sediment weights (Fig. 91).

ANOVA tests of larval count data of both species of 36 days from each site were used to assess supply of the two species within and between the sites. (Tables 30 – 34).

Table 30

Larval traps: within-site comparison of captured larval species at Site T over 36 days

Source	<i>df</i>	SS	MS	<i>F</i>	<i>p</i>
Species	1	0.030	0.031	0.03	0.864
Day	35	8.970	0.256	3.14	<0.001
Species x Day	35	35.738	1.021	12.52	<0.001
Error	216	17.611	0.082		
Total	287	62.349			

ANOVA for trapped cyprid counts ($\log x + 1$) from $n=4$ traps sampled daily over 36 days. Factors were Species (fixed) and Day (random).

Variation between species was not found to be significant at Site T, although the expected Day effect occurred. A significant interaction also occurred which was caused by non-temporal correlation of supply of the two species.

Table 31

Larval traps: within-site comparison of captured larval species at Site J / K over 36 days

Source	<i>df</i>	SS	MS	<i>F</i>	<i>p</i>
Species	1	19.721	19.721	145.36	0.021
Day	35	7.585	0.217	3.61	<0.001
Species x Day	35	4.749	0.136	2.26	<0.001
Error	216	12.959	0.060		
Total	287	45.014			

ANOVA for trapped cyprid counts ($\log x + 1$) from $n=4$ traps sampled daily over 36 days. Factors were Species (fixed) and Day (random).

All factors and interactions were significant at Site J / K, as would be expected due to the very poor larval counts of *B. crenatus* and the variation of supply over the season (Fig.107).

Table 32
Larval traps: within-site comparison of captured larval species at Site L / M over 36 days

Source	<i>df</i>	SS	MS	<i>F</i>	<i>p</i>
Species	1	17.541	17.541	63.06	<0.001
Day	35	11.531	0.329	6.39	<0.001
Species x Day	35	9.765	0.278	5.40	<0.001
Error	216	11.132	0.052		
Total	287	49.940			

ANOVA for trapped cyprid counts ($\log x + 1$) from n=4 traps sampled daily over 36 days. Factors were Species (fixed) and Day (random).

All factors of the larval trap data at Site L / M were found to be statistically significant, as counts of *B. crenatus* larvae were very low. The expected Day factor was seen, and the Species x Day interaction can be attributed to the fluctuations in counts of *S. balanoides* larvae.

Table 33
Larval traps: between-site comparison of captured larval species at Sites T, J / K and L / M over 36 days

Source	<i>df</i>	SS	MS	<i>F</i>	<i>p</i>
Species	1	23.824	23.824	3.26	0.193
Site	2	1.632	0.816	3.99	0.023
Day	35	13.785	0.394	1.9	0.010
Species x Site	2	13.459	6.765	23.58	<0.001
Species x Day	35	30.229	0.864	3.02	<0.001
Site x Day	70	14.301	0.204	3.17	<0.001
Species x Site x Day	70	19.993	0.286	4.44	<0.001
Error	648	41.702	0.064		
Total	863	158.935			

ANOVA for trapped cyprid counts ($\log x + 1$) from n=4 traps sampled daily at each site, over 36 days. Factors were Species (fixed), Site (random) and Day (random).

Comparison of the captured larval counts of both species were not significant over the three sites. This was attributable to the higher larval counts of *B. crenatus* at Site T. The non-significant variance between species at Site T also led to the significant Site term and all interactions involved. Therefore the analysis was repeated, using only Site J / K and L / M data (Table 34).

Table 34
Larval traps: between-site comparison of captured larval species at Sites J / K and L / M over 36 days

Source	<i>df</i>	SS	MS	<i>F</i>	<i>p</i>
Species	1	37.231	37.231	310.8	<0.001
Site	1	0.075	0.075	0.39	0.537
Day	35	12.347	0.353	1.82	0.040
Species x Site	1	0.032	0.032	0.20	0.0661
Species x Day	35	8.780	0.251	1.54	0.104
Site x Day	35	6.769	0.193	3.47	<0.001
Species x Site x Day	35	5.704	0.163	2.92	<0.001
Error	432	24.091	0.056		
Total	575	95.029			

ANOVA for trapped cyprid counts ($\log x + 1$) from n=4 traps sampled daily at each site, over 36 days. Factors were Species (fixed), Site (random) and Day (random).

Following the omission of Site T data, there is significant variation in the larval supply of barnacles at Site J / K and L / M, which did not alter with Site (non significant interaction). The same predominance of *S. balanoides* cyprids compared to *B. crenatus* cyprids was found at both sites and the lack of a significant Species x Day interaction can be attributed to the persistent low numbers of *B. crenatus* larvae throughout the season.

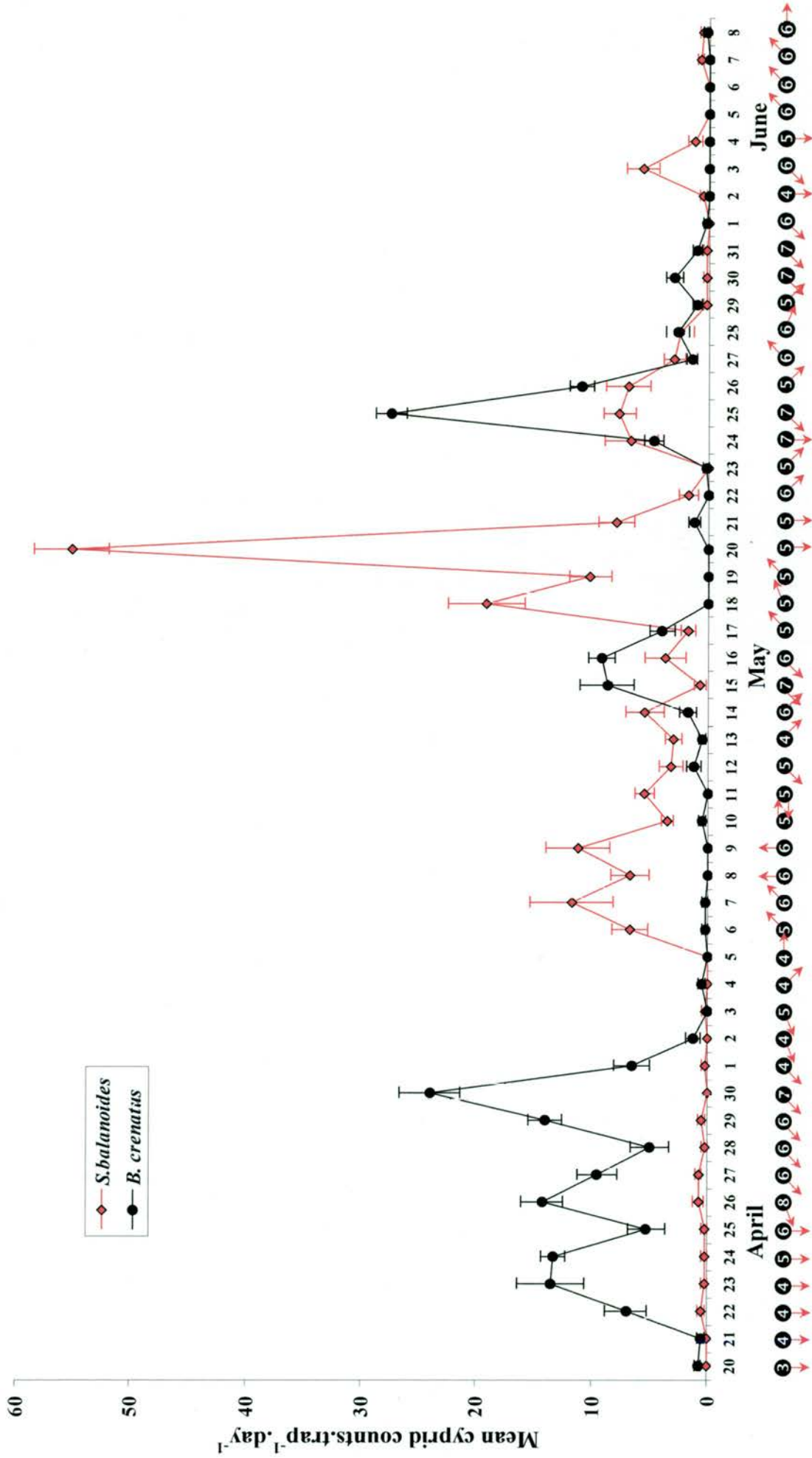


Fig. 106 – Mean daily trapped larval counts for *S. balanoides* and *B. crenatus* sampled daily from Site T at St Andrews from the 20th April until the 8th June inclusive. Each point represents four larval traps situated on the panel backplates sampled daily for 50 days. S.E.M. shown as vertical lines. Wind data shown as maximum Beaufort strength and predominant direction over each daily period, calculated from 10 minute averages.

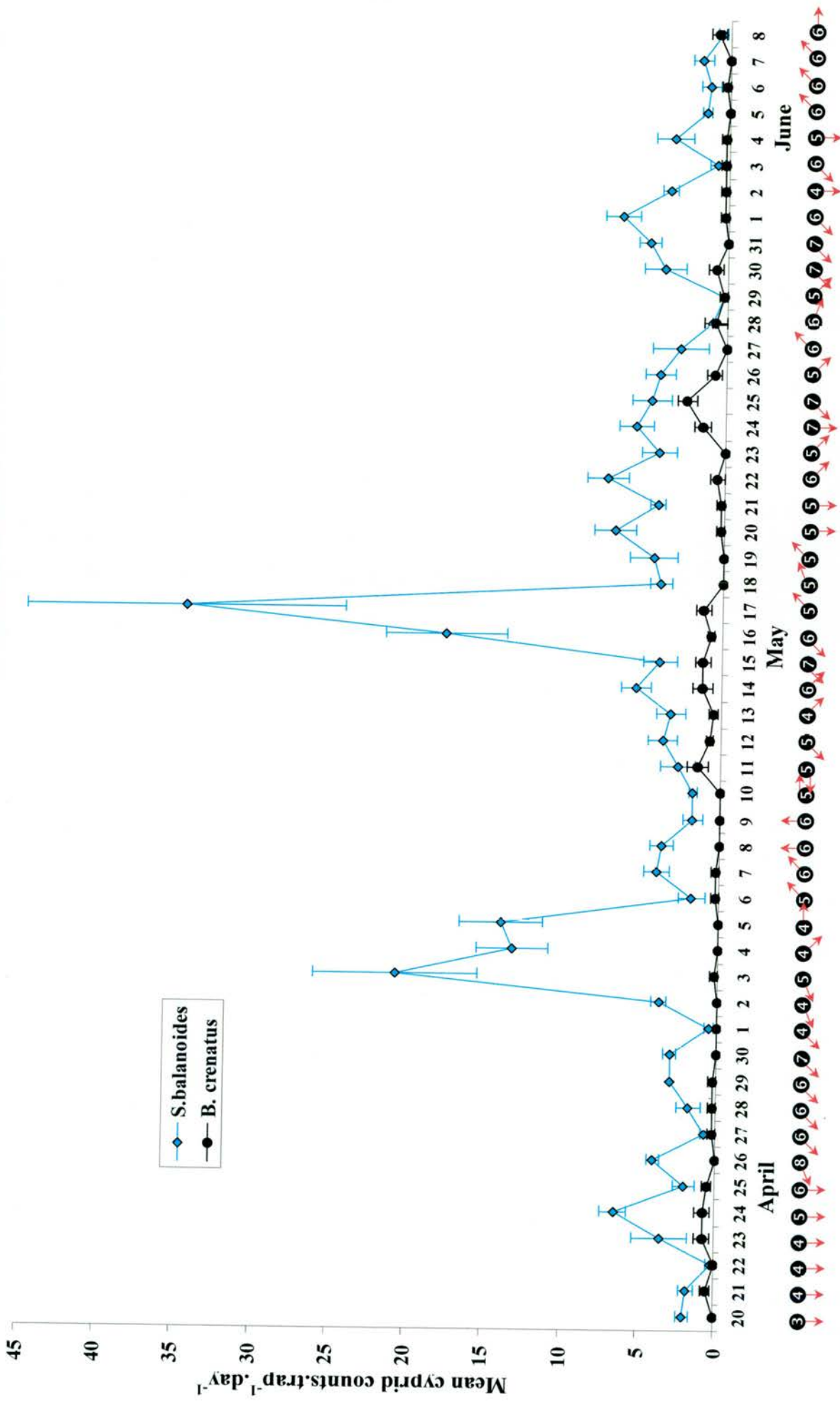


Fig. 107 – Mean daily trapped larval counts for *S. balanooides* and *B. crenatus* sampled daily from Site J / K at Fife Ness from the 20th April until the 8th June inclusive. Each point represents four larval traps situated on the panel backplates sampled daily for 50 days. S.E.M. shown as vertical lines. Wind data shown as maximum Beaufort strength and predominant direction over each daily period, calculated from 10 minute averages.

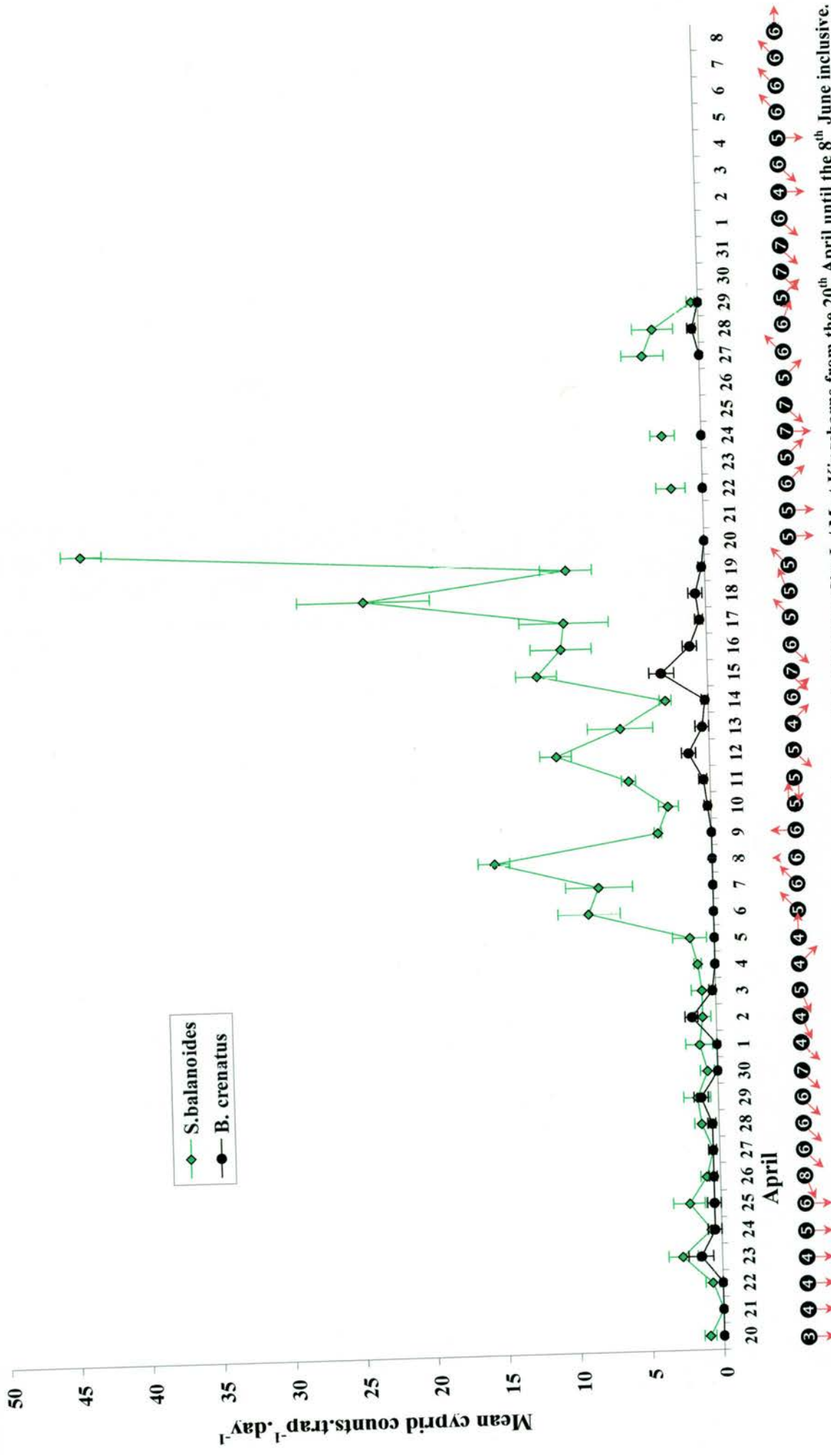


Fig. 108 – Mean daily trapped larval counts for *S. balanooides* and *B. crenatus* sampled daily from Site L / M at Kingsbarns from the 20th April until the 8th June inclusive. Each point represents four larval traps situated on the panel backplates sampled daily for 50 days. S.E.M. shown as vertical lines. Broken lines are unavailable data as traps not sampled due to vandalism. Wind data shown as maximum Beaufort strength and predominant direction over each daily period, calculated from 10 minute averages.

3. 4. Larval settlement over seasons

3. 4. 1. Site C

During the first sampled settlement season in 2000, plane panels with extract performed well with cyprid counts per panel of up to 191 ± 37 cyprids at Site C. Therefore these panels were considered to be suitable for use for the subsequent settlement experiments. However in 2001 settlement had dropped to 119 ± 28 cyprids and to 4 ± 1 cyprid in 2002 on the same panel type in the same location. This year decrease in settlement on plane panels with extract at Site C corresponds to panel per season means of 6.08 ± 0.18 , 1.05 ± 0.11 and 0.15 ± 0.01 cyprids in 2000, 2001 and 2002 respectively. During 2000 and 2001 Site C was part of a panel block consisting also of four plane panels without extract, whereas in the final year four multiple grooved panels with extract were deployed along side. Therefore this reduction in settlement on plane panels may be related to substrate preference, with the greater densities seen in the first two years caused by lack of available preferred substratum. Kruskal-Wallis analysis found that all years were significantly different from each other ($p < 0.001$, $n=104$ for 2000, $n=144$ for 2001, $n= 176$ for 2002). This non-parametric statistical test was used as the design was unbalanced, and therefore this conservative test was more suitable.

3. 4. 2. Site T

During 2001 three horizontally grooved panels (12cm^2 groove area) with extract were exposed to settlement at Site T as part of a block of panels. In 2002 four of the same type of horizontally grooved panels were deployed at Site T. Maximum mean daily settlement counts of 161 ± 30 and 82 ± 8 cyprids were found per horizontal panel

during the 2001 and 2002 settlement years. This shows an obvious decrease in settlement in the second year of ~50%. When translated into per panel means over the season, 2001 data has a mean of 5.42 ± 0.06 cyprids per panel, whereas during 2002 there are 4.11 ± 0.05 cyprids per panel. Statistically this is not significant ($t = 1.34$, $df = 202$, $p = 0.18$) although the maximum peaks may be greater in 2001. Therefore settlement levels of larvae to the panel substratum did not differ between years.

During 2001 triplicate plane panels with extract were also deployed at Site T, and had a maximum settled density of only 8 ± 3 cyprids per panel. The high comparative settlement of horizontal panels of 161 ± 30 cyprids suggests that the pattern of very poor performance of plane panels in the final year at Site C is due to panel preference and not a change in larval supply to the site.

CHAPTER 4

DISCUSSION



4. Discussion

4. 1. *Effect of conspecific extract on settlement*

The presence of the painted conspecific cue on the panels was found to have a significant effect on increasing *S. balanoides* larval settlement. This has been found in previous studies as this cue is reported to convey the suitability of the area for settlement (Crisp & Meadows, 1962, Crisp & Meadows, 1963). Specificity of settlement on panels with extract was found at all sites in 2001 and 2002. However this was not the case in 2000. Although the general pattern was for increased settlement on panels with extract, the major peaks of settlers on May 15th am and pm tides correspond to altered cyprid specificity behaviour (Figs. 44 and 45). The 15th May am tide settlement was greater on panels with extract, and Site C had a mean panel density of 191 ± 37 cyprids.panel⁻¹. This tidal count was taken *in situ* with the May 15th pm data corresponding to laboratory counts. During the second tide settlement increased on panels *without* extract and decreased on those with extract. Therefore cyprids had actually left this supposedly favourable settlement substrata, and moved onto the panels without extract; on panels with extract mean the counts decreased from 191 ± 37 cyprids to 164 ± 41 cyprids, on panels without extract mean increased from 65 ± 8 to 180 ± 27 cyprids. This movement from the panels with extract to those without extract may be the result of a 'spacing out' effect, as the large initial settlement on the *in situ* tide would have led to a competition for space (Bertness, 1989, Mullineaux & Butman, 1991). This second tide also corresponded to increased settlement on the upper intertidal Site D (as discussed further in section 4.3., (Connell, 1961).

Moreover as this event occurred with an onshore N maximum Force 2 wind, it is possible that the less selective behaviour of the larvae is linked to delayed metamorphosis in the field, which if extended for long periods decreases the energy content of the non-feeding cyprid larvae (Thiyagarajan *et al.*, 2002). As these two tides were the maximum settlement observations for Site C and D during 2000, and little settled subsequently, these larvae may have had reduced fitness. Offshore winds could have pushed the larvae away from settlement sites, and therefore on their return to shore with these onshore N winds, energy reserves may have been low resulting in less discriminate settlement (Crisp, 1988). The settlement on panels without extracts has been linked to cyprid age, with increasing age corresponding to a decrease in cue specificity (Olivier *et al.*, 2000). Therefore should larvae be exported offshore as passive particles in large-scale water movements, they will be of a greater age before they would be able to encounter a substratum again, i.e. when they are blown back onshore. As the cyprid larvae are non-feeding, any extension of the pelagic period will lead to a decrease in energy reserves and an increase in the likelihood of settlement on the first available substratum, be it favourable or not (Crisp, 1988). This occurrence of decreased specificity for the adult cue was only seen on this occasion throughout the three settlement seasons.

As settlement of *S. balanoides* is rugotropic and gregarious, experiments using multiple grooved panels with extract and without extract found that groove was more influential in determining settlement patterns (Site D 2002). In these experiments grooves rather than pits were used to create suitable refuges for settling larvae, as this facilitated an easily regulated form of surface texture across the panels. The use of unpainted multiple grooved panels increased settlement ~4 times when compared to

plane panels, and this agrees with the work of Hills *et al.*, (1998), where the presence of pits alone was sufficient to promote settlement. However the combination of groove and extract cues performed consistently better than the unpainted versions, where settlement was lower and erratic throughout the season (Fig. 81, Table 16). The presence of extract with groove yielded ~17 times more cyprids than those grooved panels without. Hills *et al.*, (1998) also found that the combination of groove and extract induced chemical-mediated exploratory behaviour, whereas cyprids settled rapidly in pits alone.

The application of the adsorbed extract cue was also found to significantly increase settlement on smooth polished panels (Figs. 55, 56a). Such smooth surfaces are not generally chosen by cyprids, who prefer settlement in cracks and pits (Crisp & Ryland, 1960), yet the presence of the extract was sufficient to induce settlement ($F_{1,10} = 15.40, p = 0.017$).

4. 2. Effects of panel choice on settlement patterns

4. 2. 1. Settlement on unsanded panels

Previous studies have described the rugotrophic nature of *Semibalanus balanoides* cyprids (Wethey, 1986) therefore settlement was compared on sanded and unsanded panels with extract. The sanded panel showed more uniform distribution of settled cyprids whereas larvae settled on the upper portion of the unsanded panel, around a 'tide mark' (Fig. 56b and 57b). Settlement on the smooth, unsanded panels was unexpectedly twice that of the sanded panels on the 8th May am tide (Fig. 55). This observation occurred during a maximum Force 2 N wind, which would have gently pushed the larvae onshore to the sampling site (C 2000) and cyprids would have been

able to explore panel surfaces fully in such low shear stresses. The adsorption of the cue may have decreased the surface wettability of the smooth panels (Taylor *et al.*, 1994), so this reduction in surface free energy and the presence of the extract itself, may have been sufficient to promote the upward exploratory movement seen with the subsequent settlement at the top of the panels (Mullineaux, 1991; Hills and Thomason, 1998). Additionally as this occurred during very light winds, this behaviour may not be seen in more turbulent conditions. The observed 'tide mark' is most likely the cause of cellular leakage on the panels prior to photographs being taken (Fig. 56b). As the cyprids dried and hence died, due to unnaturally prolonged periods out of water, the carapace tended to collapse. This caused the internal contents to be transferred onto the panel surface beneath, which created the observed white marks.

4. 2. 2. *Settlement on plane sanded panels*

A large peak in settlement in 2000 on plane sanded panels at Sites C and D (Fig. 44 and 45) suggested that these panel types could be used for estimation of settlement in the field. However poor performance of these panel types at Fife Ness and Kingsbarns in 2001 suggested these were not correctly assessing the nature of settlement patterns at the different locations. At Site C plane panels with extract were used for all three settlement seasons alongside four plane panels without extract in 2000 and 2001, and four multiple grooved panels with extract in 2002 (renamed C left). Settlement densities were found to significantly decrease to 17% in 2001, and to 2% in 2002. Therefore the drop in larvae settling in 2001 may have occurred due to yearly fluctuations in adult output, onshore winds, and reduced larval quality between seasons as panel conditions had remained the same. In 2002 however the massive

decrease to just 2% was caused by the preferential settlement on the grooved panels with extract, located in the same backplate. Therefore lack of available space and less discriminatory larval settlement was responsible for the settlement seen in the first and second year. Moreover as plane panels did not perform consistently over the 2002 season when compared to grooved panels, i.e. no relative increase was seen when settlement increased on grooved panels, it is suggested that these larvae were of decreased larval fitness.

4. 2. 3. *Settlement on horizontally and vertically grooved panels*

As small-scale substratum heterogeneity occurs naturally on rocks, milled grooves in panels were used to emulate this varied surface texture and to encourage greater numbers of the rugotrophic cyprid settlers. During 2001 the horizontally and vertically grooved panels deployed performed consistently better than plane panels at all sites (12cm² groove area, 92cm² plane ungrooved surface), as seen in Figs. 64, 69 and 74. Settlement was significantly lower on plane panels with horizontal panels having higher settlement densities than vertically grooved panels at Sites T (Table 8, Fig 64). This preference for horizontal panels may have been caused by local hydrodynamic processes, such as changes in horizontal and vertical orbital velocities (Elgar *et al.*, 2001). Cyprids are able to respond to light through their two compound eyes (Walker, 1995), and the frontal filament vesicles have been suggested as regions of pressure perception (Walker, 1974) However it is likely that the positive phototactic upward movement on panels seen with settlement on the smooth panels also occurs with the grooved panels (Hills and Thomason, 1998). This would result in the greater settlement in horizontal grooves than the vertical grooves, where there is less chance of encountering a groove before leaving a panel. Unlike Site T, Site K at Fife Ness

showed that vertical grooved panels had significantly greater settlement than horizontal grooved panels ($F_{1, 34} = 8.64, p = 0.010$), which may be a result of increased wave exposure at Site K.

Whilst horizontal and vertically grooved panels were temporally correlated at St Andrews and Fife Ness, no correlation was found at Kingsbarns (Fig. 74) as the peaks of settlement on each groove type did not coincide. ANOVA analysis revealed that both horizontally and vertically grooved panels performed equally in settlement conditions ($F_{1, 34} = 1.42, p = 0.242$). As this site was only sampled with grooved panels for the second half of the season in 2001, reduced larval fitness may have caused the lack of significance of panel type. When compared among sites the use of the horizontal or vertical groove treatments did not have a significantly different effect on settlement ($F_{1, 96} = 0.11, p = 0.763$). Settlement means on panel type between sites and between days indicated that although means of cyprid densities at the sites were different, due to variation of input at each location, no significant difference was found between the factors. Therefore the performance of the panel did not alter significantly with locations and days sampled, hence these 12cm² grooved panel types were more reliable estimators of settlement than plane panels.

Horizontally grooved panels were deployed at Site T in St Andrews during the 2000 and 2001 seasons. Although the maximum observed peaks of settlement were different between the years (161 ± 30 and 82 ± 8 cyprids per panel), comparison of per panel means over the season found that settlement was not significantly different ($t = 1.34, df = 202, p = 0.18$). Further work with the comparison of supply to settlement relationships between years would be needed to assess if this was simply a

function of similar densities of larvae available in the water column near the site, or dissimilar levels of larval availability but reduced larval fitness between years.

4. 2. 4. *Settlement on multiple grooved panels*

Multiple grooved panels performed significantly better than any other panel type and provided a reliable estimate of larval settlement across sites. Therefore this suggests that the presence of the grooves creates a substratum more akin to that of the natural rock surface, providing structure and refuge crevices. The 48cm² groove area panel did not enhance settlement four-fold when compared to 12cm² horizontal treatments (Site T 2001, Table 17). Indeed settlement on the two panels types was frequently only ~65% smaller, indicating that the multiple grooved panels could easily accommodate panel densities exceeding the maximum of 104 ± 17 cyprids observed in 2002 (Site T, Fig. 82) and therefore would be viable for use in further settlement experimentation. When log $x + 1$ cyprid counts are compared to the plane panels with extract, multiple grooved panels had significantly greater settlement at all sites (Table 23). When settlement between sites is compared at St Andrews (Sites C left, C right, D and T) settlement was temporally correlated at all sites, while Site T had significantly less settlement than the other three sites. Therefore the increase in the vertical dimension of tidal height (~28cm) is not significant whereas meso-scale horizontal variations (~30m) are indeed significant (discussed further in 4.3.).

4. 2. 5. *Settlement within multiple grooved panels*

As larvae were observed to move upwards on plane panels in 2000 and on horizontally grooved panels in 2001, nested GLM analysis of cyprid settlement spatial data (log $x + 1$) was used to examine settlement within grooves, within panel sections,

within panel replicates and within sites for the multiple grooved panel data collected in 2002 i.e. (Site (Panel replicate (Half (Grooves)))) (Underwood, 1997). Day was not included in the analysis as daily fluctuations in the numbers of cyprids settling was known to occur within and between sites, and the multiple comparisons would be uninformative. All levels of the analysis were significantly different except for Panel replicate which had a very high probability value ($F_{12, 4480} = 0.29, p = 0.991$, Table 24). This shows the lack of variation in the experimental unit in this analysis, the panel, thereby confirming that all panel replicates are indeed replicates. The nested GLM analysis then proceeded again without the inclusion of panel replicate, with no change in the significant factors.

Interaction bar plots of the resultant data (93a) showed that while settlement is higher on upper grooves, settlement on the bottom half of the panel is greater than that on the top (Fig. 93a). Therefore it is suggested that larvae are concentrated in the surface waters and are encountering grooves on the bottom half of the panel first with the incoming tide (De Wolf, 1973, Roughgarden *et al.*, 1987, Roughgarden *et al.*, 1988). They then encounter and explore the groove and may not move further up the panel as the lip of the upper groove would provide shade and a suitable refuge for the larvae. Additionally, were the panel to remain in the field and the larvae develop, this groove would then provide an ideal place for feeding as the thoracic limb could be extended out above the extent of the groove into a region of fast flowing water across the surface of the panel (Wethey, 1984). S-N-K analysis (Table 25) of the significant effect of upper or lower groove within panel half (top or bottom) found that groove was the main effect with the predominance of larvae settling on the upper groove. Tukey's HSD unplanned multiple comparison tests for the effect of Site (Half

(Groove)) revealed no clear correlation between any treatment at any site; although Fife Ness and Kingsbarns were at the extremes of the ranking for small and large means respectively, varied performance of treatments at Site CR and D led to the formation of many intermediate pairings so that no distinctive relationships could be observed. Therefore although the $H_0 = 0$ was rejected, a further unplanned Tukey test was used to examine the variation within each site separately.

At Sites C left, C right, T, J / K and Alpha the main variation in the settlement analysis was the effect of groove, with greater densities of larvae settling on the upper groove (Hills and Thomason, 1998; Fig. 93b). This is more pronounced for sites JK and Alpha, where cyprid densities were the least. However Tukey groupings for the sites with the largest means (Site LM and Beta) reveals that there was no significant difference between upper and lower grooves, and upper grooves on the lower half of the panel have the highest mean settlement at each site. Therefore it can be concluded that in higher cyprid densities a spacing-out effect of larvae will occur in the grooves as the channels are colonised and reach a 'capacity' level, and that greater settlement occurs on the lower half of the panels as cyprids encounter the panels and settle as the tide rises over the panels (Hui & Moyse, 1987). This latter effect explains the mildly significant Half (Groove) interaction seen in Fig. 93 a and Table 25 ($(F_{2, 4480} = 3.19, p = 0.041)$).

Additionally Tukey's analysis revealed no significant correlation in settlement in any of the treatments at Site D. This site was located in the upper intertidal where increased dessication pressure will occur, whereas all of the others are from the mid intertidal. Therefore this result shows that these larvae settling in the upper intertidal

were less selective than those settling in the mid intertidal, and as such had a lower larval fitness (Bertness *et al.*, 1992, Miron *et al.*, 1999, Menge, 2000).

4. 2. 6. *Settlement on natural and artificial substrata*

During the final year daily settlement on triplicate cleared quadrats on the rocks at each site was assessed. Comparison of settlement per cm² natural substrata to per cm² multiple grooved artificial substrata of the panels revealed a significant correlation at all the sites (Fig. 105). Regression analysis revealed that rock substrata was preferred by the larvae, as would be expected, but that the grooved panels performed consistently over the season and are therefore a useful tool in the assessment of settlement. For every 10 cyprids settling on the rocks 0.3, 0.5. and 1.1 cyprids settled on grooved panels at Fife Ness, St Andrews and Kingsbarns respectively. Although numbers settling at the sites were therefore different due to natural variations between shores, the relationship between settlement on natural and artificial substrata was not significant between the sites and therefore confirms that the multiple grooved panels are reliable estimators of settlement.

4. 3. *Influence of tidal height on settlement*

Cyprid settlement on panels at Sites C, D and E were temporally correlated with one another during the 2000 sampling period, although magnitudes of cyprid settlement differed significantly over the small distances of tidal height (Table 2, Fig, 20). The mid intertidal Site C had considerably greater mean settlement than the upper intertidal Site D, although on the 15th May pm 2000 the pattern was reversed. This incident was caused by high settlement densities at Site C on panels with extract during an intermediary tide (panels were not retrieved from the field); lack of

available space and larva-larva interactions occurred during the second tidal exposure and resulted in the high settlement on panels without extract and on the upper intertidal Site D (as mentioned in 4. 1.). This colonisation of upper sites after more desirable sites have little available space remaining agrees with studies by Raimondi (1988) and Pineda and Caswell (1997). This lack of specificity for adult cues and tidal height occurred during the main peak of settlement with onshore winds, therefore it is suggested that increased cyprid age / depleted energy reserves was responsible for the selection of upper intertidal sites, as in Bertness *et al.*, (1992). Dessication pressures will be increased with upper intertidal sites due to greater exposure times, and larvae generally avoid these in preference for the mid intertidal region (Raimondi, 1988).

In 2001 settlement was again found to be increased on upper intertidal sites rather than mid intertidal sites (May 12th Sites C and D, Figs. 58 and 59). Mean panel counts on plane panels with extract of 53 ± 6 cyprids and 186 ± 47 cyprids were recorded at Sites C and D respectively. However unlike in the previous year, this occasion did not coincide with a lack of specificity for the conspecific cue, as plane panel settlement without extract was 4 ± 1 and 29 ± 7 cyprids respectively. Additionally for this tidal period the wind was a strong easterly (Force 7) and therefore large waves and strong winds would be transporting the larvae over the front of the panels. These weather conditions, the still determinate response to the adult cue, and lower settlement at Site C suggests that this event was not a result of reduced larval quality, but rather related to increased wave crash upon the upper shores.

The lower intertidal Site E was located ~38cm below Site C and had significantly lower settlement during 2000 (Table 2) and the presence or absent of extract at this

site had no effect. These combined factors of low settlement site (increased predation pressure), little surface topography (plane panels) and lack of response to conspecific cues confirms that such larvae are reduced in fitness (Tukey groupings, Fig. 48) (Minchinton & Scheibling, 1991). Moreover Site E was located within a gully, and increased pebble movement through the space in front of the panels in high wave conditions is likely to abrade settlers from the rocks, therefore increasing the chance of post-settlement mortality. In 2001 settlement at Site E was very low (Fig. 60), again suggesting that only poor quality larvae would settle in this low intertidal area. Comparison of Site E to Sites F and G in 2000, also located in the lower intertidal region, should these had similar settlement densities and were significantly lower than the mid intertidal sites (Fig. 51). Again those larvae settling at these Sites F and G are likely to be indiscriminate settlers and suffer post-settlement mortalities due to movement of pebbles within the gully between the panel blocks and increased predation levels (Connell, 1961).

4. 4. Settlement patterns within and between locations

Correlation analysis found that settlement in all sites at St Andrews was temporally correlated, as although differences in means were seen among the group locations, the peaks of settlement occurred at the same time. For example, during the 2002 season settlement on grooved panels between C left, C right, D and T were significantly temporally correlated (Fig. 83). However statistical analysis of the grooved panels over the four sites found that Site T had significantly lower settlement counts across the season. This was despite the fact that Site T was located at the same approximate tidal height as Site C, and geographically separated by only ~30m in a linear direction across the shore (Table 18). The major contribution to this variation was site

orientation towards the incoming tide; Site C is relatively protected from wave crash as it faces SW, whereas Site T faces N towards the incoming tide and is therefore unprotected from direct wave action. Therefore while the peaks may occur at the same time, the magnitude of settlement observed is related to meso-scale hydrodynamic variations on the shore.

Settlement at all the Kinkell Braes sites occurred during periods of N / NE / E winds, with winds from the SW to the WNW resulting in low wave action and settlement (Figs. 47, 58, 83). This was consistent within and among years. As the experimental location of these sites was in the south section of a bay facing NE, the settlement at this site is significantly wind driven, as was found by Hawkins and Hartnoll (1982) and Bertness *et al.*, (1996). In 2001 large peaks of settlement were found correlated either on the same day or one day after heavy collection of trapped sediments, which were all found during NE winds (Fig. 58, $r^s = 0.4559$, $n=36$, $p = 0.005$). This suggests that NE winds were moving larvae onshore, hence the turbidity of water movement, and larvae are then able to position themselves in the water column before subsequent settlement (De Wolf, 1973, Gaines & Roughgarden, 1985). In 2002 trapped sediment decreases are correlated to increases in settlement (Fig. 80). In these instances peaks in sand collection in the traps occur mainly during SE winds, therefore this may be correlated to Eckman transport of the surface layer and upwelling of lower waters.

Although only studied for a short period of time, Sites H and I at Boarhills also showed the same settlement peaks as those sites at Kinkell Braes in 2000 (Fig. 54) and were temporally closely correlated even though the locations were separated by ~ 5 km. Sites HI face SE with Site C facing SW, therefore the low settlement seen and

correlation between the two sites is likely due to periods of SW winds. However as this site was not sampled in subsequent years, no firm conclusions as to the patterns of settlement can be made.

The location used at Kingsbarns faced NNW and was subject to direct wave action upon the panels in winds from the N to the E. Weights of captured ashed sediment corroborate the force of the direct wave action as all the increases were seen during N or NE winds (Figs. 72, 91). A negative correlation was apparent for settlement with water flux, as expressed by the weight of captured sediment, and this occurred in both 2001 and 2001. Settlement in 2001 was seen only during SW winds and resultant periods of low wave action; as this site was only sampled with the informative horizontal and vertical panels during the latter half of the season, during predominantly SW winds, it cannot be surmised that this pattern occurs only during SW winds and that the N winds have poor settlement (Fig. 72).

However in 2002 the main settlement peaks occurred in both periods of SW and NE winds (Fig. 91). These patterns of settlement with two opposing wind directions leads to the conclusion that the settlement peaks are correlated to a closely located larval pool, as shown by Pineda (2000). This theory was supported by the shapes of the settlement peaks. It would be expected that if the larvae settling came from a far-off larval pool, the peaks would fall to zero when the wind moved offshore. However this did not occur, suggesting that a near shore larval pool was also contributing to settlement (Fig. 91). This site may also have had significant contributions from other larval pools, but with a base level of supply from the local population. If this was the case then NE winds would push the nearshore larvae further onshore onto the panels,

and as SW winds cause minimal wave action the larvae would therefore remain in the area near the beach. Kingsbarns is a long, flat, shallow beach, often with long waves running parallel to the coast, therefore indicating that a localised advective transport process may aid the retention of larvae due to shoreline topography (Shanks & Wright, 1987). Topographical features have been documented as of greater significance to larval settlement than large currents (Eckman, 1996), but the collection of further information such as internal water temperatures, wind speed and direction offshore (Farrell *et al.*, 1991) at the site over a number of years are needed to provide a greater accuracy in determination of the settlement relationship.

Settlement sites at Fife Ness were found to be temporally correlated (Fig. 86) with no significant differences in settlement between the two locales. Sediment collection was very low at Fife Ness, reaching a maximum of $0.035 \text{ g} \pm 0.003$, even though this is the most wave exposed site of the three, facing due east on a promontory. This was caused by the low levels of fine sediment quantities seen at this exposed site, and therefore pressure inducers would provide a more accurate assessment of water conditions. Settlement on the panels was seen to increase mainly with SE / SW winds (Fig. 87), but settlement was also seen during NE winds; this relates to the shoreline position of this site as only with winds between the NW and WSW would not result in onshore winds. However although the NE winds would indeed transport larvae towards Fife Ness, the northern side of the panel block was dominated by tall blocks of bedrock, whereas the southern side was open to incoming wave action. Therefore again settlement patterns can be attributed to coastline orientation to wind-driven currents and shoreline topography (Kendall *et al.*, 1982, 1985, Bertness *et al.*, 1996).

When settlement was examined across the sites in 2001 (Fig. 75) it was seen that a definite temporal correlation pattern occurred. One settlement peak was seen for each site moving from Site T in St Andrews, to Site M in Kingsbarns 5 days later and finally Site K at Fife Ness, 8 days after Kingsbarns. Mean per panel counts for each peak decreased with each site travelled from 161 ± 30 cyprids at St Andrews to 73 ± 15 cyprids at Fife Ness. During the previous 11 days before this peak at St Andrews began, 11 days of predominantly NE winds had occurred, running from 5th May to the 15th May. Therefore this suggests that a large larval pool or pools may have come from barnacle populations further up the coast towards Dundee, and then travelled down the coast of the East Neuk to all sites (Pineda, 2000). This is suggested as Site T shows two large peaks that drop to negligible settlement in between, therefore suggesting separate advection events from a distant larval pool and not from a near larval pool, as described in Pineda (2000). Only one peak was seen in Fife Ness and Kingsbarns, as these sites were not sampled with grooved panels until the 21st May. Therefore the interpretation of the result is treated with caution.

However, during 2002 a similar settlement event occurs, this time with settlement peaks moving from Fife Ness to St Andrews after 14 days of S / SW winds. Two main settlement peaks occur at Fife Ness and St Andrews suggesting the presence of a larval pool moving up from below Fife Ness towards St Andrews; there was a delay of 5 days reaching Kingsbarns and 1 day after that to reach St Andrews for the first settlement burst. For the second settlement peak only 2 days delay occurs between the peak of Fife Ness and Kingsbarns, and another 3 days to reach a peak at St Andrews. As previously mentioned for Kingsbarns, the three peak pattern of settlement seen may be caused by the combination of advection events of larvae from a distant larval

pool as mentioned here and also larvae from a near pool population, i.e. from barnacles at Kingsbarns themselves (Pineda, 2000).

4. 5. Larval supply and settlement relationships

While trap percentage urea retention and trapped larval counts were seen to vary within sites due to local hydrodynamic variations on a small scale, traps were found to be efficient at collecting larvae over a range of weather conditions (Figs. 99-101) and also locations (Table 29). For example Trap 4 at Fife Ness was found to have a significantly decreased efficiency when compared to the other traps within that site (Fig. 97). On comparison with decreased cleared quadrat counts (Fig. 103) and reduced trapped sediment weight (Fig. 76) at that particular location it can be clearly seen that local eddies caused by the large rock outcrop at the site was sufficient to reduce supply and settlement to traps and panels. Increased water flux, as indicated by captured ashed sediment weight, decreased the urea retention in the traps, as expected, but while small-scale variations occurred a decrease in urea retention to ~63% did not show reduced capture efficiency.

Larval supply and settlement correlations were found to be significant within each site, with 74%, 70% and 35% of the variation in settlement upon grooved panels at St Andrews, Kingsbarns and Fife Ness respectively being explained by variations in larval supply to the sites (Fig. 108). This agrees with other studies of the supply and settlement relationship (Gaines & Roughgarden, 1985, Minchinton & Scheibling, 1991). The decreased linear relationship for Fife Ness suggests that while larvae are present in the water column, local hydrodynamics may deter settlement on the substrata. Indeed panel counts at this site were consistently lower than at the other

sites (Fig. 92), and percentage barnacle cover on natural substrata on the shore was also decreased. Hydrodynamics may then be determining this local settlement pattern, as was found in previous studies (Bertness *et al.*, 1996). However as ANCOVA analysis found that the supply / settlement relationship did not alter between the sites, this increased supply to settlement ratio was not significant.

The relationship between larval supply and settlement was also examined on natural substrata, using cleared quadrat daily counts (Fig. 104). Again the relationship was significantly correlated, with 72%, 56% and 34% of the variation in settlement on the quadrats due to variations in the larval supply to the sites at St Andrews, Fife Ness and Kingsbarns respectively. However this interpretation of a decrease in linearity of Kingsbarns should be treated with caution, as only 12 days of trap samples and quadrats were available, due to vandalism at the site. This low correlation coefficient also led to a significant difference in the comparison of natural settlement and supply at Kingsbarns to the other two sites, which again should be treated with caution. As the supply / settlement relationship on the grooved panels was significantly correlated (70%), and the natural and artificial substrata were highly correlated (90%) it suggests that the low numbers of sampled days is the contributing influence. Further experimentation of larval trap supply with settlement on grooved panels and natural quadrats would be needed to confirm this.

4. 6. Larval supply of *Semibalanus balanoides* and *Balanus crenatus*

Larval supply of *B. crenatus* larvae was very low in trap samples taken from Fife Ness and Kingsbarns throughout the 2002 season, and was significantly different from that seen in St Andrews. Mean numbers of *B. crenatus* and *S. balanoides* larvae in

traps at St Andrews did not differ significantly, although the peaks of supply were not temporally correlated and were generally mutually exclusive. These strong pulses of settlement of *B. crenatus* occur exclusively during periods of moderate to strong (Force 4 to Force 8) SW/ S / SE winds, and are therefore likely to be caused by the offshore movement of the Eckman layer (Farrell *et al.*, 1991), and the subsequent upwelling process, bringing the larvae of this sublittoral barnacle species higher in water column, and resulting in counts observed in the traps. During this period of offshore winds, *S. balanoides* larvae normally located in the top of the water column, will then move offshore which explains the lack of temporal correlation of the supply of these two species.

Conclusions

Settlement of the intertidal species *S. balanoides* was found to differ on a number of spatial and temporal scales. On a large spatial scale settlement patterns were primarily driven by site orientation to prevailing winds, by the movement of water onshore or offshore, although small-scale spatial variability was observed due to local hydrodynamics around topographical features. Within site spatial variation occurred again due the panel block orientation towards the oncoming wind, and increased wave exposure also led to the lower settlement at sites separated linearly on a differing meso-scale. Examination of tidal height with settlement found that cyprids settling in upper intertidal areas were less discriminate to settlement cues such as surface texture and conspecific cues, therefore conferring reduced larval fitness. Lower intertidal sites also conferred reduced specificity for settlement cues, again indicating poor cyprid quality. Settlement was significantly influenced by the surface texture of settlement panels, with grooved panels with a groove area of 48cm² yielding the highest numbers

of settlers. Larvae were found to show a phototactic response for the upper portion of grooves, although larva-larva interactions at high densities caused a 'spacing out' effect of settlement on upper and lower grooves.

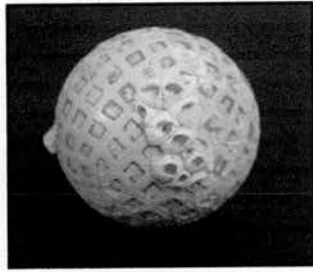
Supply and settlement relationships between larval trap counts and natural and artificial substrata found that up to 74% of the variation on 48cm² grooved panels could be explained by variations in larval supply at Fife Ness. The relationship between supply and settlement decreased to 35%, as whilst larvae were present in the water column little settlement was observed due to localised eddies near the settlement site. Larval supply to natural rock surfaces was highly correlated, with that of artificial substratum, indicating that larval supply is the major influence structuring distribution patterns of *S. balanoides* cyprids in Fife. Larval supply of the sublittoral barnacle *B. crenatus* was directly correlated to the presence of SW offshore winds, which resulted in larval upwelling into the mid intertidal section of the shore.

This combination of sampled factors shows the complexity of the intertidal barnacle settlement pattern. For future studies the use of multiple grooved panels, with cleared quadrats and larval traps would provide a useful indicator of settlement and supply relationships. However, pressure inducers, thermal plotters, offshore and inshore wind buoys and offshore larval sampling should be used to provide a full picture of the influence of wind, shore topography and currents on the movement of cyprid larvae and therefore an estimation of supply to the settlement substratum. Additionally use of cyprid sizing, the quantification of cyprid energy reserves using ratios of triacylglycerols to cholesterol, and post-settlement mortalities of cyprids settling on

differing panel types at the varying sites will provide a comprehensive quantification of larval cyprid quality and its response to settlement cues.

CHAPTER 5

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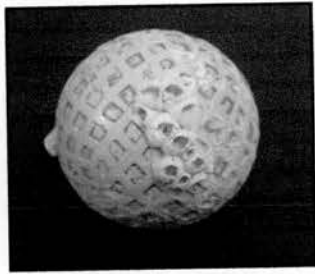
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CHAPTER 6

APPENDICES



	A	Y	Z	AA	AB	AC	AD	AE	AF	AG	AH	AI	AJ	AK	AL	AM	AN	AO	AP	AQ	AR	AS	AT	AU	AV	AW	AX	AY	AZ	BA	BB	BC	BD			
1	Date	C1	C2	C3	C4	C5	C6	C7	C8	D1	D2	D3	D4	D5	D6	D7	D8	E1	E2	E3	E4	E5	E6	E7	E8	F1	F2	F3	F4	F5	F6	F7	F8			
48	May29 pm																																			
49	May30 am																																			
50	May30 pm	0	0	0	0	0	0	0	0																											
51	May31 am																																			
52	May31 pm	0	1	0	0	0	0	0	0																											
53	June1 am																																			
54	June1 pm	0	0	0	0	0	0	0	0																											
55	June2 am																																			
56	June2 pm																																			
57	June3 am	0	0	0	0	0	0	0	0																											
58	June3 pm	0	0	0	0	0	0	0	0																											
59	June4 am	0	0	0	0	0	0	0	0																											
60	June4 pm	0	0	0	0	0	0	0	0																											

	A	BE	BF	BG	BH	BI	BJ	BK	BL	BM	BN	BO	BP	BQ	BR	BS	BT	BU	BV	BW	BX	BY	BZ	CA	CB
1	Date	G1	G2	G3	G4	G5	G6	G7	G8	H1	H2	H3	H4	H5	H6	H7	H8	I1	I2	I3	I4	I5	I6	I7	I8
48	May29 pm																								
49	May30 am																								
50	May30 pm																								
51	May31 am																								
52	May31 pm									0	0	0	0	0	0	0	0	0							
53	June1 am																								
54	June1 pm									1	0	0	0	0	0	0	0	0							
55	June2 am																								
56	June2 pm																								
57	June3 am									0	0	0	0	0	0	0	0	0							
58	June3 pm									0	0	0	0	0	0	0	0	0							
59	June4 am									0	0	0	0	0	0	0	0	0							
60	June4 pm									0	0	0	0	0	0	0	0	0							

Tide	Date	Day	SITE C										SITE D										SITE E									
			P1+	P2+	P3+	P4+	P1-	P2-	P3-	P4-	P1+	P2+	P3+	P4+	P1-	P2-	P3-	P4-	P1+	P2+	P3+	P4+	P1-	P2-	P3-	P4-						
28/04/2001	28 April	5	1	2	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0								
29/04/2001	29 April	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0								
30/04/2001	30 April	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0								
01/05/2001	01 May	8	40	1	10	4	0	0	0	0	0	0	0	1	8	0	3	1	0	0	0	0	0	0								
02/05/2001	02 May	9	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0								
03/05/2001	3 May	10	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0								
04/05/2001	4 May	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0								
05/05/2001	5 May	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0								
06/05/2001	6 May	13	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0								
07/05/2001	7 May	14	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0								
08/05/2001	8 May	15	0	0	1	1	0	2	2	0	1	2	0	1	2	0	2	0	0	1	0	0	0	0								
09/05/2001	9 May	16	0	1	3	0	0	0	0	0	0	4	2	0	2	0	4	0	0	1	0	0	0	0								
10/05/2001	10 May	17	6	3	3	2	2	0	0	1	8	2	2	0	0	1	0	0	0	0	0	0	0	0								
11/05/2001	11 May	18	1	1	0	5	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0								
12/05/2001	12 May	19	55	44	44	67	7	5	5	0	135	169	116	324	24	49	30	14	3	2	1	2	1	0								
13/05/2001	13 May	20	7	5	8	1	3	0	0	3	28	21	1	40	6	7	1	21	0	1	2	0	0	0								
14/05/2001	14 May	21	1	2	4	1	3	0	0	2	7	6	4	2	6	2	4	6	*	*	*	*	*	*								
15/05/2001	15 May	22	19	24	58	92	7	13	27	1	8	40	48	71	4	15	4	9	*	*	*	*	*	*								
16/05/2001	16 May	23	4	1	0	3	1	1	0	0	0	0	0	1	0	0	0	0	*	*	*	*	*	*								
17/05/2001	17 May	24	113	83	80	198	10	20	30	21	23	31	21	20	5	2	6	20	*	*	*	*	*	*								
18/05/2001	18 May	25	1	3	0	0	1	1	3	1	0	0	0	0	0	0	1	0	*	*	*	*	*	*								
19/05/2001	19 May	26	10	5	10	8	3	0	1	3	7	8	5	9	1	6	2	3	*	*	*	*	*	*								
20/05/2001	20 May	27	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	*	*	*	*	*	*								
21/05/2001	21 May	28	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	*	*	*	*	*	*								
22/05/2001	22 May	29	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	*	*	*	*	*	*								
23/05/2001	23 May	30	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	*	*	*	*	*	*								
24/05/2001	24 May	31	0	0	0	0	1	0	0	0	2	2	1	3	0	3	0	1	*	*	*	*	*	*								
25/05/2001	25 May	32	0	0	0	1	0	0	0	0	2	0	4	4	0	0	1	1	*	*	*	*	*	*								
26/05/2001	26 May	33	0	0	0	1	0	0	0	0	1	0	0	2	1	0	0	1	*	*	*	*	*	*								
27/05/2001	27 May	34	0	0	0	0	0	0	0	0	1	0	3	0	1	0	0	0	*	*	*	*	*	*								
28/05/2001	28 May	35	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*	*	*	*	*	*								
29/05/2001	29 May	36	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	*	*	*	*	*	*								

Tide	Date	Day	SITE C								SITE D								SITE E							
			P1+	P2+	P3+	P4+	P1-	P2-	P3-	P4-	P1+	P2+	P3+	P4+	P1-	P2-	P3-	P4-	P1+	P2+	P3+	P4+	P1-	P2-	P3-	P4-
30/05/2001	30 May	37	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*
31/05/2001	31 May	38	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*
01/06/2001	01 June	39	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*
02/06/2001	02 June	40	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*
03/06/2001	03 June	41	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
04/06/2001	04 June	42	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
05/06/2001	05 June	43	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
06/06/2001	06 June	44	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*

Tide	Date	Day	SITE T										SITE J								SITE K						
			H1	H2	H3	V1	V2	V3	P1	P2	P3	P1+	P2+	P3+	P4+	P1-	P2-	P3-	P4-	P1+	P2+	P3+	H1	P4+	H2	P1-	
28/04/2001	28 April	5	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
29/04/2001	29 April	6	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
30/04/2001	30 April	7	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
01/05/2001	01 May	8	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
02/05/2001	02 May	9	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
03/05/2001	3 May	10	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
04/05/2001	4 May	11	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
05/05/2001	5 May	12	3	0	0	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
06/05/2001	6 May	13	3	4	3	4	5	6	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
07/05/2001	7 May	14	4	5	1	7	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
08/05/2001	8 May	15	10	6	9	9	6	8	1	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
09/05/2001	9 May	16	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10/05/2001	10 May	17	102	27	16	69	54	32	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11/05/2001	11 May	18	27	8	35	19	11	8	1	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12/05/2001	12 May	19	45	50	22	75	9	18	7	6	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13/05/2001	13 May	20	3	4	8	3	1	6	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14/05/2001	14 May	21	11	3	11	1	3	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15/05/2001	15 May	22	98	45	27	38	11	42	0	2	1	2	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16/05/2001	16 May	23	31	19	14	16	12	20	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17/05/2001	17 May	24	216	156	111	103	136	69	13	7	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18/05/2001	18 May	25	33	46	26	22	28	29	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19/05/2001	19 May	26	34	48	43	30	19	30	1	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20/05/2001	20 May	27	7	5	8	1	8	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21/05/2001	21 May	28	4	3	2	1	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22/05/2001	22 May	29	4	4	3	3	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23/05/2001	23 May	30	2	3	0	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24/05/2001	24 May	31	3	3	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25/05/2001	25 May	32	5	3	11	2	11	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
26/05/2001	26 May	33	5	4	3	6	13	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27/05/2001	27 May	34	0	2	2	3	2	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28/05/2001	28 May	35	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29/05/2001	29 May	36	11	10	15	15	13	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Tide	Date	Day	SITE T															SITE J								SITE K														
			H 1	H 2	H 3	V 1	V 2	V 3	P 1	P 2	P 3	P 1+	P 2+	P 3+	P 4+	P 1-	P 2-	P 3-	P 4-	P 1+	P 2+	P 3+	P 4+	H 1	H 2	P 1-														
30/05/2001	30 May	37	2	1	2	3	3	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	88	58	0
31/05/2001	31 May	38	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	21	26	0	
01/06/2001	01 June	39	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	63	52	0			
02/06/2001	02 June	40	2	4	2	1	2	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19	12	0			
03/06/2001	03 June	41	6	5	5	4	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	8	0				
04/06/2001	04 June	42	*	*	*	*	*	*	*	*	*	*	*	*	*	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	8	1				
05/06/2001	05 June	43	2	4	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	7	15	0					
06/06/2001	06 June	44	1	1	0	1	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	7	0					

Tide	Date	Day	SITE L										Site M						
			P2-	P3- / V1	P4- / V2	P1+	P2+	p3+	P4+	P1-	P2-	P3-	P4-	P1+	P2+	P3+ / H1	P4+ / H2	P1-	P2-
28/04/2001	28 April	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29/04/2001	29 April	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30/04/2001	30 April	7	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
01/05/2001	01 May	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
02/05/2001	02 May	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
03/05/2001	3 May	10	0	8	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
04/05/2001	4 May	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
05/05/2001	5 May	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
06/05/2001	6 May	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
07/05/2001	7 May	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
08/05/2001	8 May	15	0	0	0	2	1	1	0	0	0	0	0	0	1	1	0	0	0
09/05/2001	9 May	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10/05/2001	10 May	17	0	0	0	0	0	0	0	0	0	0	0	0	8	5	0	1	0
11/05/2001	11 May	18	0	0	0	0	0	0	2	0	0	0	0	0	0	1	0	0	0
12/05/2001	12 May	19	0	0	0	0	0	0	3	0	0	0	0	0	8	6	0	0	0
13/05/2001	13 May	20	0	0	0	1	1	2	1	0	0	0	0	0	0	1	1	0	0
14/05/2001	14 May	21	1	0	1	0	1	0	0	0	0	0	0	0	0	2	0	1	0
15/05/2001	15 May	22	0	0	0	0	1	1	0	0	0	0	0	0	0	2	0	0	0
16/05/2001	16 May	23	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
17/05/2001	17 May	24	0	0	0	1	0	1	0	1	0	0	0	0	2	1	0	0	0
18/05/2001	18 May	25	0	1	0	1	2	0	2	0	0	0	0	0	0	0	0	0	0
19/05/2001	19 May	26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20/05/2001	20 May	27	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0
21/05/2001	21 May	28	1	19	28	0	0	0	0	0	0	0	0	0	33	32	0	0	43
22/05/2001	22 May	29	1	5	2	2	0	0	0	2	0	2	0	0	142	115	1	0	137
23/05/2001	23 May	30	0	7	7	0	0	0	1	1	0	1	0	1	25	23	1	0	44
24/05/2001	24 May	31	0	1	5	1	1	1	0	0	0	0	0	0	46	83	1	1	107
25/05/2001	25 May	32	0	5	10	0	2	0	1	0	0	0	0	1	85	95	1	0	71
26/05/2001	26 May	33	0	19	3	0	0	1	1	0	0	0	0	1	66	55	0	0	41
27/05/2001	27 May	34	0	10	19	0	0	0	0	0	0	0	0	1	88	58	0	0	61
28/05/2001	28 May	35	0	24	6	0	0	1	1	0	2	0	0	0	50	58	0	1	68
29/05/2001	29 May	36	0	13	18	0	0	0	0	0	0	0	0	0	13	23	0	0	33

Tide	Date	Day	SITE L												Site M								
			P2-	P3-	V1	P4-	V2	P1+	P2+	p3+	P4+	P1-	P2-	P3-	P4-	P1+	P2+	P3+	H1	P4+	H2	P1-	P2-
30/05/2001	30 May	37	1	96	76	0	1	0	0	0	0	0	0	0	0	0	0	6	2	0	0	0	3
31/05/2001	31 May	38	0	36	41	0	0	0	0	0	0	0	0	0	0	0	0	3	5	0	0	0	4
01/06/2001	01 June	39	0	49	52	0	0	0	0	0	0	0	0	0	0	0	0	2	3	0	0	0	7
02/06/2001	02 June	40	0	35	23	0	0	0	0	0	0	0	0	0	0	0	10	7	0	0	0	9	
03/06/2001	03 June	41	0	14	17	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2	
04/06/2001	04 June	42	0	11	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
05/06/2001	05 June	43	0	28	23	0	0	0	0	0	0	0	0	0	0	0	3	1	0	0	0	7	
06/06/2001	06 June	44	0	10	11	0	0	0	0	0	0	1	0	0	0	0	7	4	0	0	0	8	

Tide	Date	Day	P4- / V2
28/04/2001	28 April	5	0
29/04/2001	29 April	6	0
30/04/2001	30 April	7	0
01/05/2001	01 May	8	0
02/05/2001	02 May	9	0
03/05/2001	3 May	10	0
04/05/2001	4 May	11	0
05/05/2001	5 May	12	0
06/05/2001	6 May	13	0
07/05/2001	7 May	14	0
08/05/2001	8 May	15	0
09/05/2001	9 May	16	0
10/05/2001	10 May	17	0
11/05/2001	11 May	18	0
12/05/2001	12 May	19	0
13/05/2001	13 May	20	0
14/05/2001	14 May	21	0
15/05/2001	15 May	22	0
16/05/2001	16 May	23	1
17/05/2001	17 May	24	0
18/05/2001	18 May	25	0
19/05/2001	19 May	26	0
20/05/2001	20 May	27	0
21/05/2001	21 May	28	50
22/05/2001	22 May	29	137
23/05/2001	23 May	30	27
24/05/2001	24 May	31	96
25/05/2001	25 May	32	82
26/05/2001	26 May	33	68
27/05/2001	27 May	34	56
28/05/2001	28 May	35	104
29/05/2001	29 May	36	42

Tide	Date	Day	P4- / V2
	30/05/2001	30 May	37
	31/05/2001	31 May	38
	01/06/2001	01 June	39
	02/06/2001	02 June	40
	03/06/2001	03 June	41
	04/06/2001	04 June	42
	05/06/2001	05 June	43
	06/06/2001	06 June	44
			6
			4
			1
			12
			1
			1
			4
			2

Site	Date out	Date in	No tides	P1	P2	P3	P4	G1	G2	G3	G4
C left	19/04/2002	20/04/2002	2	0	0	0	0	3	0	0	0
C left	20/04/2002	21/04/2002	2	0	0	0	0	0	1	0	0
C left	21/04/2002	22/04/2002	2	0	0	0	0	1	0	0	0
C left	22/04/2002	23/04/2002	2	0	0	0	0	0	0	0	0
C left	23/04/2002	24/04/2002	2	0	0	0	0	1	2	0	0
C left	24/04/2002	25/04/2002	2	0	0	0	0	1	0	0	0
C left	25/04/2002	26/04/2002	2	0	0	0	0	2	2	2	7
C left	26/04/2002	27/04/2002	1	0	0	0	0	2	3	1	2
C left	27/04/2002	28/04/2002	2	0	0	0	0	0	0	1	2
C left	28/04/2002	29/04/2002	2	0	0	0	1	2	8	7	4
C left	29/04/2002	30/04/2002	2	0	1	0	1	6	7	5	3
C left	30/04/2002	01/05/2002	2	0	0	1	0	2	1	3	0
C left	01/05/2002	02/05/2002	2	0	0	0	0	4	0	0	1
C left	02/05/2002	03/05/2002	2	1	0	0	0	1	1	1	9
C left	03/05/2002	04/05/2002	2	0	0	0	0	1	1	0	0
C left	04/05/2002	05/05/2002	2	0	0	0	0	5	5	0	5
C left	05/05/2002	06/05/2002	2	0	0	0	0	24	24	24	22
C left	06/05/2002	07/05/2002	2	1	1	1	0	118	58	109	105
C left	07/05/2002	08/05/2002	2	2	1	0	0	36	35	16	30
C left	08/05/2002	09/05/2002	2	0	0	1	0	104	156	144	111
C left	09/05/2002	10/05/2002	2	0	0	0	0	69	62	56	72
C left	10/05/2002	11/05/2002	2	0	0	0	0	13	10	7	11
C left	11/05/2002	12/05/2002	2	0	0	0	1	13	12	8	6
C left	12/05/2002	13/05/2002	1	0	0	0	0	5	6	0	9
C left	13/05/2002	14/05/2002	2	1	1	3	0	47	32	23	29
C left	14/05/2002	15/05/2002	2	0	0	0	0	12	9	18	20
C left	15/05/2002	16/05/2002	2	0	0	0	0	14	48	8	23
C left	16/05/2002	17/05/2002	2	1	0	0	0	37	17	38	15
C left	17/05/2002	18/05/2002	2	0	3	0	0	136	130	112	110
C left	18/05/2002	19/05/2002	2	0	0	0	1	140	76	195	186
C left	19/05/2002	20/05/2002	2	3	3	6	3	172	75	73	139
C left	20/05/2002	21/05/2002	2	2	1	0	1	45	24	34	56
C left	21/05/2002	22/05/2002	2	0	0	0	0	3	5	1	2
C left	22/05/2002	23/05/2002	2	0	0	0	0	1	1	0	0
C left	23/05/2002	24/05/2002	2	0	0	0	0	8	3	2	6
C left	24/05/2002	25/05/2002	2	0	0	0	0	25	13	6	12
C left	25/05/2002	26/05/2002	2	0	1	1	0	14	35	21	14
C left	26/05/2002	27/05/2002	2	0	0	0	0	2	1	1	5
C left	27/05/2002	28/05/2002	2	0	0	0	0	2	1	2	3
C left	28/05/2002	29/05/2002	1	0	0	0	0	0	1	0	0
C left	29/05/2002	30/05/2002	2	0	0	0	0	1	1	2	2
C left	30/05/2002	31/05/2002	2	0	0	0	0	2	0	6	6
C left	31/05/2002	01/06/2002	2	0	0	0	0	1	0	0	0
C left	01/06/2002	02/06/2002	2	0	0	0	0	0	1	0	0
C right	19/04/2002	20/04/2002	2	0	0	0	0	3	5	3	2
C right	20/04/2002	21/04/2002	2	0	0	0	0	1	1	0	0
C right	21/04/2002	22/04/2002	2	0	0	0	0	1	1	0	1
C right	22/04/2002	23/04/2002	2	0	0	0	0	0	0	1	0
C right	23/04/2002	24/04/2002	2	0	0	0	0	2	0	0	2
C right	24/04/2002	25/04/2002	2	0	0	0	0	0	1	1	2
C right	25/04/2002	26/04/2002	2	0	0	0	0	3	3	2	5
C right	26/04/2002	27/04/2002	1	0	0	0	0	3	2	3	5
C right	27/04/2002	28/04/2002	2	0	0	0	1	2	5	4	3
C right	28/04/2002	29/04/2002	2	0	0	0	0	14	10	8	8
C right	29/04/2002	30/04/2002	2	0	0	1	0	8	13	3	10
C right	30/04/2002	01/05/2002	2	0	0	0	0	2	2	0	1
C right	01/05/2002	02/05/2002	2	0	0	0	0	4	0	3	1
C right	02/05/2002	03/05/2002	2	1	0	0	0	7	5	0	2
C right	03/05/2002	04/05/2002	2	0	0	0	0	2	2	3	1
C right	04/05/2002	05/05/2002	2	0	0	0	0	6	3	0	0
C right	05/05/2002	06/05/2002	2	0	0	0	0	13	14	26	13

Site	Date out	Date in	No tides	P1	P2	P3	P4	G1	G2	G3	G4
D	23/05/2002	24/05/2002	2	0	1	0	0	2	3	5	14
D	24/05/2002	25/05/2002	2	3	0	0	0	19	15	13	14
D	25/05/2002	26/05/2002	2	2	1	1	2	22	40	45	51
D	26/05/2002	27/05/2002	2	1	1	0	0	8	3	5	2
D	27/05/2002	28/05/2002	2	0	0	1	0	2	1	0	1
D	28/05/2002	29/05/2002	1	0	0	0	0	1	1	0	1
D	29/05/2002	30/05/2002	2	0	0	0	0	1	2	0	1
D	30/05/2002	31/05/2002	2	0	0	0	0	0	1	2	2
D	31/05/2002	01/06/2002	2	0	1	0	0	0	0	1	0
D	01/06/2002	02/06/2002	2	0	0	0	0	0	1	0	1
T	19/04/2002	20/04/2002	2	0	0	0	0	0	1	1	0
T	20/04/2002	21/04/2002	2	0	0	0	0	1	0	0	0
T	21/04/2002	22/04/2002	2	0	0	0	0	0	3	0	1
T	22/04/2002	23/04/2002	2	0	0	0	0	4	1	0	0
T	23/04/2002	24/04/2002	2	0	0	0	0	0	2	0	0
T	24/04/2002	25/04/2002	2	5	3	0	2	4	4	2	3
T	25/04/2002	26/04/2002	2	3	3	3	7	3	9	8	6
T	26/04/2002	27/04/2002	1	1	2	1	2	2	5	3	2
T	27/04/2002	28/04/2002	2	1	2	1	1	2	1	2	1
T	28/04/2002	29/04/2002	2	3	5	0	2	4	3	5	2
T	29/04/2002	30/04/2002	2	5	4	2	1	4	4	2	3
T	30/04/2002	01/05/2002	2	1	0	0	2	2	3	3	1
T	01/05/2002	02/05/2002	2	0	1	0	0	0	2	1	2
T	02/05/2002	03/05/2002	2	0	0	0	1	0	1	0	1
T	03/05/2002	04/05/2002	2	0	2	0	0	0	0	0	0
T	04/05/2002	05/05/2002	2	0	0	0	0	0	2	0	0
T	05/05/2002	06/05/2002	2	15	3	8	5	8	12	10	8
T	06/05/2002	07/05/2002	2	70	28	44	40	103	55	53	36
T	07/05/2002	08/05/2002	2	15	4	10	15	15	23	15	16
T	08/05/2002	09/05/2002	2	95	82	93	59	85	111	92	105
T	09/05/2002	10/05/2002	2	75	79	70	33	102	60	75	73
T	10/05/2002	11/05/2002	2	20	7	17	17	38	25	8	24
T	11/05/2002	12/05/2002	2	2	7	4	11	12	22	5	8
T	12/05/2002	13/05/2002	1	16	15	4	5	13	23	14	12
T	13/05/2002	14/05/2002	2	6	9	2	3	12	11	8	3
T	14/05/2002	15/05/2002	2	9	6	2	6	12	14	5	4
T	15/05/2002	16/05/2002	2	10	2	3	3	12	18	14	6
T	16/05/2002	17/05/2002	2	4	7	4	7	15	17	23	17
T	17/05/2002	18/05/2002	2	33	27	45	16	146	87	112	70
T	18/05/2002	19/05/2002	2	52	62	36	32	64	115	120	104
T	19/05/2002	20/05/2002	2	57	59	20	31	42	53	30	40
T	20/05/2002	21/05/2002	2	17	18	15	18	20	10	19	34
T	21/05/2002	22/05/2002	2	1	1	3	12	2	8	2	0
T	22/05/2002	23/05/2002	2	14	0	1	0	1	3	3	0
T	23/05/2002	24/05/2002	2	1	7	6	9	5	12	12	6
T	24/05/2002	25/05/2002	2	19	15	5	16	8	17	8	10
T	25/05/2002	26/05/2002	2	8	5	2	9	10	5	13	5
T	26/05/2002	27/05/2002	2	3	1	6	1	11	13	4	9
T	27/05/2002	28/05/2002	2	4	4	4	0	2	1	2	5
T	28/05/2002	29/05/2002	1	0	0	0	1	2	1	0	1
T	29/05/2002	30/05/2002	2	1	0	0	0	0	0	1	0
T	30/05/2002	31/05/2002	2	0	1	1	0	2	0	0	0
T	31/05/2002	01/06/2002	2	0	0	0	1	0	0	0	0
T	01/06/2002	02/06/2002	2	0	0	0	0	0	0	0	0
JK	19/04/2002	20/04/2002	2	0	0	0	0	4	4	1	3
JK	20/04/2002	21/04/2002	2	0	0	0	0	1	0	1	0
JK	21/04/2002	22/04/2002	2	0	0	0	0	0	0	0	0
JK	22/04/2002	23/04/2002	2	0	0	0	0	8	2	2	1
JK	23/04/2002	24/04/2002	2	0	0	0	0	9	5	2	3
JK	24/04/2002	25/04/2002	2	0	0	0	0	0	1	0	0
JK	25/04/2002	26/04/2002	2	0	0	0	0	2	0	1	5

Site	Date out	Date in	No tides	P1	P2	P3	P4	G1	G2	G3	G4
JK	26/04/2002	27/04/2002	1	0	0	0	0	7	3	0	8
JK	27/04/2002	28/04/2002	2	0	0	0	0	4	15	15	10
JK	28/04/2002	29/04/2002	2	0	0	0	0	3	13	8	14
JK	29/04/2002	30/04/2002	2	0	0	0	0	9	13	20	13
JK	30/04/2002	01/05/2002	2	1	0	0	0	4	2	0	4
JK	01/05/2002	02/05/2002	2	0	0	0	0	2	2	9	2
JK	02/05/2002	03/05/2002	2	0	1	0	0	28	22	17	19
JK	03/05/2002	04/05/2002	2	0	0	0	0	4	1	2	0
JK	04/05/2002	05/05/2002	2	0	0	0	0	5	10	4	11
JK	05/05/2002	06/05/2002	2	0	0	0	0	3	8	1	4
JK	06/05/2002	07/05/2002	2	0	0	0	0	5	5	3	3
JK	07/05/2002	08/05/2002	2	0	0	0	0	0	2	1	3
JK	08/05/2002	09/05/2002	2	0	0	0	0	5	1	0	3
JK	09/05/2002	10/05/2002	2	0	1	0	0	5	5	2	1
JK	10/05/2002	11/05/2002	2	0	0	0	0	4	4	7	5
JK	11/05/2002	12/05/2002	2	0	0	0	0	6	11	4	7
JK	12/05/2002	13/05/2002	1	0	0	0	0	2	3	2	4
JK	13/05/2002	14/05/2002	2	0	0	0	1	34	33	44	36
JK	14/05/2002	15/05/2002	2	0	0	0	0	52	18	30	20
JK	15/05/2002	16/05/2002	2	0	1	0	1	59	23	34	33
JK	16/05/2002	17/05/2002	2	0	0	0	1	45	33	21	17
JK	17/05/2002	18/05/2002	2	0	0	0	0	38	17	15	19
JK	18/05/2002	19/05/2002	2	0	0	0	0	9	7	10	11
JK	19/05/2002	20/05/2002	2	0	0	0	0	2	11	5	14
JK	20/05/2002	21/05/2002	2	0	0	0	0	9	23	16	13
JK	21/05/2002	22/05/2002	2	0	0	0	0	20	16	25	1
JK	22/05/2002	23/05/2002	2	0	0	0	0	22	5	8	21
JK	23/05/2002	24/05/2002	2	0	0	0	0	11	20	9	15
JK	24/05/2002	25/05/2002	2	0	0	0	0	12	14	10	2
JK	25/05/2002	26/05/2002	2	1	0	0	0	1	2	5	0
JK	26/05/2002	27/05/2002	2	0	0	0	0	3	3	3	1
JK	27/05/2002	28/05/2002	2	0	0	0	0	3	1	0	4
JK	28/05/2002	29/05/2002	1	0	0	0	0	1	3	0	0
JK	29/05/2002	30/05/2002	2	0	0	0	0	11	2	2	5
JK	30/05/2002	31/05/2002	2	0	0	0	0	4	3	6	5
JK	31/05/2002	01/06/2002	2	0	0	0	0	7	3	4	0
JK	01/06/2002	02/06/2002	2	0	0	0	0	3	1	0	1
ALPHA	19/04/2002	20/04/2002	2	0	0	0	0	4	7	2	3
ALPHA	20/04/2002	21/04/2002	2	0	0	0	0	1	0	0	1
ALPHA	21/04/2002	22/04/2002	2	0	0	0	0	0	0	0	0
ALPHA	22/04/2002	23/04/2002	2	0	0	0	0	1	3	1	1
ALPHA	23/04/2002	24/04/2002	2	0	0	0	0	2	2	2	3
ALPHA	24/04/2002	25/04/2002	2	0	0	1	0	0	1	0	1
ALPHA	25/04/2002	26/04/2002	2	0	0	0	0	0	0	3	2
ALPHA	26/04/2002	27/04/2002	1	0	0	0	0	6	1	3	2
ALPHA	27/04/2002	28/04/2002	2	0	1	0	1	5	3	4	16
ALPHA	28/04/2002	29/04/2002	2	0	0	0	0	9	6	15	5
ALPHA	29/04/2002	30/04/2002	2	0	0	0	0	5	8	8	12
ALPHA	30/04/2002	01/05/2002	2	0	0	0	0	8	4	6	3
ALPHA	01/05/2002	02/05/2002	2	0	0	0	0	3	4	3	7
ALPHA	02/05/2002	03/05/2002	2	0	2	0	0	24	27	15	50
ALPHA	03/05/2002	04/05/2002	2	2	0	0	0	0	1	0	0
ALPHA	04/05/2002	05/05/2002	2	0	0	0	0	8	7	2	4
ALPHA	05/05/2002	06/05/2002	2	0	0	0	0	3	4	1	2
ALPHA	06/05/2002	07/05/2002	2	0	0	0	0	5	3	2	4
ALPHA	07/05/2002	08/05/2002	2	0	0	0	0	4	0	3	7
ALPHA	08/05/2002	09/05/2002	2	0	0	0	0	4	0	3	1
ALPHA	09/05/2002	10/05/2002	2	0	0	0	0	3	5	5	12
ALPHA	10/05/2002	11/05/2002	2	0	0	0	0	3	10	10	7
ALPHA	11/05/2002	12/05/2002	2	0	0	0	0	20	15	17	18
ALPHA	12/05/2002	13/05/2002	1	0	0	0	0	5	6	8	5

Date	High tide (when sett occurs)	From this low tide	From date	To this low tide	To date	Median speed knots	Mean in Beaufort	Direction	Max BF	Med speed knots	Median speed knots
05/05/2000											
06/05/2000	348	2130	05/05/2000	952	06/05/2000	6	2	N	3	3	6
	1605	952	06/05/2000	2212	06/05/2000	8	3	E	3	3	8
07/05/2000	431	2212	06/05/2000	1037	07/05/2000	4	2	NE	3	4	4
	1652	1037	07/05/2000	2255	07/05/2000	6	2	E	3	3	6
08/05/2000	517	2255	07/05/2000	1124	08/05/2000	0	0	N	2	0	0
	1744	1124	08/05/2000	2341	08/05/2000	5	2	E	3	5	5
09/05/2000	608	2341	08/05/2000	1217	09/05/2000	1	1	NNE	3	1	1
	1841	1217	09/05/2000	37	10/05/2000	7	3	E	3	7	7
10/05/2000	708	37	10/05/2000	1324	10/05/2000	6	6	2	5	6	6
	1950	1324	10/05/2000	152	11/05/2002	13	4	E	5	13	13
11/05/2000	823	152	11/05/2002	1448	11/05/2002	11.5	4	ENE	5	11.5	11.5
	2108	1448	11/05/2002	318	12/05/2000	12	4	NE	4	12	12
12/05/2000	937	318	12/05/2000	1609	12/05/2000	12	4	ENE	5	12	12
	2222	1609	12/05/2000	431	13/05/2000	7.5	3	ENE	4	7.5	7.5
13/05/2000	1049	431	13/05/2000	1718	13/05/2000	11	4	ENE	4	11	11
	2331	1718	13/05/2000	532	14/05/2000	5	2	NE	3	5	5
14/05/2000	1150	532	14/05/2000	1817	14/05/2000	6	2	E	3	6	6
15/05/2000	28	1817	14/05/2000	623	15/05/2000	0	0	N	2	0	0
	1243	623	15/05/2000	1903	15/05/2000	2	1	SSE	3	2	2
16/05/2000	114	1903	15/05/2000	707	16/05/2000	3	1	SW	3	3	3
	1329	707	16/05/2000	1942	16/05/2000	10.5	4	SSW	5	10.5	10.5
17/05/2000	153	1942	16/05/2000	746	17/05/2000	1.5	1	N	3	1.5	1.5
	1410	746	17/05/2000	2015	17/05/2000	17	5	WSW	17	17	17
18/05/2000	229	2015	17/05/2000	823	18/05/2000	8	3	WSW	4	8	8
	1449	823	18/05/2000	2046	18/05/2000	6	2	WSW	3	6	6
19/05/2000	304	2046	18/05/2000	858	19/05/2000	5	2	WSW	4	5	5
	1527	858	19/05/2000	2114	19/05/2000	4.5	2	SE	2	4.5	4.5
20/05/2000	337	2114	19/05/2000	929	20/05/2000	1	1	N	3	1	1
	1604	929	20/05/2000	2140	20/05/2000	8	3	SE	2	8	8
21/05/2000	410	2140	20/05/2000	957	21/05/2000	1	1	ESE	3	1	1
	1641	957	21/05/2000	2206	21/05/2000	6	2	ESE	3	6	6
22/05/2000	445	2206	21/05/2000	1025	22/05/2000	7	3	WSW	3	7	7
	1720	1025	22/05/2000	2234	22/05/2000	7.5	3	WSW	4	7.5	7.5
23/05/2000	522	2234	22/05/2000	1057	23/05/2000	3	1	SSE	3	3	3
	1801	1057	23/05/2000	2309	23/05/2000	10	3	WSW	6	10	10
24/05/2000	604	2309	23/05/2000	1137	24/05/2000	10.5	4	WSW	5	10.5	10.5
	1846	1137	24/05/2000	2355	24/05/2000	14	4	SW	5	14	14
25/05/2000	650	2355	24/05/2000	1229	25/05/2000	6	4	WSW	4	6.5	6.5
	1937	1229	25/05/2000	100	26/05/2000	11	4	WSW	5	10	11
26/05/2000	744	100	26/05/2000	1335	26/05/2000	6	2	WSW	3	6	6
	2034	1335	26/05/2000	223	27/05/2000	6	2	SE	4	6	6
27/05/2000	847	223	27/05/2000	1452	27/05/2000	8.5	3	WNW	5	8.5	8.5
	2136	1452	27/05/2000	346	28/05/2000	5	2	W	4	5	5

Date	High tide (when sett occurs)	From this low tide	From date	To this low tide	To date	Median speed knots	Mean in Beaufort	Direction	Max BF	Med speed knots	Median speed knots
28/05/2000	953	346	28/05/2000	1610	28/05/2000	3	1	W	2	3	3
	2239	1610	28/05/2000	449	29/05/2000	4	2	WNW	3	4	4
29/05/2000	1056	449	29/05/2000	1710	29/05/2000	8	3	WNW	4	8	8
	2338	1710	29/05/2000	541	30/05/2000	4.5	2	W	3	4.5	4.5
30/05/2000	1153	541	30/05/2000	1800	30/05/2000	10	3	W	4	10	10
31/05/2000	30	1800	30/05/2000	627	31/05/2000	6	2	W	3	6	6
	1243	627	31/05/2000	1847	31/05/2000	10	3	W	4	10	10
01/06/2000	117	1847	31/05/2000	714	01/06/2000	5.5	2	S	4	5.5	5.5
	1330	714	01/06/2000	1935	01/06/2000	15.5	5	SW	5	15.5	15.5
02/06/2000	200	1935	01/06/2000	802	02/06/2000	11	4	WSW	5	11	11
	1416	802	02/06/2000	2023	02/06/2000	11	4	E	4	11	11
03/06/2000	244	2023	02/06/2000	852	03/06/2000	1	1	N	3	1	1
	1503	852	03/06/2000	2113	03/06/2000	12	4	E	5	12	12
04/06/2000	328	2113	03/06/2000	942	04/06/2000	14	4	ENE	5	14	14
	1551	942	04/06/2000	2202	04/06/2000	12	4	ENE	5	12	12

Date	High tide (when sett occurs)	Time taken in	No tides	From this low tide	From date	To this low tide	To date	Max speed ms-1	Max speed kph	Max speed BF	Median speed ms-1	Median kph	Median BF
27/04/01	1707												
28/04/01	0530 1754	pm	2	1028	27/04/01	1103	28/04/2001	11	39.6	6	5.7	20.52	4
29/04/01	0617 1848	pm	2	1103	28/04/2001	1155	2904/01	12	43.2	6	4.5	16.2	3
30/04/01	0713 1954	pm	2	1155	29/04/01	1315	30/04/01	12.3	44.28	6	6.5	23.4	4
01/05/01	0827 2114	pm		1315	30/04/01	1455	01/05/01	9	32.4	5	2.5	9	2
02/05/01	0950 2234	1500	2	1455	01/05/01	1622	02/05/01	15.1	54.36	7	6.5	23.4	4
03/05/01	1102 2342	pm		1622	02/05/01	1730	03/05/01	15.1	54.36	7	4.3	15.48	3
04/05/01	1202	1800		1730	03/05/01	1828	04/05/01	6.8	24.48	4	3.7	13.32	3
05/05/01	0037 1253	1900		1828	04/05/01	1918	05/05/01	9.4	33.84	5	5	18	3
06/05/01	0123 1338	2000		1918	05/05/01	2002	06/05/01	7.2	25.92	4	3.3	11.88	2
07/05	0205 1422	am	1	2002	06/05/01	0810	07/05	5.7	20.52	4	2	7.2	2
08/05	0245 1506	1100	2	0810	07/05	0852	08/05	9	32.4	5	3.7	13.32	3
09/05	0325 1550	1115		0852	08/05	0931	09/05	8	28.8	5	4.1	14.76	3
10/05	0405 1634	1115		0931	09/05	1006	10/05	9.8	35.28	5	7.8	28.08	5
11/05	0445 1718	1130		1006	10/05	1034	11/05	10.6	38.16	6	6.5	23.4	4
12/05	0524 1803	1130		1034	11/05	1100	12/05	14.8	53.28	7	2.5	9	2
13/05	0606 1851	1145		1100	12/05	1135	13/05	6.5	23.4	4	2.9	10.44	2
14/05	0654 1944	1215		1135	13/05	1225	14/05	8	28.8	5	6.1	21.96	4
15/05	0751 2041	1245		1225	14/05	1334	15/05	9	32.4	5	6.5	23.4	4
16/05	0856 2143	1545		1334	15/05	1518	16/05	7.2	25.92	4	3.3	11.88	2
17/05	1002 2247	1545		1518	16/05	1638	17/05	7.2	25.92	4	2.5	9	2
18/05	1105 2346	1630		1638	17/05	1728	18/05	14.3	51.48	7	6.7	24.12	4
19/05	1200	1900		1728	18/05	1809	19/05	11.8	42.48	6	6.5	23.4	4
20/05	0034 1247	1850		1809	19/05	1846	20/05	12.8	46.08	7	6.1	21.96	4

Date	High tide (when sett occurs)	Time taken in	No tides	From this low tide	From date	To this low tide	To date	Max speed ms-1	Max speed kph	Max speed BF	Median speed ms-1	Median kph	Median BF
21/05	0116	2000		1846	20/05	1924	21/05	8.8	31.68	5	4.1	14.76	3
	1328								0			0	
22/05	0154	1850		1924	21/05	2202	22/05	8	28.8	5	4.1	14.76	3
	1406								0			0	
23/05	0232	0920	1	2202	22/05	0825	23/05	6.1	21.96	4	2	7.2	2
	1445								0			0	
24/05	0309	1000	2	0825	23/05	0906	24/05	9.4	33.84	5	4.1	14.76	3
	1526								0			0	
25/05	0349	1015		0906	24/05	0949	25/05	9.4	33.84	5	6.5	23.4	4
	1609								0			0	
26/05	0430	1145		0949	25/05	1034	26/05	8.2	29.52	5	3.8	13.68	3
	1655								0			0	
27/05	0515	1330		1034	26/05	1124	27/05	11.4	41.04	6	6.9	24.84	4
	1745								0			0	
28/05	0605	1400		1124	27/05	1219	28/05	12.7	45.72	7	8	28.8	5
	1841								0			0	
29/05	0704	1410		1219	28/05	1324	29/05	18.8	67.68	9	11.9	42.84	6
	1946								0			0	
30/05	0815	1530		1324	29/05	1440	30/05	15.2	54.72	7	6.4	23.04	4
	2100								0			0	
31/05	0930	1720		1440	30/05	1556	31/05	12.7	45.72	7	7.4	26.64	5
	2211								0			0	
01/06	1037	1700		1556	31/05	1703	01/06	14.2	51.12	7	9	32.4	5
	2316								0			0	
02/06	1137	1930		1703	01/06	1802	02/06	18	64.8	8	8.6	30.96	5
									0			0	
03/06	0013	2000		1802	02/06	1852	03/06	14	50.4	7	7.2	25.92	4
	1232								0			0	
04/06	0102	2030		1852	03/06	1935	04/06	13.1	47.16	7	9	32.4	5
	1320								0			0	
05/06	0145	1845		1935	04/06	2015	05/06	14.7	52.92	7	8.8	31.68	5
	1406								0			0	
06/06	0226	1930		2015	05/06	2051	06/06	10.2	36.72	6	6.8	24.48	4
	1451								0			0	

Date	High tides	Time taken in No tides	From this low tide	From date	To this low tide	To date	Direction	Max speed mph	Max speed BF	Median speed mph	Median BF
19/04/2002	1905										
20-Apr	729	1345	2	1143	1303	19-Apr	20-Apr S	8.8	3	4.5	2
	2008										
21-Apr	842	1445	2	1303	1506	20-Apr	21-Apr S	12	4	5.3	2
	2129										
22-Apr	1006	1700	2	1506	1638	21-Apr	22-Apr S	14.8	4	10.9	3
	2249										
23-Apr	1118	1700	2	1638	1743	22-Apr	23-Apr S	13.6	4	8.9	3
	2355										
24-Apr	1216	1850	2	1743	1839	23-Apr	24-Apr S	21.8	5	6.6	2
	48	1835	2								
25-Apr	1305			1839	1929	24-Apr	25-Apr S	24	6	14.4	4
	134	2000	2								
26-Apr	1350			1929	2016	25-Apr	26-Apr WSW	34.9	8	18	5
	217	1030	1	2016	826	26-Apr	27-Apr SW	23.2	6	13.2	4
27-Apr	1434										
28-Apr	300	1050	2	826	910	27-Apr	28-Apr SW	24	6	10.3	3
	1520										
29-Apr	344	1040	2	910	953	28-Apr	29-Apr SW	26.7	6	13.7	4
	1608										
30-Apr	428	1135	2	953	1033	29-Apr	30-Apr SW	29.7	7	18.5	5
	1657										
01-May	513	1200	2	1033	1110	30-Apr	01-May SW	14.4	4	8.1	3
	1749										
02-May	601	1300	2	1110	1146	01-May	02-May WSW	15.4	4	8.9	3
	1845										
03-May	655	1445	2	1146	1235	02-May	03-May WSW	18.4	5	5.6	2
	1945										
04-May	758	1515	2	1235	1400	03-May	04-May SE	14.8	4	6.4	2
	2050										
05-May	907	1620	2	1400	1557	04-May	05-May E	16.1	4	6.5	2
	2200										
06-May	1018	1730	2	1557	1707	05-May	06-May NE	19.4	5	12	4
	2313										
07-May	1127	1815	2	1707	1757	06-May	07-May NE	22.7	6	8	3
	12										
08-May	1222	1950	2	1757	1834	07-May	08-May N	22.8	6	11	3
	56										
09-May	1303	1935	2	1834	1904	08-May	09-May N	26.7	6	17.3	5
	130										
10-May	1339	1930	2	1904	1932	09-May	10-May E	16.9	5	6.8	2
	202										
11-May	1411	1825	2	1932	2002	10-May	11-May W	21.4	5	12.9	4
	233										
12-May	1444	2050	2	2002	2033	11-May	12-May SW	19.3	5	10.1	3
	305	1050	1	2033	853	12-May	13-May SE	16.1	4	12.8	4
13-May	1518										
14-May	338	1045	2	853	926	13-May	14-May SE	25.7	6	12.8	4
	1554										
15-May	413	1030	2	926	958	14-May	15-May SW	32.2	7	21.2	5
	1632										
16-May	450	1115	2	958	1031	15-May	16-May SW	23.4	6	14	4

Date	High tides 1714	Time taken in No tides	From this low tide	From date	To this low tide	To date	Direction	Max speed mph	Max speed BF	Median speed mph	Median BF
17-May	531 1800	1110 2	1031	16-May	1110	17-May	NE	19.6	5	13.5	4
18-May	618 1853	1300 2	1110	17-May	1207	18-May	ENE	21.9	5	19.1	5
19-May	713 1956	1400 2	1207	18-May	1322	19-May	NE	20.3	5	11.1	3
20-May	823 2109	1450 2	1322	19-May	1449	20-May	S	17.5	5	9.9	3
21-May	940 2222	1615 2	1449	20-May	1609	21-May	S	18.9	5	11.2	3
22-May	1049 2327	1530 2	1609	21-May	1713	22-May	SE	25.4	6	16.7	5
23-May	1147	2015	1713	22-May	1810	23-May	SE	21.8	5	12.4	4
24-May	21										
25-May	1239 110	1715 2	1810	23-May	1902	24-May	S	29.4	7	14.7	4
26-May	1328 155	1735 2	1902	24-May	1950	25-May	SW	31.3	7	17.2	5
27-May	1416 239	2110 2	1950	25-May	2035	26-May	SE	20.1	5	12.1	4
28-May	1504 323	2000 2	2035	26-May	2118	27-May	NE	26.5	6	12	4
29-May	1553 408	2135 1	2118 2157	27-May 28-May	2157 1020	28-May 29-May	ESE SE	25.6 22	6 5	12 10.4	4 3
30-May	1642 453	1642 2	1020	29-May	1059	30-May	SW	29.1	7	13.6	4
31-May	1732 539	1010 2	1059	30-May	1134	31-May	SW	28	7	14.8	4
01-Jun	1822 628	1400 2	1134	31-May	1213	01-Jun	SW	24.3	6	8.8	3
02-Jun	1915 723 pm 2009		1213	01-Jun	1306	02-Jun	S	14.4	4	6.4	2
03-Jun	822 2106		1306	02-Jun	1423	03-Jun	SW	22.5	6	12	4
04-Jun	923 2206		1423	03-Jun	1548	04-Jun	S	20.1	5	9	3
05-Jun	1024 2305		1548	04-Jun	1647	05-Jun	NE	25	6	13	4
06-Jun	1121 2359		1647	05-Jun	1734	06-Jun	NE	24.1	6	17.7	5
07-Jun	1213		1734	06-Jun	1814	07-Jun	NE	22.6	6	17	5
08-Jun	44 1258		1814	07-Jun	1851	08-Jun	E	23.8	6	14.4	4

Sample	Tides	Crucible wt	Crucible + Dry sed	Dry sed (g)	Crucible + Ash	Ash wt (g)	% Ash
Cleft Apr15/16	2	8.325	8.581	0.256	8.566	0.241	94.14
Cleft Apr16/17	2	8.084	8.193	0.109	8.187	0.103	94.50
Cleft Apr17/18	2	7.685	8.566	0.881	8.512	0.827	93.87
Cleft Apr18/19	2	8.39			9.409	1.019	
Cleft Apr19/20	2	7.677	8.763	1.086	8.555	0.878	80.85
Cleft Apr20/21	2	8.385	8.73	0.345	8.647	0.262	75.94
Cleft Apr21/22	2	9.187	9.193	0.006	9.191	0.004	66.67
Cleft Apr22/23	2	7.969	8.031	0.062	8.009	0.04	64.52
Cleft Apr23/24	2	8.398	8.418	0.02	8.412	0.014	70.00
Cleft Apr24/25	2	9.185	9.24	0.055	9.225	0.04	72.73
Cleft Apr25/26	2	9.185	9.509	0.324	9.447	0.262	80.86
Cleft Apr26/28	3	8.083	8.091	0.008	8.089	0.006	75.00
Cleft Apr28/29	2	8.129	8.133	0.004	8.132	0.003	75.00
Cleft Apr29/30	2	8.685	8.8	0.115	8.78	0.095	82.61
Cleft Apr30/May01	2	8.352	8.363	0.011	8.361	0.009	81.82
Cleft May01/02	2	9.406	9.417	0.011	9.41	0.004	36.36
Cleft May02/03	2	8.396	8.411	0.015	8.411	0.015	100.00
Cleft May03/04	2	9.315	9.333	0.018	9.331	0.016	88.89
Cleft May04/05	2	8.324	8.346	0.022	8.341	0.017	77.27
Cleft May05/06	2	9.451	9.493	0.042	9.483	0.032	76.19
Cleft May06/07	1	9.707	9.72	0.013	9.718	0.011	84.62
Cleft May07/08	2	9.36	9.378	0.018	9.371	0.011	61.11
Cleft May08/09	2	9.186	9.197	0.011	9.196	0.01	90.91
Cleft May09/10	2	9.772			9.786	0.014	
Cleft May10/11	2	8.143			8.229	0.086	
Cleft May11/12	2	8.396	8.437	0.041	8.435	0.039	95.12
Cleft May12/13	2	7.518	7.517	0.001	7.517	0.001	100.00
Cleft May13/14	2	9.453	9.46	0.007	9.458	0.005	71.43
Cleft May14/15	2	8.397	8.496	0.099	8.485	0.088	88.89
Cleft May15/16	2	7.486	7.554	0.068	7.537	0.051	75.00
Cleft May16/17	2	8.696	8.705	0.009	8.701	0.005	55.56
Cleft May17/18	2	8.986	9	0.014	8.998	0.012	85.71
Cleft May18/19	2	9.708	9.71	0.002	9.71	0.002	100.00
Cleft May 19/20	2	8.398	8.401	0.003	8.4	0.002	66.67
Cleft May 20/21	2	8.084	8.09	0.006	8.088	0.004	66.67
Cleft May 21/22	2	8.041	8.043	0.002	8.042	0.001	50.00
Cleft May 22/23	2	9.775	9.776	0.001	9.776	0.001	100.00
Cleft May 23/24	2	8.928	8.936	0.008	8.936	0.008	100.00
Cleft May 24/25	2	8.399	8.418	0.019	8.415	0.016	84.21
Cleft May 25/26	2	9.456	9.464	0.008	9.462	0.006	75.00
Cleft May 26/27	2	9.776	9.777	0.001	9.777	0.001	100.00
Cleft May 27/28	2	7.967	7.976	0.009	7.975	0.008	88.89
Cleft May 28/29	2	8.397	8.399	0.002	8.399	0.002	100.00
Cleft May 29/30	2	9.773	9.781	0.008	9.779	0.006	75.00
Cleft May 30/31	2	8.129	8.133	0.004	8.133	0.004	100.00
Cleft May 31/June01	2	9.774	9.786	0.012	9.784	0.01	83.33
Cleft June 01/02	2	9.455	9.626	0.171	9.6	0.145	84.80
Cleft June 02/03	2	7.966	8.154	0.188	8.118	0.152	80.85
Cright Apr15/16	2	8.384	8.616	0.232	8.603	0.219	94.40
Cright Apr16/17	2	8.34	8.485	0.145	8.479	0.139	95.86
Cright Apr17/18	2	7.834	9.566	1.732	9.471	1.637	94.52
Cright Apr18/19	2	7.968			9.456	1.488	
Cright Apr19/20	2	8.353	9.483	1.13	9.238	0.885	78.32
Cright Apr20/21	2	8.035	8.392	0.357	8.296	0.261	73.11
Cright Apr21/22	2	8.355	8.369	0.014	8.366	0.011	78.57
Cright Apr22/23	2	8.55	8.616	0.066	8.593	0.043	65.15
Cright Apr23/24	2	8.129	8.156	0.027	8.148	0.019	70.37
Cright Apr24/25	2	8.25	8.308	0.058	8.293	0.043	74.14
Cright Apr25/26	2	8.354	8.667	0.313	8.559	0.205	65.50
Cright Apr26/28	3	8.353	8.368	0.015	8.367	0.014	93.33
Cright Apr28/29	2	8.389	8.394	0.005	8.394	0.005	100.00
Cright Apr29/30	2	8.073	8.186	0.113	8.164	0.091	80.53
Cright Apr30/May01	2	9.708	9.713	0.005	9.712	0.004	80.00
Cright May01/02	2	9.479	9.504	0.025	9.5	0.021	84.00
Cright May02/03	2	7.515	7.53	0.015	7.528	0.013	86.67
Cright May03/04	2	9.16	9.163	0.003	9.162	0.002	66.67
Cright May04/05	2	8.083	8.113	0.03	8.106	0.023	76.67
5th to 6th							
Cright May06/07	1	9.653	9.668	0.015	9.665	0.012	80.00
Cright May07/08	2	9.314	9.343	0.029	9.335	0.021	72.41
Cright May08/09	2	8.354	8.376	0.022	8.374	0.02	90.91
Cright May09/10	2	10.019			10.039	0.02	
Cright May10/11	2	8.686			8.745	0.059	
Cright May11/12	2	8.389	8.393	0.004	8.393	0.004	100.00
Cright May12/13	2	8.035	8.042	0.007	8.041	0.006	85.71
Cright May13/14	2	9.939	9.945	0.006	9.943	0.004	66.67
Cright May14/15	2	8.39	8.516	0.126	8.503	0.113	89.68
Cright May15/16	2	8.339	8.413	0.074	8.401	0.062	83.78
Cright May16/17	2	8.844	8.86	0.016	8.855	0.011	68.75
Cright May17/18	2	9.025	9.034	0.009			
Cright May17/18	2	9.602	9.611	0.009	9.609	0.007	77.78
Cright May18/19	2	9.653	9.659	0.006	9.658	0.005	83.33
Cright May 19/20	2	7.517	7.524	0.007	7.524	0.007	100.00
Cright May 20/21	2	8.684	8.689	0.005	8.688	0.004	80.00
Cright May 21/22	2	9.601	9.606	0.005	9.606	0.005	100.00

Sample	Tides	Crucible wt	Crucible + Dry sed	Dry sed (g)	Crucible + Ash	Ash wt (g)	% Ash
Crigh May 22/23	2	10.022	10.023	0.001	10.022	0	0.00
Crigh May 23/24	2	9.709	9.712	0.003	9.711	0.002	66.67
Crigh May 24/25	2	7.518	7.523	0.005	7.52	0.002	40.00
Crigh May 25/26	2	9.601	9.609	0.008	9.609	0.008	100.00
Crigh May 26/27	2	10.023	10.029	0.006	10.03	0.007	116.67
Crigh May 27/28	2	7.485	7.493	0.008	7.493	0.008	100.00
Crigh May 28/29	2	7.517	7.519	0.002	7.519	0.002	100.00
Crigh May 29/30	2	10.021	10.025	0.004	10.024	0.003	75.00
Crigh May 30/31	2	8.353	8.359	0.006	8.359	0.006	100.00
Crigh May 31/June01	2	10.021	10.035	0.014	10.034	0.013	92.86
Crigh June 01/02	2	9.601	9.667	0.066	9.65	0.049	74.24
Crigh June 02/03	2	8.397	8.595	0.198	8.558	0.161	81.31
Dleft Apr15/16	2	8.063	8.101	0.038	8.097	0.034	89.47
Dleft Apr16/17	2	8.39	8.45	0.06	8.446	0.056	93.33
Dleft Apr17/18	2	8.13	8.644	0.514	8.602	0.472	91.83
Dleft Apr18/19	2	8.13			9.009	0.879	
Dleft Apr19/20	2	8.144	8.997	0.853	8.766	0.622	72.92
Dleft Apr20/21	2	8.142	8.386	0.244	8.317	0.175	71.72
Dleft Apr21/22	2	8.25	8.251	0.001	8.25	0	0.00
Dleft Apr22/23	2	8.392	8.437	0.045	8.423	0.031	68.89
Dleft Apr23/24	2	8.04	8.052	0.012	8.051	0.011	91.67
Dleft Apr24/25	2	7.487	7.513	0.026	7.505	0.018	69.23
Dleft Apr25/26	2	8.143	8.347	0.204	8.308	0.163	79.90
Dleft Apr26/28	3	7.485	7.495	0.01	7.492	0.007	70.00
Dleft Apr28/29	2	8.547	8.55	0.003	8.55	0.003	100.00
Dleft Apr29/30	2	8.035	8.078	0.043	8.066	0.031	72.09
Dleft Apr30/May01	2	9.655	9.659	0.004	9.657	0.002	50.00
Dleft May01/02	2	7.485					
Dleft May02/03	2	8.388	8.399	0.011	8.397	0.009	81.82
3rd to 4th							
Dleft May04/05	2	8.34	8.371	0.031	8.36	0.02	64.52
5th to 6th							
Dleft May06/07	1	9.966	9.974	0.008	9.973	0.007	87.50
Dleft May07/08	2	9.159	9.173	0.014	9.169	0.01	71.43
Dleft May08/09	2	8.23	8.232	0.002	8.232	0.002	100.00
Dleft May09/10	2	9.452			9.469	0.017	
Dleft May10/11	2	8.103			8.109	0.006	
Dleft May11/12	2	8.546	8.552	0.006	8.552	0.006	100.00
Dleft May12/13	2	8.685	8.686	0.001	8.686	0.001	100.00
Dleft May13/14	2	9.773	9.775	0.002	9.774	0.001	50.00
Dleft May14/15	2	8.548	8.588	0.04	8.584	0.036	90.00
Dleft May15/16	2	8.323	8.348	0.025	8.344	0.021	84.00
Dleft May16/17	2	9.192	9.197	0.005	9.195	0.003	60.00
Dleft May17/18	2	8.984	8.99	0.006	8.987	0.003	50.00
Dleft May18/19	2	9.36	9.362	0.002	9.362	0.002	100.00
Dleft May 19/20	2	8.39	8.393	0.003	8.393	0.003	100.00
Dleft May 20/21	2	8.143	8.146	0.003	8.146	0.003	100.00
Dleft May 21/22	2	8.694	8.696	0.002	8.696	0.002	100.00
Dleft May 22/23	2	9.454	9.455	0.001	9.454	0	0.00
Dleft May 23/24	2	8.392	8.396	0.004	8.393	0.001	25.00
Dleft May 24/25	2	9.479	9.496	0.017	9.493	0.014	82.35
Dleft May 25/26	2	8.695	8.701	0.006	8.699	0.004	66.67
Dleft May 26/27	2	9.455	9.458	0.003	9.46	0.005	166.67
Dleft May 27/28	2	8.339	8.346	0.007	8.346	0.007	100.00
Dleft May 28/29	2	8.389	8.392	0.003	8.39	0.001	33.33
Dleft May 29/30	2	9.454	9.457	0.003	9.455	0.001	33.33
Dleft May 30/31	2	8.929	8.934	0.005	8.934	0.005	100.00
Dleft May 31/June01	2	9.455	9.465	0.01	9.465	0.01	100.00
Dleft June 01/02	2	8.694	8.901	0.207	8.867	0.173	83.57
Dleft June 02/03	2	8.549	8.654	0.105	8.628	0.079	75.24
Drigh Apr15/16	2	8.548	8.651	0.103	8.646	0.098	95.15
Drigh Apr16/17	2	7.968	8.035	0.067	8.031	0.063	94.03
Drigh Apr17/18	2	7.486	8.244	0.758	8.187	0.701	92.48
Drigh Apr18/19	2	8.064			9.038	0.974	
Drigh Apr19/20	2	8.037	8.901	0.864	8.697	0.66	76.39
Drigh Apr20/21	2	7.677	7.945	0.268	7.875	0.198	73.88
Drigh Apr21/22	2	8.041	8.045	0.004	8.044	0.003	75.00
Drigh Apr22/23	2	7.519	7.567	0.048	7.549	0.03	62.50
Drigh Apr23/24	2	7.517	7.53	0.013	7.527	0.01	76.92
Drigh Apr24/25	2	8.04	8.085	0.045	8.069	0.029	64.44
Drigh Apr25/26	2	8.073	8.311	0.238	8.263	0.19	79.83
Drigh Apr26/28	3	8.323	8.333	0.01	8.33	0.007	70.00
Drigh Apr28/29	2	7.968	7.972	0.004	7.972	0.004	100.00
Drigh Apr29/30	2	8.142	8.209	0.067	8.195	0.053	79.10
Drigh Apr30/May01	2	9.361	9.368	0.007	9.366	0.005	71.43
Drigh May01/02	2	9.455	9.466	0.011	9.461	0.006	54.55
Drigh May02/03	2	8.034	8.047	0.013	8.046	0.012	92.31
3rd to 4th							
Drigh May04/05	2	7.833	7.861	0.028	7.856	0.023	82.14
Drigh May05/05	2	9.937	9.965	0.028	9.957	0.02	71.43
Drigh May06/07	1	9.413	9.422	0.009	9.42	0.007	77.78
Drigh May07/08	2	8.925	8.94	0.015	8.936	0.011	73.33
Drigh May08/09	2	8.25	8.254	0.004	8.254	0.004	100.00
Drigh May09/10	2	9.938			9.957	0.019	
Drigh May10/11	2	8.073			8.167	0.094	

Sample	Tides	Crucible wt	Crucible + Dry sed	Dry sed (g)	Crucible + Ash	Ash wt (g)	% Ash
Dright May11/12	2	7.967	7.981	0.014	7.977	0.01	71.43
Dright May12/13	2	8.141	8.147	0.006	8.145	0.004	66.67
Dright May13/14	2	10.021	10.031	0.01	10.029	0.008	80.00
Dright May14/15	2	7.968	8.018	0.05	8.007	0.039	78.00
Dright May15/16	2	7.833	7.87	0.037	7.864	0.031	83.78
Dright May16/17	2	9.364	9.372	0.008	9.371	0.007	87.50
Dright May 17/18	2	9.025	9.034	0.009	9.031	0.006	66.67
Dright May18/19	2	9.315	9.317	0.002	9.316	0.001	50.00
Dright May 19/20	2	8.551	8.553	0.002	8.553	0.002	100.00
Dright May 20/21	2	8.073	8.076	0.003	8.076	0.003	100.00
Dright May 21/22	2	8.932	8.935	0.003	8.935	0.003	100.00
Dright May 22/23	2	9.941	9.942	0.001	9.941	0	0.00
Dright May 23/24	2	9.408	9.43	0.022	9.429	0.021	95.45
Dright May 24/25	2	8.551	8.558	0.007	8.555	0.004	57.14
Dright May 25/26	2	8.983	8.986	0.003	8.985	0.002	66.67
Dright May 26/27	2	9.941	9.944	0.003	9.945	0.004	133.33
Dright May 27/28	2	8.324	8.327	0.003	8.327	0.003	100.00
Dright May 28/29	2	8.548	8.552	0.004	8.552	0.004	100.00
Dright May 29/30	2	9.939	9.94	0.001	9.94	0.001	100.00
Dright May 30/31	2	9.363	9.369	0.006	9.369	0.006	100.00
Dright May 31/June01	2	9.94	9.955	0.015	9.956	0.016	106.67
Dright June 01/02	2	8.983	9.096	0.113	9.076	0.093	82.30
Dright June 02/03	2	8.389	8.523	0.134	8.49	0.101	75.37
Eleft 22/23 Apr	2	8.084	8.158	0.074	8.127	0.043	58.11
Eleft 23/24 Apr	2	8.23	8.251	0.021	8.24	0.01	47.62
Eleft 24/25 Apr	2	8.354	8.427	0.073	8.402	0.048	65.75
Eleft 25/26 Apr	2	8.23	8.548	0.318	8.483	0.253	79.56
Eleft 26/28 Apr	3	8.339	8.358	0.019	8.355	0.016	84.21
Eleft 28/29 Apr	2	7.517	7.524	0.007	7.524	0.007	100.00
Eleft 29/30 Apr	2	9.185	9.349	0.164	9.318	0.133	81.10
Eleft 30Apr/01 May	2	9.184	9.191	0.007	9.188	0.004	57.14
Eleft 01/02 May	2	9.706	9.728	0.022	9.718	0.012	54.55
Eleft 02/03 May	2	8.139	8.155	0.016	8.147	0.008	50.00
Erigh 22/23 Apr	2	8.4	8.516	0.116	8.473	0.073	62.93
Erigh 23/24 Apr	2	8.249	8.287	0.038	8.271	0.022	57.89
Erigh 24/25 Apr	2	8.229	8.326	0.097	8.294	0.065	67.01
Erigh 25/26 Apr	2	8.25	8.741	0.491	8.646	0.396	80.65
Erigh 26/28 Apr	3	7.832	7.84	0.008	7.837	0.005	62.50
Erigh 28/29 Apr	2	8.397	8.4	0.003	8.4	0.003	100.00
Erigh 29/30 Apr	2	8.354	8.601	0.247	8.556	0.202	81.78
Erigh 30Apr/01 May	2	8.072	8.089	0.017	8.086	0.014	82.35
Erigh 01/02 May	2	9.926	9.951	0.025	9.936	0.01	40.00
Erigh 02/03 May	2	8.683	8.692	0.009	8.692	0.009	100.00
Jleft Apr23/24	2	8.385	8.429	0.044	8.425	0.04	90.91
Jleft Apr24/25	2	8.142	8.161	0.019	8.16	0.018	94.74
Jleft Apr25/26	2	8.397	8.418	0.021	8.416	0.019	90.48
Jleft Apr26/27	2	8.128	8.144	0.016	8.142	0.014	87.50
Jleft Apr27/28	2	8.385	8.419	0.034	8.416	0.031	91.18
Jleft Apr28/29	2	8.324	8.326	0.002	8.326	0.002	100.00
Jleft Apr29/30	2	8.398	8.414	0.016	8.413	0.015	93.75
Jleft Apr30/May01	2	9.939	9.945	0.006	9.943	0.004	66.67
Jleft May01/02	2	7.486	7.494	0.008	7.491	0.005	62.50
Jleft May02/03	2	9.773	9.833	0.06	9.828	0.055	91.67
Jleft May03/04	2	8.397	8.409	0.012	8.409	0.012	100.00
Jleft May04/05	2	8.383	8.4	0.017	8.4	0.017	100.00
Jleft May05/06	2	8.353	8.391	0.038	8.387	0.034	89.47
Jleft May06/07	1	7.485	7.503	0.018	7.498	0.013	72.22
Jleft May07/08	1	9.455	9.458	0.003	9.458	0.003	100.00
Jleft May08/09	2	8.383	8.393	0.01	8.389	0.006	60.00
Jleft May09/10	2	9.654			9.673	0.019	
Jleft May10/11	2	9.479			9.498	0.019	
Jleft May11/12	2	7.484	7.494	0.01	7.493	0.009	90.00
Jleft May12/13	2	8.353	8.358	0.005	8.357	0.004	80.00
Jleft May13/14	2	9.654	9.664	0.01	9.662	0.008	80.00
Jleft May14/15	2	9.478	9.486	0.008	9.485	0.007	87.50
Jleft May15/16	2	8.143	8.153	0.01	8.15	0.007	70.00
Jleft May16/17	2	9.187	9.206	0.019	9.203	0.016	84.21
Jleft May17/18	2	9.771	9.779	0.008	9.777	0.006	75.00
Jleft May18/19	2	9.158	9.166	0.008	9.163	0.005	62.50
Jleft May 19/20	2	7.969	7.973	0.004	7.973	0.004	100.00
Jleft May 20/21	2	8.038	8.048	0.01	8.048	0.01	100.00
Jleft May 21/22	2	9.192	9.205	0.013	9.201	0.009	69.23
Jleft May 22/23	2	9.97	9.973	0.003	9.972	0.002	66.67
Jleft May 23/24	2	7.97	7.978	0.008	7.975	0.005	62.50
Jleft May 24/25	2	8.687	8.737	0.05	8.728	0.041	82.00
Jleft May 25/26	2	9.193	9.266	0.073	9.249	0.056	76.71
Jleft May 26/27	2	9.971	9.978	0.007	9.977	0.006	85.71
Jleft May 27/28	2	8.928	8.93	0.002	8.93	0.002	100.00
Jleft May 28/29	2	7.832	7.842	0.01	7.836	0.004	40.00
Jleft May 29/30	2	9.97	9.977	0.007	9.975	0.005	71.43
Jleft May 30/31	2	8.927	8.933	0.006	8.932	0.005	83.33
Jleft May 31/June01	2	9.655	9.664	0.009	9.663	0.008	88.89
Jleft June 01/02	2	9.193	9.234	0.041	9.217	0.024	58.54
Jleft June 02/03	2	8.339	8.431	0.092	8.418	0.079	85.87
Jleft June 03/04	2	8.039	8.055	0.016	8.051	0.012	75.00

Sample	Tides	Crucible wt	Crucible + Dry sed	Dry sed (g)	Crucible + Ash	Ash wt (g)	% Ash
Jleft June 04/05	2	9.404	9.412	0.008	9.412	0.008	100.00
Jleft June 05/06	2	8.93	8.944	0.014	8.944	0.014	100.00
J/K Apr23/24	2	8.036	8.076	0.04	8.073	0.037	92.50
J/K Apr24/25	2	8.684	8.707	0.023	8.705	0.021	91.30
J/K Apr25/26	2	7.517	7.558	0.041	7.554	0.037	90.24
J/K Apr26/27	2	8.549	8.557	0.008	8.555	0.006	75.00
J/K Apr27/28	2	8.036	8.078	0.042	8.075	0.039	92.86
J/K Apr28/29	2	8.084	8.091	0.007	8.089	0.005	71.43
J/K Apr29/30	2	7.517	7.541	0.024	7.532	0.015	62.50
J/K Apr30/May01	2	9.969	9.97	0.001	9.97	0.001	100.00
J/K May01/02	2	8.325	8.327	0.002	8.327	0.002	100.00
J/K May02/03	2	10.02	10.029	0.009	10.026	0.006	66.67
J/K May03/04	2	7.517	7.521	0.004	7.52	0.003	75.00
J/K May04/05	2	8.036	8.047	0.011	8.047	0.011	100.00
J/K May05/06	2	8.23	8.242	0.012	8.24	0.01	83.33
J/K May06/07	1	8.322	8.335	0.013	8.331	0.009	69.23
J/K May07/08	1	8.398	8.406	0.008	8.403	0.005	62.50
J/K May08/09	2	8.141	8.156	0.015	8.154	0.013	86.67
J/K May09/10	2	9.36			9.379	0.019	
J/K May10/11	2	9.406			9.429	0.023	
J/K May11/12	2	8.323	8.333	0.01	8.331	0.008	80.00
J/K May12/13	2	8.229	8.234	0.005	8.232	0.003	60.00
J/K May13/14	2	9.361	9.363	0.002	9.363	0.002	100.00
J/K May14/15	2	9.406	9.421	0.015	9.416	0.01	66.67
J/K May15/16	2	8.074	8.09	0.016	8.086	0.012	75.00
J/K May16/17	2	8.25	8.271	0.021	8.269	0.019	90.48
J/K May17/18	2	10.019	10.026	0.007	10.022	0.003	42.86
J/K May18/19	2	8.923	8.94	0.017	8.938	0.015	88.24
J/K May 19/20	2	7.486	7.491	0.005	7.491	0.005	100.00
J/K May 20/21	2	8.13	8.139	0.009	8.137	0.007	77.78
J/K May 21/22	2	8.981	8.989	0.008	8.987	0.006	75.00
J/K May 22/23	2	9.415	9.42	0.005	9.419	0.004	80.00
J/K May 23/24	2	7.487	7.492	0.005	7.492	0.005	100.00
J/K May 24/25	2	8.144	8.19	0.046	8.183	0.039	84.78
J/K May 25/26	2	8.041	8.101	0.06	8.088	0.047	78.33
J/K May 26/27	2	9.417	9.428	0.011	9.427	0.01	90.91
J/K May 27/28	2	9.708	9.711	0.003	9.711	0.003	100.00
J/K May 28/29	2	8.382	8.39	0.008	8.388	0.006	75.00
J/K May 29/30	2	9.414	9.422	0.008	9.418	0.004	50.00
J/K May 30/31	2	9.708	9.712	0.004	9.71	0.002	50.00
J/K May 31/June01	2	9.362	9.394	0.032	9.392	0.03	93.75
J/K June 01/02	2	8.041	8.105	0.064	8.076	0.035	54.69
J/K June 02/03	2	8.146	8.228	0.082	8.21	0.064	78.05
J/K June 03/04	2	9.157	9.168	0.011	9.168	0.011	100.00
J/K June 04/05	2	9.706	9.712	0.006	9.712	0.006	100.00
J/K June 05/06	2	8.128	8.135	0.007	8.134	0.006	85.71
Kright Apr23/24	2	8.143	8.26	0.117	8.251	0.108	92.31
Kright Apr24/25	2	8.073	8.116	0.043	8.111	0.038	88.37
Kright Apr25/26	2	8.39	8.456	0.066	8.445	0.055	83.33
Kright Apr26/27	2	7.988	7.988	0.02	7.982	0.014	70.00
Kright Apr27/28	2	8.141	8.165	0.024	8.163	0.022	91.67
Kright Apr28/29	2	7.485	7.495	0.01	7.493	0.008	80.00
Kright Apr29/30	2	8.39	8.451	0.061	8.437	0.047	77.05
Kright Apr30/ May01	2	9.415	9.418	0.003	9.417	0.002	66.67
Kright May01/02	2	8.085	8.102	0.017	8.096	0.011	64.71
Kright May02/03	2	9.454	9.486	0.032	9.473	0.019	59.38
Kright May03/04	2	8.389	8.397	0.008	8.396	0.007	87.50
Kright May04/05	2	8.142	8.163	0.021	8.161	0.019	90.48
Kright May05/06	2	8.249	8.292	0.043	8.288	0.039	90.70
Kright May06/07	1	8.083	8.098	0.015	8.097	0.014	93.33
Kright May07/08	1	7.517	7.527	0.01	7.523	0.006	60.00
Kright May08/09	2	8.684	8.707	0.023	8.696	0.012	52.17
Kright May09/10	2	9.314			9.349	0.035	
Kright May10/11	2	9.458			9.514	0.058	
Kright May11/12	2	8.083	8.113	0.03	8.11	0.027	90.00
Kright May12/13	2	8.249	8.266	0.017	8.266	0.017	100.00
Kright May13/14	2	9.315	9.324	0.009	9.322	0.007	77.78
Kright May14/15	2	9.455	9.493	0.038	9.484	0.029	76.32
Kright May15/16	2	8.037	8.083	0.046	8.079	0.042	91.30
Kright May16/17	2	8.041	8.21	0.169	8.195	0.154	91.12
Kright May17/18	2	9.452	9.471	0.019	9.468	0.016	84.21
Kright May18/19	2	9.706	9.715	0.009	9.714	0.008	88.89
Kright May 19/20	2	8.323	8.362	0.039	8.357	0.034	87.18
Kright May 20/21	2	8.354	8.37	0.016	8.368	0.014	87.50
Kright May 21/22	2	8.844	8.89	0.046	8.883	0.039	84.78
Kright May 22/23	2	9.708	9.717	0.009	9.715	0.007	77.78
Kright May 23/24	2	8.326	8.343	0.017	8.34	0.014	82.35
Kright May 24/25	2	8.075	8.307	0.232	8.28	0.205	88.36
Kright May 25/26	2	8.251	8.44	0.189	8.409	0.158	83.60
Kright May 26/27	2	9.71	9.731	0.021	9.727	0.017	80.95
Kright May 27/28	2	9.48	9.487	0.007	9.486	0.006	85.71
Kright May 28/29	2	8.686	8.708	0.022	8.7	0.014	63.64
Kright May 29/30	2	9.709	9.716	0.007	9.716	0.007	100.00
Kright May 30/31	2	9.481	9.493	0.012	9.492	0.011	91.67
Kright May 31/June01	2	9.16	9.189	0.029	9.188	0.028	96.55

Sample	Tides	Crucible wt	Crucible + Dry sed	Dry sed (g)	Crucible + Ash	Ash wt (g)	% Ash
Kright June 01/02	2	8.249	8.337	0.088	8.308	0.057	64.77
Kright June 02/03	2	8.073	8.223	0.15	8.202	0.129	86.00
Kright June 03/04	2	9.412	9.431	0.019	9.431	0.019	100.00
Kright June 04/05	2	8.249	8.26	0.011	8.258	0.009	81.82
Kright June 05/06	2	8.352	8.359	0.007	8.359	0.007	100.00
Lieft Apr23/24	2	7.685	10.474	2.789	10.34	2.655	95.20
Lieft Apr24/25	2	7.832	8.127	0.295	8.076	0.244	82.71
Lieft Apr25/26	2	8.13	13.817	5.687	13.629	5.499	96.69
Lieft Apr26/27	2	8.397	8.785	0.388	8.771	0.374	96.39
Lieft Apr27/28	2	9.185	9.197	0.012	9.196	0.011	91.67
Lieft Apr28/29	2	8.338	8.361	0.023	8.361	0.023	100.00
Lieft Apr29/30	2	8.229	10.984	2.755	10.899	2.67	96.91
Lieft Apr30/May01	2	8.34	8.374	0.034	8.37	0.03	88.24
Lieft May01/02	2	8.13	8.18	0.05	8.176	0.046	92.00
Lieft May02/03	2	8.228	8.298	0.07	8.295	0.067	95.71
Lieft May03/04	2	8.128	8.177	0.049	8.176	0.048	97.96
Lieft May04/05	2	8.685	9.679	0.994	9.649	0.964	96.98
Lieft May05/06	2	8.04	8.603	0.563	8.581	0.541	96.09
Lieft May06/07	1	8.388	8.424	0.036	8.421	0.033	91.67
Lieft May07/08	1	9.706	9.759	0.053	9.756	0.05	94.34
Lieft May08/09	2	7.833	7.856	0.023	7.855	0.022	95.65
Lieft May09/10	2	9.968			10.12	0.152	
Lieft May10/11	2	9.159			11.707	2.548	
Lieft May11/12	2	8.339	8.522	0.183	8.515	0.176	96.17
Lieft May12/13	2	8.072	8.098	0.026	8.098	0.026	100.00
Lieft May13/14	2	9.97	10.013	0.043	10.01	0.04	93.02
Lieft May14/15	2	9.16	12.755	3.595	12.667	3.507	97.55
Lieft May15/16	2	8.383	11.968	3.585	11.881	3.498	97.57
Lieft May16/17	2	8.13	8.529	0.399	8.518	0.388	97.24
Lieft May17/18	2	9.939	10.739	0.8	10.715	0.776	97.00
Lieft May18/19	2	9.478	9.52	0.042	9.518	0.04	95.24
Lieft May 19/20	2	8.337	8.472	0.135	8.468	0.131	97.04
Lieft May 20/21	2	8.23	8.257	0.027	8.256	0.026	96.30
Lieft May 21/22	2	8.988	9.001	0.013	9.001	0.013	100.00
Lieft May 22/23	2	9.656	9.658	0.002	9.658	0.002	100.00
Lieft May 23/24	2	8.341	8.346	0.005	8.344	0.003	60.00
Lieft May 24/25	2	8.037	8.217	0.18	8.208	0.171	95.00
Lieft May 25/26	2	8.085	8.488	0.403	8.47	0.385	95.53
Lieft May 26/27	2	9.655	9.691	0.036	9.691	0.036	100.00
Lieft May 27/28	2	9.408	9.409	0.001	9.408	0	0.00
Lieft May 28/29	2	8.143	8.149	0.006	8.147	0.004	66.67
Lieft May 29/30	2	9.655	9.677	0.022	9.677	0.022	100.00
Lieft May 30/31	2	9.405	9.446	0.041	9.446	0.041	100.00
Lieft May 31/June01	2	9.97	9.977	0.007	9.979	0.009	128.57
Lieft June 01/02	2	8.084	11.837	3.753	11.734	3.65	97.26
Lieft June 02/03	2	7.486	12.808	5.322	12.672	5.186	97.44
Lieft June 03/04	2	8.227	8.737	0.51	8.726	0.499	97.84
Lieft June 04/05	2	8.841	8.876	0.035	8.876	0.035	100.00
Lieft June 05/06	2	9.363	9.377	0.014	9.377	0.014	100.00
L/M Apr23/24	2	8.341	12.222	3.881	12.076	3.735	96.24
L/M Apr24/25	2	8.384	8.695	0.311	8.66	0.276	88.75
L/M Apr25/26	2	8.549	15.473	6.924	15.277	6.728	97.17
L/M Apr26/27	2	7.517	8.119	0.602	8.097	0.58	96.35
L/M Apr27/28	2	8.072	8.105	0.033	8.094	0.022	86.67
L/M Apr28/29	2	7.832	7.847	0.015	7.847	0.015	100.00
L/M Apr29/30	2	8.25	10.934	2.684	10.85	2.6	96.87
L/M Apr30/May01	2	7.833	7.864	0.031	7.86	0.027	87.10
L/M May01/02	2	7.969	8.011	0.042	8.006	0.037	88.10
L/M May02/03	2	8.247	8.296	0.049	8.293	0.046	93.88
L/M May03/04	2	8.549	8.59	0.041	8.589	0.04	97.56
L/M May04/05	2	8.074	8.976	0.902	8.939	0.865	95.90
L/M May05/06	2	9.772	10.253	0.481	10.235	0.463	96.26
L/M May06/07	1	8.548	8.597	0.049	8.596	0.048	97.96
L/M May07/08	1	9.476	9.607	0.131	9.601	0.125	95.42
L/M May08/09	2	8.339	8.357	0.018	8.357	0.018	100.00
L/M May09/10	2	9.414			9.584	0.17	
L/M May10/11	2	8.926			12.348	3.422	
L/M May11/12	2	7.832	8.088	0.256	8.081	0.249	97.27
L/M May12/13	2	8.129	8.206	0.077	8.203	0.074	96.10
L/M May13/14	2	9.414	9.483	0.069	9.481	0.067	97.10
L/M May14/15	2	8.926	12.836	3.91	12.743	3.817	97.62
L/M May15/16	2	8.084	12.197	4.113	12.098	4.014	97.59
L/M May16/17	2	8.354	8.796	0.442	8.785	0.431	97.51
L/M May17/18	2	9.969	10.915	0.946	10.881	0.912	96.41
L/M May18/19	2	9.404	9.477	0.073	9.474	0.07	95.89
L/M May 19/20	2	7.832	7.98	0.148	7.973	0.141	95.27
L/M May 20/21	2	9.167	9.226	0.039	9.224	0.037	94.87
L/M May 21/22	2	9.365	9.386	0.021	9.386	0.021	100.00
L/M May 22/23	2	9.361	9.372	0.011	9.372	0.011	100.00
L/M May 23/24	2	7.834	7.847	0.013	7.845	0.011	84.62
L/M May 24/25	2	8.132	8.346	0.214	8.337	0.205	95.79
L/M May 25/26	2	8.23	8.715	0.485	8.689	0.459	94.64
L/M May 26/27	2	9.361	9.46	0.099	9.457	0.096	96.97
L/M May 27/28	2	8.845	8.862	0.017	8.86	0.015	88.24
L/M May 28/29	2	8.074	8.088	0.014	8.087	0.013	92.86

Sample	Tides	Crucible wt	Crucible + Dry sed	Dry sed (g)	Crucible + Ash	Ash wt (g)	% Ash
L/M May 29/30	2	9.362	9.389	0.027	9.388	0.026	96.30
L/M May 30/31	2	8.844	8.879	0.035	8.875	0.031	88.57
L/M May 31/June01	2	9.416	9.418	0.002	9.418	0.002	100.00
L/M June 01/02	2	8.229	12.733	4.504	12.617	4.388	97.42
L/M June 02/03	2	8.685	14.908	6.223	14.744	6.059	97.36
L/M June 03/04	2	9.021	9.637	0.616	9.623	0.602	97.73
L/M June 04/05	2	8.083	8.128	0.045	8.123	0.04	88.89
L/M June 05/06	2	8.925	8.938	0.013	8.935	0.01	76.92
Mright Apr23/24	2	7.833	12.1	4.267	11.901	4.068	95.34
Mright Apr24/25	2	8.036	8.385	0.349	8.342	0.306	87.68
Mright Apr25/26	2	7.968	14.458	6.49	14.265	6.297	97.03
Mright Apr26/27	2	8.389	9.029	0.64	9.007	0.618	96.56
Mright Apr27/28	2	8.684	8.691	0.007	8.689	0.005	71.43
Mright Apr28/29	2	8.383	8.418	0.035	8.418	0.035	100.00
Mright Apr29/30	2	8.041	10.642	2.601	10.563	2.522	96.96
Mright Apr30/May01	2	8.383	8.441	0.058	8.436	0.053	91.38
Mright May 01/02	2	8.549	8.569	0.02	8.568	0.019	95.00
Mright May 02/03	2	8.039	8.066	0.027	8.063	0.024	88.89
Mright May 03/04	2	7.967	8.014	0.047	8.013	0.046	97.87
Mright May 04/05	2	9.185	10.198	1.013	10.167	0.982	96.94
Mright May 05/06	2	10.019	10.593	0.574	10.575	0.556	96.86
Mright May 06/07	1	7.968	8.032	0.064	8.027	0.059	92.19
Mright May 07/08	2	9.407	9.472	0.065	9.468	0.061	93.85
Mright May 08/09	2	8.036	8.06	0.024	8.057	0.021	87.50
Mright May 09/10	2	9.708			9.876	0.168	
Mright May 10/11	2	9.708			12.928	3.22	
Mright May 11/12	2	8.384	8.703	0.319	8.695	0.311	97.49
Mright May 12/13	2	8.185	9.278	1.093	9.274	1.089	99.63
Mright May 13/14	2	9.708	9.831	0.123	9.827	0.119	96.75
Mright May 14/15	2	9.707	13.283	3.576	13.206	3.499	97.85
Mright May 15/16	2	8.685	12.427	3.742	12.34	3.655	97.68
Mright May 16/17	2	8.23	8.813	0.583	8.799	0.569	97.60
Mright May 17/18	2	9.413	10.24	0.827	10.213	0.8	96.74
Mright May 18/19	2	9.455	9.496	0.041	9.494	0.039	95.12
Mright May 19/20	2	8.383	8.56	0.177	8.554	0.171	96.61
Mright May 20/21	2	8.25	8.326	0.076	8.324	0.074	97.37
Mright May 21/22	2	9.025	9.057	0.032	9.055	0.03	93.75
Mright May 22/23	2	9.161	9.165	0.004	9.163	0.002	50.00
Mright May 23/24	2	8.386	8.414	0.028	8.411	0.025	89.29
Mright May 24/25	2	8.365	8.559	0.194	8.552	0.187	96.39
Mright May 25/26	2	9.186	9.659	0.473	9.636	0.45	95.14
Mright May 26/27	2	9.159	9.18	0.021	9.18	0.021	100.00
Mright May 27/28	2	8.989	9.001	0.012	9.001	0.012	100.00
Mright May 28/29	2	8.036	8.042	0.006	8.04	0.004	66.67
Mright May 29/30	2	9.161	9.205	0.044	9.204	0.043	97.73
Mright May 30/31	2	8.989	9.03	0.041	9.018	0.029	70.73
Mright May 31/June01	2	9.709	9.714	0.005	9.714	0.005	100.00
Mright June 01/02	2	9.185	12.932	3.747	12.835	3.65	97.41
Mright June 02/03	2	8.383	13.635	5.252	13.515	5.132	97.72
Mright June 03/04	2	9.476	10.089	0.613	10.072	0.596	97.23
Mright June 04/05	2	9.184	9.228	0.044	9.225	0.041	93.18
Mright June 05/06	2	8.986	8.997	0.011	8.997	0.011	100.00

Site	Date out	Date In	No tides	Empty wgt	Prior ash	After ash	Sand wgt	+500uM fraction
STA L	19/04/2002	20/04/2002	2	8.324	8.327	8.327	0.003	0.000
STA R	19/04/2002	20/04/2002	2	8.041	8.044	8.046	0.005	0.003
STA L	20/04/2002	21/04/2002	2	8.397	8.395	8.396	-0.001	0.000
STA R	20/04/2002	21/04/2002	2	7.967	7.967	7.967	0.000	0.000
STA L	21/04/2002	22/04/2002	2	7.516	7.523	7.526	0.010	0.007
STA R	21/04/2002	22/04/2002	2	8.387	8.414	8.413	0.026	0.018
STA L	22/04/2002	23/04/2002	2	9.413	9.417	9.417	0.004	0.000
STA R	22/04/2002	23/04/2002	2	9.191	9.194	9.194	0.003	0.000
STA L	23/04/2002	24/04/2002	2	9.183	9.188	9.188	0.005	0.000
STA R	23/04/2002	24/04/2002	2	9.360	9.364	9.364	0.004	0.002
STA L	24/04/2002	25/04/2002	2	9.938	9.939	9.939	0.001	0.000
STA R	24/04/2002	25/04/2002	2	9.022	9.024	9.024	0.002	0.000
STA L	25/04/2002	26/04/2002	2	8.544	8.565	8.569	0.025	0.017
STA R	25/04/2002	26/04/2002	2	8.339	8.364	8.369	0.030	0.011
STA L	26/04/2002	27/04/2002	1	8.684	8.684	8.686	0.002	0.000
STA R	26/04/2002	27/04/2002	1	8.388	8.389	8.390	0.002	0.000
STA L	27/04/2002	28/04/2002	2	7.516	7.523	7.523	0.007	0.000
STA R	27/04/2002	28/04/2002	2	8.039	8.046	8.046	0.007	0.000
STA L	28/04/2002	29/04/2002	2	9.936	9.939	9.942	0.006	0.000
STA R	28/04/2002	29/04/2002	2	9.359	9.361	9.364	0.005	0.000
STA L	29/04/2002	30/04/2002	2	9.599	9.606	9.607	0.008	0.003
STA R	29/04/2002	30/04/2002	2	9.411	9.416	9.418	0.007	0.000
STA L	30/04/2002	01/05/2002	2	8.692	8.697	8.699	0.007	0.000
STA R	30/04/2002	01/05/2002	2	8.986	8.997	8.995	0.009	0.004
STA L	01/05/2002	02/05/2002	2	9.702	9.706	9.709	0.007	0.000
STA R	01/05/2002	02/05/2002	2	9.448	9.455	9.456	0.008	0.000
STA L	02/05/2002	03/05/2002	2	9.360	9.367	9.369	0.009	0.000
STA R	02/05/2002	03/05/2002	2	9.705	9.711	9.714	0.009	0.000
STA L	03/05/2002	04/05/2002	2	8.071	8.083	8.083	0.012	0.007
STA R	03/05/2002	04/05/2002	2	8.141	8.143	8.145	0.004	0.000
STA L	04/05/2002	05/05/2002	2	9.361	9.365	9.369	0.008	0.003
STA R	04/05/2002	05/05/2002	2	9.186	9.198	9.202	0.016	0.009
STA L	05/05/2002	06/05/2002	2	9.970	10.360	10.339	0.369	0.031
STA R	05/05/2002	06/05/2002	2	8.987	9.370	9.353	0.366	0.024
STA L	06/05/2002	07/05/2002	2	9.940	9.976	9.976	0.036	0.000
STA R	06/05/2002	07/05/2002	2	9.192	9.239	9.236	0.044	0.000
STA L	07/05/2002	08/05/2002	2	8.983	8.995	8.995	0.012	0.000
STA R	07/05/2002	08/05/2002	2	8.933	8.939	8.939	0.006	0.000
STA L	08/05/2002	09/05/2002	2	7.833	8.053	8.029	0.196	0.003
STA R	08/05/2002	09/05/2002	2	8.324	8.526	8.505	0.181	0.002
STA L	09/05/2002	10/05/2002	2	9.364	9.507	9.489	0.125	0.001
STA R	09/05/2002	10/05/2002	2	9.453	9.595	9.582	0.129	0.003
STA L	10/05/2002	11/05/2002	2	9.191	11.321	11.191	2.000	0.023
STA R	10/05/2002	11/05/2002	2	10.019	12.101	11.974	1.955	0.030
STA L	11/05/2002	12/05/2002	2	8.228	8.271	8.267	0.039	0.000
STA R	11/05/2002	12/05/2002	2	8.249	8.299	8.297	0.048	0.000
STA L	12/05/2002	13/05/2002	1	7.967	7.974	7.974	0.007	0.000
STA R	12/05/2002	13/05/2002	1	8.339	8.351	8.349	0.010	0.000
STA L	13/05/2002	14/05/2002	2	8.931	8.952	8.949	0.018	0.000
STA R	13/05/2002	14/05/2002	2	8.981	9.009	9.004	0.023	0.000
STA L	14/05/2002	15/05/2002	2	8.037	8.058	8.056	0.019	0.016
STA R	14/05/2002	15/05/2002	2	7.832	7.837	7.836	0.004	0.000
STA L	15/05/2002	16/05/2002	2	8.390	8.425	8.421	0.031	0.029
STA R	15/05/2002	16/05/2002	2	8.324	8.328	8.328	0.004	0.001
STA L	16/05/2002	17/05/2002	2	9.183	9.194	9.194	0.011	0.000
STA R	16/05/2002	17/05/2002	2	9.412	9.428	9.427	0.015	0.000
STA L	17/05/2002	18/05/2002	2	8.694	8.720	8.741	0.047	0.000
STA R	17/05/2002	18/05/2002	2	9.025	9.042	9.040	0.015	0.000
STA L	18/05/2002	19/05/2002	2	8.229	8.258	8.256	0.027	0.000
STA R	18/05/2002	19/05/2002	2	7.968	7.999	7.997	0.029	0.000
STA L	19/05/2002	20/05/2002	2	8.324	8.328	8.328	0.004	0.000
STA R	19/05/2002	20/05/2002	2	7.835	7.837	7.837	0.002	0.000
STA L	20/05/2002	21/05/2002	2	8.144	8.159	8.159	0.015	0.006
STA R	20/05/2002	21/05/2002	2	8.354	8.360	8.360	0.006	0.000
STA L	21/05/2002	22/05/2002	2	9.707	9.871	9.858	0.151	0.024
STA R	21/05/2002	22/05/2002	2	9.453	9.613	9.599	0.146	0.028
STA L	22/05/2002	23/05/2002	2	9.364	10.621	10.536	1.172	0.004
STA R	22/05/2002	23/05/2002	2	8.844	10.053	9.990	1.146	0.009

Site	Date out	Date In	No tides	Empty wgt	Prior ash	After ash	Sand wgt	+500uM fraction
STA L	23/05/2002	24/05/2002	2	8.694	8.733	8.728	0.034	0.000
STA R	23/05/2002	24/05/2002	2	8.933	8.965	8.960	0.027	0.000
STA L	24/05/2002	25/05/2002	2	9.772	9.782	9.782	0.010	0.000
STA R	24/05/2002	25/05/2002	2	9.453	9.460	9.460	0.007	0.002
STA L	25/05/2002	26/05/2002	2	9.476	9.479	9.479	0.003	0.000
STA R	25/05/2002	26/05/2002	2	8.844	8.847	8.847	0.003	0.000
STA L	26/05/2002	27/05/2002	2	8.925	8.992	8.984	0.059	0.000
STA R	26/05/2002	27/05/2002	2	8.389	8.446	8.442	0.053	0.000
STA L	27/05/2002	28/05/2002	2	7.485	7.524	7.521	0.036	0.000
STA R	27/05/2002	28/05/2002	2	8.142	8.179	8.175	0.033	0.000
STA L	28/05/2002	29/05/2002	1	9.707	9.715	9.715	0.008	0.000
STA R	28/05/2002	29/05/2002	1	8.249	8.265	8.264	0.015	0.000
STA L	29/05/2002	30/05/2002	2	9.184	9.189	9.189	0.005	0.000
STA R	29/05/2002	30/05/2002	2	8.396	8.401	8.401	0.005	0.000
STA L	30/05/2002	31/05/2002	2	8.390	8.393	8.392	0.002	0.000
STA R	30/05/2002	31/05/2002	2	7.832	7.837	7.835	0.003	0.000
STA L	31/05/2002	01/06/2002	2	9.023	9.026	9.026	0.003	0.000
STA R	31/05/2002	01/06/2002	2	9.772	9.773	9.773	0.001	0.000
STA L	01/06/2002	02/06/2002	2	9.191	9.193	9.191	0.000	0.000
STA R	01/06/2002	02/06/2002	2	9.476	9.482	9.482	0.006	0.003
STA L	02/06/2002	03/06/2002	2	8.700	8.700	8.700	0.000	0.000
STA R	02/06/2002	03/06/2002	2	8.933	8.937	8.936	0.003	0.001
STA L	03/06/2002	04/06/2002	2	8.142	8.209	8.201	0.059	0.001
STA R	03/06/2002	04/06/2002	2	8.352	8.413	8.406	0.054	0.000
STA L	04/06/2002	05/06/2002	2	9.598	9.642	9.637	0.039	0.000
STA R	04/06/2002	05/06/2002	2	9.413	9.454	9.449	0.036	0.000
STA L	05/06/2002	06/06/2002	2	8.128	9.115	9.033	0.905	0.044
STA R	05/06/2002	06/06/2002	2	9.359	10.442	10.337	0.978	0.036
STA L	06/06/2002	07/06/2002	2	8.323	9.167	9.064	0.741	0.045
STA R	06/06/2002	07/06/2002	2	8.547	9.303	9.198	0.651	0.019
STA L	07/06/2002	08/06/2002	2	8.337	9.087	9.013	0.676	0.041
STA R	07/06/2002	08/06/2002	2	8.228	8.947	8.868	0.640	0.002

Site	Date out	Date In	No tides	Empty wgt	Prior ash	After ash	Sand wgt	+500uM fraction
KB L	19/04/2002	20/04/2002	2	7.834	7.947	7.945	0.111	0.009
KB R	19/04/2002	20/04/2002	2	7.486	7.612	7.610	0.124	0.010
KB L	20/04/2002	21/04/2002	2	8.383	8.799	8.793	0.410	0.000
KB R	20/04/2002	21/04/2002	2	8.685	9.106	9.099	0.414	0.000
KB L	21/04/2002	22/04/2002	2	8.227	8.403	8.400	0.173	0.021
KB R	21/04/2002	22/04/2002	2	8.246	8.406	8.403	0.157	0.012
KB L	22/04/2002	23/04/2002	2	8.339	9.353	8.353	0.014	0.001
KB R	22/04/2002	23/04/2002	2	8.924	9.939	8.937	0.013	0.001
KB L	23/04/2002	24/04/2002	2	8.986	8.992	8.992	0.006	0.000
KB R	23/04/2002	24/04/2002	2	9.771	9.780	9.780	0.009	0.000
KB L	24/04/2002	25/04/2002	2	8.028	8.063	8.062	0.034	0.020
KB R	24/04/2002	25/04/2002	2	7.964	7.972	7.972	0.008	0.000
KB L	25/04/2002	26/04/2002	2	8.074	8.100	8.100	0.026	0.002
KB R	25/04/2002	26/04/2002	2	8.143	8.172	8.172	0.029	0.000
KB L	26/04/2002	27/04/2002	1	8.396	8.402	8.403	0.007	0.000
KB R	26/04/2002	27/04/2002	1	8.323	8.329	8.331	0.008	0.002
KB L	27/04/2002	28/04/2002	2	9.451	9.646	9.638	0.187	0.018
KB R	27/04/2002	28/04/2002	2	8.035	8.256	8.247	0.212	0.011
KB L	28/04/2002	29/04/2002	2	9.769	9.867	9.869	0.100	0.012
KB R	28/04/2002	29/04/2002	2	8.128	8.235	8.235	0.107	0.003
KB L	29/04/2002	30/04/2002	2	8.248	8.285	8.285	0.037	0.005
KB R	29/04/2002	30/04/2002	2	9.183	9.220	9.220	0.037	0.002
KB L	30/04/2002	01/05/2002	2	8.228	8.354	8.353	0.125	0.014
KB R	30/04/2002	01/05/2002	2	8.396	8.506	8.502	0.106	0.008
KB L	01/05/2002	02/05/2002	2	8.839	8.907	8.884	0.045	0.006
KB R	01/05/2002	02/05/2002	2	8.683	8.748	8.738	0.055	0.005
KB L	02/05/2002	03/05/2002	2	8.546	8.567	8.564	0.018	0.000
KB R	02/05/2002	03/05/2002	2	8.353	8.368	8.367	0.014	0.000
KB L	03/05/2002	04/05/2002	2	7.484	7.499	7.498	0.014	0.004
KB R	03/05/2002	04/05/2002	2	8.034	8.043	8.043	0.009	0.000
KB L	04/05/2002	05/05/2002	2	9.025	9.112	9.110	0.085	0.010
KB R	04/05/2002	05/05/2002	2	8.340	8.425	8.420	0.080	0.008
KB L	05/05/2002	06/05/2002	2	8.695	13.563	13.430	4.735	0.617
KB R	05/05/2002	06/05/2002	2	8.251	12.874	12.735	4.484	0.631
KB L	06/05/2002	07/05/2002	2	9.772	12.041	11.975	2.203	0.292
KB R	06/05/2002	07/05/2002	2	8.230	10.410	10.353	2.123	0.322
KB L	07/05/2002	08/05/2002	2	8.925	9.111	9.102	0.177	0.012
KB R	07/05/2002	08/05/2002	2	8.353	8.531	8.522	0.169	0.016
KB L	08/05/2002	09/05/2002	2	9.707	16.249	16.099	6.392	1.096
KB R	08/05/2002	09/05/2002	2	8.075	14.985	14.841	6.766	1.253
KB L	09/05/2002	10/05/2002	2	8.519	19.583	19.366	10.847	2.101
KB R	09/05/2002	10/05/2002	2	7.486	18.984	18.776	11.290	2.272
KB L	10/05/2002	11/05/2002	2	19.710	34.149	33.890	14.180	1.857
KB R	10/05/2002	11/05/2002	2	18.109	32.119	31.887	13.778	1.975
KB L	11/05/2002	12/05/2002	2	9.361	9.993	9.980	0.619	0.042
KB R	11/05/2002	12/05/2002	2	9.186	9.858	9.844	0.658	0.042
KB L	12/05/2002	13/05/2002	1	9.478	9.727	9.723	0.245	0.027
KB R	12/05/2002	13/05/2002	1	9.161	9.382	9.377	0.216	0.019
KB L	13/05/2002	14/05/2002	2	8.845	12.183	12.033	3.188	0.326
KB R	13/05/2002	14/05/2002	2	9.453	12.544	12.403	2.950	0.300
KB L	14/05/2002	15/05/2002	2	9.363	9.506	9.494	0.131	0.023
KB R	14/05/2002	15/05/2002	2	9.706	9.806	9.799	0.093	0.003
KB L	15/05/2002	16/05/2002	2	8.925	8.944	8.941	0.016	0.004
KB R	15/05/2002	16/05/2002	2	9.707	9.720	9.719	0.012	0.000
KB L	16/05/2002	17/05/2002	2	9.969	10.299	10.272	0.303	0.012
KB R	16/05/2002	17/05/2002	2	9.476	9.794	9.768	0.292	0.014
KB L	17/05/2002	18/05/2002	2	10.019	10.894	10.856	0.837	0.050
KB R	17/05/2002	18/05/2002	2	9.360	10.201	10.161	0.801	0.051
KB L	18/05/2002	19/05/2002	2	8.399	12.137	12.039	3.640	0.810
KB R	18/05/2002	19/05/2002	2	8.338	11.352	11.278	2.940	0.340
KB L	19/05/2002	20/05/2002	2	8.926	9.395	9.375	0.449	0.316
KB R	19/05/2002	20/05/2002	2	9.707	9.835	9.835	0.128	0.036
KB L	20/05/2002	21/05/2002						
KB R	20/05/2002	21/05/2002						
KB L	21/05/2002	22/05/2002	2	8.685	13.207	12.987	4.302	0.225
KB R	21/05/2002	22/05/2002	2	8.036	12.411	12.193	4.157	0.218
KB L	22/05/2002	23/05/2002	2					
KB R	22/05/2002	23/05/2002	2					

Site	Date out	Date In	No tides	Empty wgt	Prior ash	After ash	Sand wgt	+500uM fraction
KB L	23/05/2002	24/05/2002	2	9.023	11.104	11.001	1.978	0.065
KB R	23/05/2002	24/05/2002	2	9.969	12.053	11.924	1.955	0.098
KB L	24/05/2002	25/05/2002	2					
KB R	24/05/2002	25/05/2002	2					
KB L	25/05/2002	26/05/2002	2					
KB R	25/05/2002	26/05/2002	2					
KB L	26/05/2002	27/05/2002	2	8.230	10.037	9.987	1.757	0.039
KB R	26/05/2002	27/05/2002	2	8.129	9.954	9.902	1.773	0.038
KB L	27/05/2002	28/05/2002	2	7.969	11.378	11.302	3.333	0.049
KB R	27/05/2002	28/05/2002	2	8.341	11.806	11.728	3.387	0.045
KB L	28/05/2002	29/05/2002	1	8.324	9.002	8.980	0.656	0.012
KB R	28/05/2002	29/05/2002	1	8.549	9.234	9.211	0.662	0.024
KB L	29/05/2002	30/05/2002	2					
KB R	29/05/2002	30/05/2002	2					
KB L	30/05/2002	31/05/2002	2					
KB R	30/05/2002	31/05/2002	2					
KB L	31/05/2002	01/06/2002	2					
KB R	31/05/2002	01/06/2002	2					
KB L	01/06/2002	02/06/2002	2					
KB R	01/06/2002	02/06/2002	2					
KB L	02/06/2002	03/06/2002	2					
KB R	02/06/2002	03/06/2002	2					
KB L	03/06/2002	04/06/2002	2					
KB R	03/06/2002	04/06/2002	2					
KB L	04/06/2002	05/06/2002	2					
KB R	04/06/2002	05/06/2002	2					
KB L	05/06/2002	06/06/2002	2					
KB R	05/06/2002	06/06/2002	2					
KB L	06/06/2002	07/06/2002	2					
KB R	06/06/2002	07/06/2002	2					
KB L	07/06/2002	08/06/2002	2					
KB R	07/06/2002	08/06/2002	2					
Red type denotes data missing due to vandalism								

Site	Date out	Date In	No tides	Empty wgt	Prior ash	After ash	Sand wgt	+500uM fraction
FN L	19/04/2002	20/04/2002	2	8.550	8.549	8.550	0.000	0.002
FN R	19/04/2002	20/04/2002	2	8.354	8.353	8.353	-0.001	0.003
FN L	20/04/2002	21/04/2002	2	8.036	8.037	8.037	0.001	0.048
FN R	20/04/2002	21/04/2002	2	8.142	8.148	8.149	0.007	0.045
FN L	21/04/2002	22/04/2002	2	8.081	8.089	8.088	0.007	0.000
FN R	21/04/2002	22/04/2002	2	8.070	8.082	8.081	0.011	0.000
FN L	22/04/2002	23/04/2002	2	9.452	9.454	9.453	0.001	0.000
FN R	22/04/2002	23/04/2002	2	9.600	9.602	9.600	0.000	0.000
FN L	23/04/2002	24/04/2002	2	8.693	8.699	8.698	0.005	0.005
FN R	23/04/2002	24/04/2002	2	9.969	9.984	9.984	0.015	0.000
FN L	24/04/2002	25/04/2002	2	8.129	8.130	8.130	0.001	0.000
FN R	24/04/2002	25/04/2002	2	8.240	8.250	8.250	0.010	0.000
FN L	25/04/2002	26/04/2002	2	8.382	8.387	8.389	0.007	0.002
FN R	25/04/2002	26/04/2002	2	7.827	7.844	7.844	0.017	0.011
FN L	26/04/2002	27/04/2002	1	8.228	8.228	8.229	0.001	0.000
FN R	26/04/2002	27/04/2002	1	8.083	8.083	8.084	0.001	0.000
FN L	27/04/2002	28/04/2002	2	7.485	7.506	7.505	0.020	0.012
FN R	27/04/2002	28/04/2002	2	8.926	8.949	8.947	0.021	0.016
FN L	28/04/2002	29/04/2002	2	8.336	9.348	8.351	0.015	0.002
FN R	28/04/2002	29/04/2002	2	9.021	9.033	9.033	0.012	0.000
FN L	29/04/2002	30/04/2002	2	9.967	9.968	9.970	0.003	0.000
FN R	29/04/2002	30/04/2002	2	9.188	9.193	9.195	0.007	0.000
FN L	30/04/2002	01/05/2002	2	7.967	7.978	7.979	0.012	0.002
FN R	30/04/2002	01/05/2002	2	10.020	10.036	10.036	0.016	0.009
FN L	01/05/2002	02/05/2002	2	8.386	8.392	8.392	0.006	0.000
FN R	01/05/2002	02/05/2002	2	8.921	8.927	8.929	0.008	0.000
FN L	02/05/2002	03/05/2002	2	7.831	7.833	7.835	0.004	0.000
FN R	02/05/2002	03/05/2002	2	8.928	8.932	8.933	0.005	0.000
FN L	03/05/2002	04/05/2002	2	8.322	8.327	8.327	0.005	0.002
FN R	03/05/2002	04/05/2002	2	8.382	8.394*	*		
FN L	04/05/2002	05/05/2002	2	7.969	7.965	7.970	0.001	0.000
FN R	04/05/2002	05/05/2002	2	9.415	9.416	9.418	0.003	0.003
FN L	05/05/2002	06/05/2002	2	8.131	8.141	8.143	0.012	0.000
FN R	05/05/2002	06/05/2002	2	10.021	10.026	10.026	0.005	0.000
FN L	06/05/2002	07/05/2002	2	8.399	8.402	8.401	0.002	0.000
FN R	06/05/2002	07/05/2002	2	9.601	9.615	9.615	0.014	0.009
FN L	07/05/2002	08/05/2002	2	8.036	8.056	8.056	0.020	0.018
FN R	07/05/2002	08/05/2002	2	9.707	9.710	9.710	0.003	0.002
FN L	08/05/2002	09/05/2002	2	8.390	8.400	8.399	0.009	0.001
FN R	08/05/2002	09/05/2002	2	8.844	8.851	8.851	0.007	0.003
FN L	09/05/2002	10/05/2002	2	8.685	8.695	8.695	0.010	0.000
FN R	09/05/2002	10/05/2002	2	8.143	8.151	8.151	0.008	0.000
FN L	10/05/2002	11/05/2002	2	8.128	8.161	8.159	0.031	0.000
FN R	10/05/2002	11/05/2002	2	8.396	8.420	8.417	0.021	0.008
FN L	11/05/2002	12/05/2002	2	9.600	9.606	9.604	0.004	0.000
FN R	11/05/2002	12/05/2002	2	8.987	8.994	8.994	0.007	0.000
FN L	12/05/2002	13/05/2002	1	9.024	9.031	9.031	0.007	0.000
FN R	12/05/2002	13/05/2002	1	9.968	9.979	9.979	0.011	0.000
FN L	13/05/2002	14/05/2002	2	7.484	7.515	7.512	0.028	0.000
FN R	13/05/2002	14/05/2002	2	8.353	8.388	8.386	0.033	0.000
FN L	14/05/2002	15/05/2002	2	8.685	8.694	8.693	0.008	0.000
FN R	14/05/2002	15/05/2002	2	8.073	8.082	8.080	0.007	0.000
FN L	15/05/2002	16/05/2002	2	8.144	8.146	8.145	0.001	0.000
FN R	15/05/2002	16/05/2002	2	8.548	8.554	8.552	0.004	0.000
FN L	16/05/2002	17/05/2002	2	9.190	9.194	9.194	0.004	0.000
FN R	16/05/2002	17/05/2002	2	8.249	8.251	8.251	0.002	0.000
FN L	17/05/2002	18/05/2002	2	9.159	9.176	9.175	0.016	0.010
FN R	17/05/2002	18/05/2002	2	8.129	8.133	8.133	0.004	0.000
FN L	18/05/2002	19/05/2002	2	9.938	9.944	9.944	0.006	0.000
FN R	18/05/2002	19/05/2002	2	9.600	9.608	9.608	0.008	0.000
FN L	19/05/2002	20/05/2002	2	8.394	8.399	8.396	0.002	0.004
FN R	19/05/2002	20/05/2002	2	8.550	8.554	8.554	0.004	0.001
FN L	20/05/2002	21/05/2002	2	7.487	7.504	7.502	0.015	0.004
FN R	20/05/2002	21/05/2002	2	8.074	8.089	8.087	0.013	0.001
FN L	21/05/2002	22/05/2002	2	8.981	9.002	8.998	0.017	0.000
FN R	21/05/2002	22/05/2002	2	8.932	8.955	8.950	0.018	0.000
FN L	22/05/2002	23/05/2002	2	9.772	9.813	9.810	0.038	0.000
FN R	22/05/2002	23/05/2002	2	8.988	9.022	9.020	0.032	0.000

Site	Date out	Date In	No tides	Empty wgt	Prior ash	After ash	Sand wgt	+500uM fraction
FN L	23/05/2002	24/05/2002	2	7.833	7.861	7.856	0.023	0.012
FN R	23/05/2002	24/05/2002	2	9.707	9.734	9.728	0.021	0.000
FN L	24/05/2002	25/05/2002	2	8.987	9.059	9.020	0.033	0.003
FN R	24/05/2002	25/05/2002	2	9.159	9.226	9.187	0.028	0.001
FN L	25/05/2002	26/05/2002	2	10.020	10.047	10.030	0.010	0.000
FN R	25/05/2002	26/05/2002	2	9.190	9.219	9.200	0.010	0.000
FN L	26/05/2002	27/05/2002	2	9.363	9.372	9.372	0.009	0.000
FN R	26/05/2002	27/05/2002	2	8.983	8.989	8.989	0.006	0.000
FN L	27/05/2002	28/05/2002	2	9.600	9.610	9.610	0.010	0.000
FN R	27/05/2002	28/05/2002	2	9.361	9.365	9.365	0.004	0.000
FN L	28/05/2002	29/05/2002	1	9.938	9.943	9.943	0.005	0.000
FN R	28/05/2002	29/05/2002	1	9.412	9.419	9.419	0.007	0.000
FN L	29/05/2002	30/05/2002	2	8.685	8.689	8.688	0.003	0.000
FN R	29/05/2002	30/05/2002	2	8.354	8.356	8.356	0.002	0.000
FN L	30/05/2002	31/05/2002	2	8.981	8.983	8.983	0.002	0.000
FN R	30/05/2002	31/05/2002	2	9.364	9.365	9.365	0.001	0.000
FN L	31/05/2002	01/06/2002	2	9.159	9.161	9.161	0.002	0.000
FN R	31/05/2002	01/06/2002	2	10.019	10.020	10.020	0.001	0.000
FN L	01/06/2002	02/06/2002	2	8.986	8.989	8.989	0.003	0.000
FN R	01/06/2002	02/06/2002	2	8.926	8.929	8.928	0.002	0.000
FN L	02/06/2002	03/06/2002	2	9.706	9.710	9.709	0.003	0.000
FN R	02/06/2002	03/06/2002	2	9.965	9.974	9.974	0.009	0.000
FN L	03/06/2002	04/06/2002	2	8.683	8.687	8.689	0.006	0.000
FN R	03/06/2002	04/06/2002	2	9.184	9.187	9.187	0.003	0.000
FN L	04/06/2002	05/06/2002	2	8.396	8.401	8.400	0.004	0.000
FN R	04/06/2002	05/06/2002	2	8.248	8.254	8.253	0.005	0.000
FN L	05/06/2002	06/06/2002	2	9.938	9.974	9.973	0.035	0.002
FN R	05/06/2002	06/06/2002	2	9.707	9.730	9.727	0.020	0.002
FN L	06/06/2002	07/06/2002	2	7.483	7.497	7.496	0.013	0.000
FN R	06/06/2002	07/06/2002	2	7.967	7.985	7.982	0.015	0.002
FN L	07/06/2002	08/06/2002	2	8.035	8.049	8.047	0.012	0.000
FN R	07/06/2002	08/06/2002	2	8.073	8.084	8.083	0.010	0.000
* missing data due to crucible breakage								

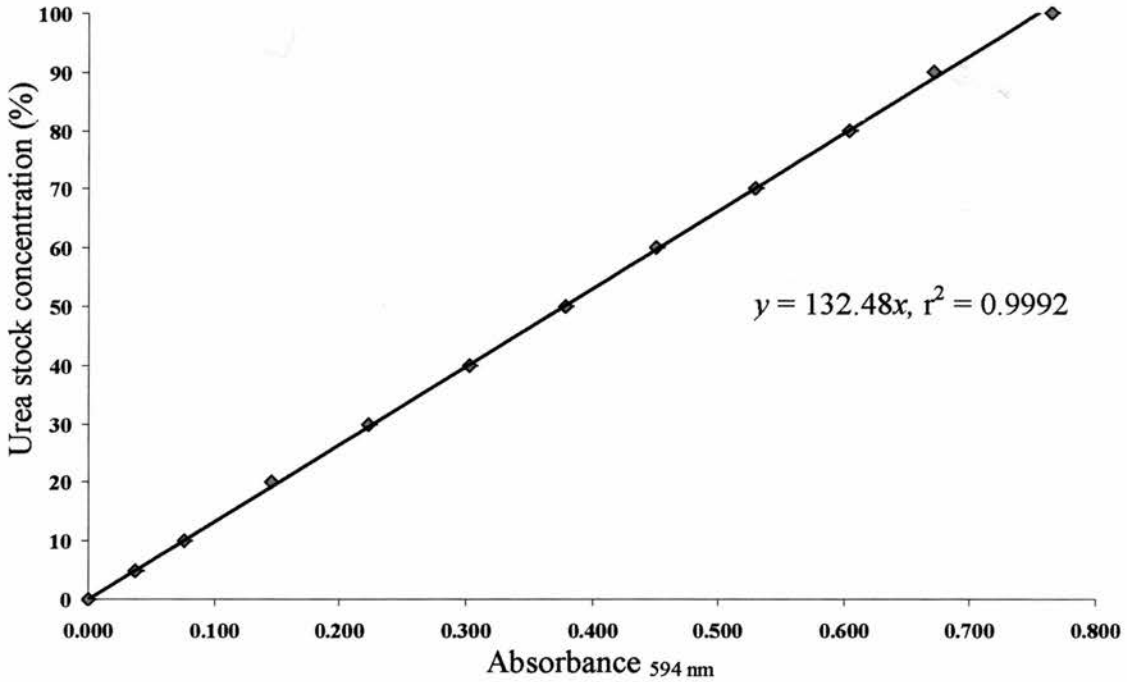
<i>Semibalanus balanoides</i>			St Andrews				Fife Ness				Kingsbarns			
Date out	Date in	No tides	Trap 1	Trap 2	Trap 3	Trap 4	Trap 1	Trap 2	Trap 3	Trap 4	Trap 1	Trap 2	Trap 3	Trap 4
19/04/2002	20/04/2002	2	0	0	0	0	2	2	1	3	1	1	2	0
20/04/2002	21/04/2002	2	0	0	0	0	3	1	1	2	0	0	0	0
21/04/2002	22/04/2002	2	1	0	0	1	0	0	1	0	2	1	0	0
22/04/2002	23/04/2002	2	0	0	1	0	6	0	1	7	5	4	1	1
23/04/2002	24/04/2002	2	0	1	0	0	7	7	8	4	1	1	0	1
24/04/2002	25/04/2002	2	0	1	0	0	1	4	2	1	5	3	1	0
25/04/2002	26/04/2002	2	1	0	0	2	3	5	4	4	1	1	0	2
26/04/2002	27/04/2002	1	0	1	1	1	0	1	1	1	1	1	0	0
27/04/2002	28/04/2002	2	0	1	0	0	1	3	3	0	2	2	0	1
28/04/2002	29/04/2002	2	0	1	1	0	3	3	3	3	2	4	0	0
29/04/2002	30/04/2002	2	0	0	0	0	2	3	3	4	2	0	1	0
30/04/2002	01/05/2002	2	0	0	0	1	1	0	1	0	4	0	0	1
01/05/2002	02/05/2002	2	0	0	0	0	4	3	5	3	0	0	2	2
02/05/2002	03/05/2002	2	0	1	0	0	22	15	35	11	0	3	1	0
03/05/2002	04/05/2002	2	0	0	0	0	9	10	15	19	1	1	1	2
04/05/2002	05/05/2002	2	0	0	0	0	15	14	20	7	5	2	0	0
05/05/2002	06/05/2002	2	4	11	5	7	2	0	4	1	13	8	3	11
06/05/2002	07/05/2002	2	11	22	6	8	4	2	6	4	13	7	2	10
07/05/2002	08/05/2002	2	5	3	9	10	3	5	5	2	14	16	13	18
08/05/2002	09/05/2002	2	10	19	10	6	3	0	2	2	4	4	3	4
09/05/2002	10/05/2002	2	4	4	2	4	2	2	2	1	5	3	2	2
10/05/2002	11/05/2002	2	6	7	6	3	5	4	2	0	5	6	7	5
11/05/2002	12/05/2002	2	2	5	1	5	5	5	4	1	10	14	9	10
12/05/2002	13/05/2002	1	1	4	3	4	2	3	2	6	12	5	1	7
13/05/2002	14/05/2002	2	10	2	5	5	3	7	5	7	3	4	2	3
14/05/2002	15/05/2002	2	2	*	1	0	2	3	4	7	12	14	14	8
15/05/2002	16/05/2002	2	1	9	3	2	16	29	15	11	12	4	12	13
16/05/2002	17/05/2002	2	2	3	2	0	50	54	21	13	7	9	5	19
17/05/2002	18/05/2002	2	25	25	13	14	2	5	4	5	21	27	13	35
18/05/2002	19/05/2002	2	11	15	7	8	8	6	1	3	9	8	15	7
19/05/2002	20/05/2002	2	61	58	46	56	8	8	3	9	46	46	43	40
20/05/2002	21/05/2002	2	4	10	11	7	4	3	5	5*	*	*	*	*
21/05/2002	22/05/2002	2	4	1	0	2	5	11	6	8	5	3	1	*
22/05/2002	23/05/2002	2	0	0	0	0	7	3	2	5*	*	*	*	*
23/05/2002	24/05/2002	2	4	12	9	2	3	7	8	5	5	2	3	1
24/05/2002	25/05/2002	2	11	9	6	5	8	2	5	4*	*	*	*	*
25/05/2002	26/05/2002	2	8	12	4	4	4	3	7	3*	*	*	*	*
26/05/2002	27/05/2002	2	4	5	2	1	0	1	8	3	8	4	3	1
27/05/2002	28/05/2002	2	4	5	1	0	1	1	1	1	1	7	4	1
28/05/2002	29/05/2002	1	0	0	0	1	0	1	0	0	0	1	1	0
29/05/2002	30/05/2002	2	0	1	0	0	5	6	5	0*	*	*	*	*
30/05/2002	31/05/2002	2	0	0	0	1	7	4	5	4*	*	*	*	*
31/05/2002	01/06/2002	2	0	0	0	0	4	8	6	9*	*	*	*	*
01/06/2002	02/06/2002	2	1	0	0	1	3	3	4	5*	*	*	*	*
02/06/2002	03/06/2002	2	7	9	3	4	2	0	1	0*	*	*	*	*
03/06/2002	04/06/2002	2	3	1	0	1	2	2	3	7*	*	*	*	*
04/06/2002	05/06/2002	2	0	0	0	0	1	2	1	2*	*	*	*	*
05/06/2002	06/06/2002	2	0	0	0	0	3	1	0	1*	*	*	*	*
06/06/2002	07/06/2002	2	1	1	1	0	2	2	3	0*	*	*	*	*
07/06/2002	08/06/2002	2	1	1	0	0	0	1	1	0*	*	*	*	*

<i>Balanus crenatus</i>		No tides	St Andrews				Fife Ness				Kingsbarns			
Date out	Date in		Trap 1	Trap 2	Trap 3	Trap 4	Trap 1	Trap 2	Trap 3	Trap 4	Trap 1	Trap 2	Trap 3	Trap 4
19/04/2002	20/04/2002	2	0	1	1	1	0	0	0	0	0	0	0	0
20/04/2002	21/04/2002	2	0	1	1	0	1	0	1	0	0	0	0	0
21/04/2002	22/04/2002	2	3	10	10	5	0	0	0	0	0	0	0	0
22/04/2002	23/04/2002	2	20	13	6	15	0	2	1	0	1	4	0	1
23/04/2002	24/04/2002	2	13	13	11	16	1	0	0	2	2	0	0	0
24/04/2002	25/04/2002	2	3	10	5	3	1	0	0	1	0	2	0	0
25/04/2002	26/04/2002	2	14	19	14	10	0	0	0	0	1	1	0	0
26/04/2002	27/04/2002	1	12	13	6	7	0	0	0	1	1	1	0	0
27/04/2002	28/04/2002	2	7	7	0	6	0	1	0	0	1	1	0	0
28/04/2002	29/04/2002	2	18	13	11	14	0	0	0	1	2	2	0	1
29/04/2002	30/04/2002	2	29	27	17	23	0	0	0	0	0	0	0	0
30/04/2002	01/05/2002	2	10	3	5	8	0	0	0	0	0	0	0	0
01/05/2002	02/05/2002	2	3	1	0	1	0	0	0	0	3	1	2	1
02/05/2002	03/05/2002	2	0	0	0	0	0	0	1	0	0	1	0	0
03/05/2002	04/05/2002	2	0	1	1	0	0	0	0	0	0	0	0	0
04/05/2002	05/05/2002	2	0	0	0	0	0	0	0	0	0	0	0	0
05/05/2002	06/05/2002	2	1	0	0	0	0	1	0	0	0	0	0	0
06/05/2002	07/05/2002	2	0	1	0	0	0	0	1	0	0	0	0	0
07/05/2002	08/05/2002	2	0	0	0	0	0	0	0	0	0	0	0	0
08/05/2002	09/05/2002	2	0	0	0	0	0	0	0	0	0	0	0	0
09/05/2002	10/05/2002	2	0	1	0	1	0	0	0	0	0	0	0	1
10/05/2002	11/05/2002	2	0	0	0	0	2	1	3	0	0	1	0	1
11/05/2002	12/05/2002	2	3	1	0	1	1	1	1	0	1	1	3	1
12/05/2002	13/05/2002	1	1	0	0	1	1	1	0	0	0	0	0	2
13/05/2002	14/05/2002	2	0	3	1	3	0	3	1	1	1	0	0	0
14/05/2002	15/05/2002	2	17*		9	9	2	1	0	2	5	3	4	1
15/05/2002	16/05/2002	2	11	11	6	9	1	0	1	1	0	2	1	2
16/05/2002	17/05/2002	2	7	3	4	2	2	2	0	1	0	0	1	1
17/05/2002	18/05/2002	2	0	0	0	0	0	0	0	0	0	2	0	1
18/05/2002	19/05/2002	2	0	0	0	0	0	0	0	0	1	0	0	0
19/05/2002	20/05/2002	2	0	0	0	0	0	0	1	0	0	0	0	0
20/05/2002	21/05/2002	2	0	1	2	2	1	0	0	0*	*	*	*	*
21/05/2002	22/05/2002	2	0	0	0	0	0	0	2	0	0	0	0	0
22/05/2002	23/05/2002	2	0	1	0	0	0	0	0	0*	*	*	*	*
23/05/2002	24/05/2002	2	7	4	3	5	1	1	1	3	0	0	0	0
24/05/2002	25/05/2002	2	26	25	31	28	2	3	4	1*	*	*	*	*
25/05/2002	26/05/2002	2	11	9	14	10	2	0	0	1*	*	*	*	*
26/05/2002	27/05/2002	2	3	1	1	1	0	0	0	0	0	0	0	0
27/05/2002	28/05/2002	2	5	3	3	0	0	0	0	3	0	1	0	1
28/05/2002	29/05/2002	1	1	0	2	1	0	1	0	0	0	0	0	0
29/05/2002	30/05/2002	2	4	3	4	1	0	2	1	0*	*	*	*	*
30/05/2002	31/05/2002	2	1	2	1	0	0	0	0	0*	*	*	*	*
31/05/2002	01/06/2002	2	0	0	1	0	0	0	0	1*	*	*	*	*
01/06/2002	02/06/2002	2	0	0	0	0	0	0	1	0*	*	*	*	*
02/06/2002	03/06/2002	2	0	0	0	0	0	0	0	1*	*	*	*	*
03/06/2002	04/06/2002	2	0	0	0	0	0	0	1	0*	*	*	*	*
04/06/2002	05/06/2002	2	0	0	0	0	0	0	0	0*	*	*	*	*
05/06/2002	06/06/2002	2	0	0	0	0	0	1	0	0*	*	*	*	*
06/06/2002	07/06/2002	2	0	0	0	0	0	0	0	0*	*	*	*	*
07/06/2002	08/06/2002	2	1	0	0	0	1	0	0	2*	*	*	*	*

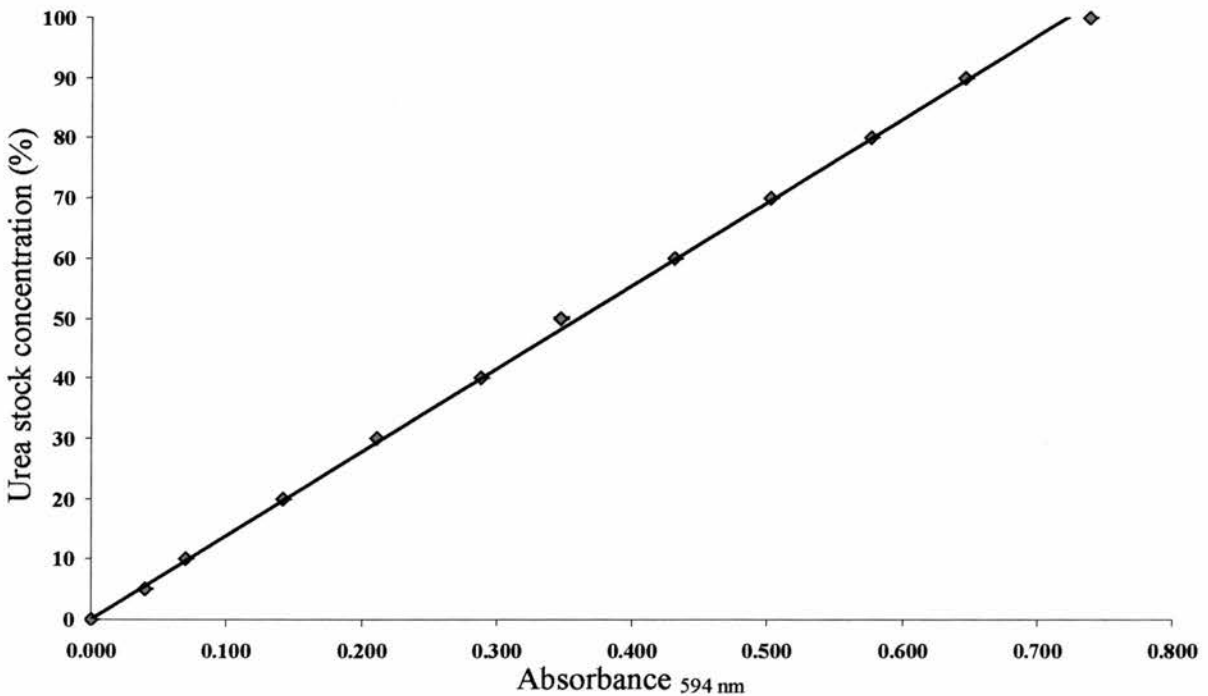
Appendix 10

Standard curves of 1ppt Bromophenol Blue 4M Urea solution, used for extrapolation of percentage retained urea from trap samples after field deployment. Absorbance at 594nm using a seawater blank.

(a) Stock 1 chart, used for field samples from 19/04/02 to 22/05/02 inclusive



(b) Stock 2 chart, used for field samples from 23/05/02 until the end of season



Percentage retention of urea		St Andrews								Fife Ness								Kingsbarns			
Date from	Date to	STA 1	STA 2	STA 3	STA 4	FN1	FN2	FN3	FN4	KB1	KB2	KB3	KB4								
19/04/2002	20/04/2002	69.51696	76.30248	74.91768	77.5488	64.11624	64.25472	66.4704	60.51576	60.2388	60.37728	22.1568	60.37728								
20/04/2002	21/04/2002	81.58472	91.67376	85.71912	86.13456	62.59296	63.42384	66.05496	59.5464	62.03904	64.3932	8.86272	59.26944								
21/04/2002	22/04/2002	85.8576	86.55	85.99608	86.96544	57.74916	63.83928	63.97776	54.4264	59.13096	65.36256	65.63952	63.28536								
22/04/2002	23/04/2002	83.91888	88.90416	88.6272	87.85784	65.50104	66.33192	69.65544	62.73144	67.71672	66.05496	67.57824	66.60888								
23/04/2002	24/04/2002	80.45688	86.41152	86.55	85.44216	71.3172	74.0868	75.4716	68.40912	67.8552	67.30128	65.778	64.11624								
24/04/2002	25/04/2002	80.45688	84.19584	86.96544	87.51936	73.11744	72.702	75.4716	66.4704	70.20936	67.8552	67.02432	65.63952								
25/04/2002	26/04/2002	85.44216	85.44216	78.79512	81.56472	66.88584	68.40912	70.20936	63.42384	69.37848	68.5476	68.27064	66.60888								
26/04/2002	27/04/2002	84.88824	86.82696	86.21176	84.0868	71.04024	74.0868	74.22528	64.94712	68.82456	68.68608	67.1628	64.53168								
27/04/2002	28/04/2002	73.67136	78.10272	78.51816	80.45688	67.1628	69.37848	47.48864	62.03904	68.82456	68.27064	65.63952	62.59296								
28/04/2002	29/04/2002	79.34904	84.61128	75.74856	82.67256	63.7008	65.36256	61.76208	61.76208	56.7768	65.63952	65.50104	63.28536								
29/04/2002	30/04/2002	76.8564	81.42624	74.64072	78.37968	68.82456	71.73264	73.11744	65.22408	63.83928	65.63952	62.45448	63.0084								
30/04/2002	01/05/2002	73.11744	79.48752	75.88704	80.87232	61.20816	63.42384	65.22408	62.316	65.50104	62.316	61.76208	59.26944								
01/05/2002	02/05/2002	74.91768	79.48752	74.0868	78.10272	63.7008	66.4704	66.33192	58.854	63.42384	62.59296	61.20816	59.68488								
02/05/2002	03/05/2002	75.74856	80.3184	72.84048	75.61008	66.88584	69.79392	70.6248	63.14688	63.0084	63.28536	64.53168	61.48512								
03/05/2002	04/05/2002	76.57944	81.14928	81.56472	80.87232	71.8712	72.56352	72.84048	64.25472	63.83928	63.14688	61.06968	59.96184								
04/05/2002	05/05/2002	72.8656	77.82576	78.10272	77.96424	71.8712	70.76328	71.59416	62.86992	61.20816	63.83928	60.9312	58.57704								
05/05/2002	06/05/2002	66.11964	70.48632	64.25472	71.59416	65.91648	63.14688	64.80864	58.1616	55.50408	67.33072	54.83808	54.42264								
06/05/2002	07/05/2002	66.74736	71.59416	65.91648	72.0096	64.11624	63.14688	66.19344	60.2388	58.02312	56.49984	55.94592	52.20696								
07/05/2002	08/05/2002	72.8656	75.61008	68.13216	72.702	66.60888	66.38584	67.43976	60.10032	61.90056	47.91408	59.40792	57.88464								
08/05/2002	09/05/2002	66.74736	70.48632	63.0084	66.60888	62.59296	63.42384	66.4704	60.10032	55.80744	55.11504	56.0844	54.6996								
09/05/2002	10/05/2002	68.82456	72.8656	64.80864	70.48632	63.7008	65.50104	67.71672	61.20816	57.06376	55.66896	55.25352	53.17632								
10/05/2002	11/05/2002	63.97776	67.43976	57.60768	61.90056	58.30008	58.02312	62.59296	58.99248	56.7768	54.83808	57.05376	51.93								
11/05/2002	12/05/2002	74.2528	77.5488	64.94712	72.56352	61.76208	63.14688	66.19344	59.82336	65.63952	67.02432	65.36256	59.40792								
12/05/2002	13/05/2002	84.4728	85.02672	78.51816	85.02672	62.59296	65.63952	65.63952	59.26944	70.34784	64.53168	63.42384	61.76208								
13/05/2002	14/05/2002	73.25592	77.5488	65.91648	74.22528	55.94592	58.30008	59.40792	57.4692	66.05496	63.0084	63.0084	61.6236								
14/05/2002	15/05/2002	77.5488	77.874	75.05616	81.0108	62.59296	63.0084	65.50104	58.57704	73.3944	76.30248	63.0084	60.2388								
15/05/2002	16/05/2002	81.14928	83.64192	78.79512	82.67256	62.86992	62.73144	61.6236	55.11504	64.53168	62.03904	60.79272	60.65424								
16/05/2002	17/05/2002	68.40912	74.91768	65.50104	73.80984	65.36256	66.4704	56.22288	60.79272	62.17752	62.86992	62.73144	61.6236								
17/05/2002	18/05/2002	68.13216	74.7792	65.778	72.702	61.06968	60.37728	65.91648	59.82336	59.82336	59.26944	57.74616	57.05376								
18/05/2002	19/05/2002	67.57824	74.36376	65.36256	73.53288	53.86872	62.316	66.05496	58.02312	74.64072	71.73264	62.17752	74.50224								
19/05/2002	20/05/2002	77.82576	81.7032	77.82576	81.7032	60.9312	63.28536	63.7008	57.74616	63.56232	62.59296	63.56232	59.40792								
20/05/2002	21/05/2002	73.11744	77.13336	67.43976	75.4716	60.51576	62.45448	63.42384	56.49984	*	*	*	*								
21/05/2002	22/05/2002	66.33192	70.20936	60.37728	66.74736	58.854	60.10032	60.65424	55.25352	58.99248	58.1616	57.33072	58.1616								
22/05/2002	23/05/2002	65.63952	65.36256	57.4692	65.0856	55.25352	57.60768	45.83688	55.53048	*	*	*	*								
23/05/2002	24/05/2002	81.28776	81.28776	69.9324	78.65664	56.64152	60.47938	53.46536	57.03854	60.47938	63.12618	61.67044	66.30234								
24/05/2002	25/05/2002	78.0806	74.63976	73.84572	82.0508	56.50918	58.62662	58.75896	56.50918	*	*	*	*								
25/05/2002	26/05/2002	75.69848	78.60996	70.53722	77.28656	58.49428	62.06746	56.9062	60.2147	*	*	*	*								
26/05/2002	27/05/2002	70.93424	74.54712	62.72916	70.40488	58.09726	59.81768	43.6722	54.9211	60.34704	59.02364	60.47938	57.5679								
27/05/2002	28/05/2002	72.1253	74.37508	62.59688	69.61084	56.50918	58.62662	52.40664	57.17088	60.47938	61.80278	59.42066	58.62662								
28/05/2002	29/05/2002	74.1104	76.22784	62.1998	74.24274	57.96492	61.27342	60.2147	58.09726	62.59682	58.8913	64.8466	58.62662								
29/05/2002	30/05/2002	77.4189	81.78612	73.71338	81.25676	61.00874	62.46448	57.30322	58.2296	*	*	*	*								
30/05/2002	31/05/2002	79.404	81.52144	74.1104	79.27166	73.84572	65.64064	64.05256	59.95002	*	*	*	*								
31/05/2002	01/06/2002	84.0359	87.60908	88.40312	88.40312	73.84572	74.7721	73.97806	64.44958	*	*	*	*								
01/06/2002	02/06/2002	80.99208	84.30058	82.97718	84.0359	57.96492	62.33214	62.33214	56.11216	*	*	*	*								
02/06/2002	03/06/2002	82.0508	85.3593	83.3742	86.94738	61.00874	62.46448	59.95002	56.9062	*	*	*	*								
03/06/2002	04/06/2002	69.61084	71.59594	66.30234	72.65466	61.67044	61.67044	62.46448	56.50918	*	*	*	*								
04/06/2002	05/06/2002	67.36106	73.58104	63.25852	71.59594	63.12618	64.05256	53.5977	51.74494	*	*	*	*								
05/06/2002	06/06/2002	61.5381	64.05256	60.61172	65.24362	62.1998	61.93512	59.553	57.83258	*	*	*	*								
06/06/2002	07/06/2002	64.97894	65.24362	57.30322	65.37596	61.40576	63.5232	51.74494	57.70024	*	*	*	*								
07/06/2002	08/06/2002	61.93512	64.44958	56.64152	66.03766	59.68534	62.8615	62.1998	59.02364	*	*	*	*								

blue type indicates substituted values, as described in results

Rank order	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32																												
Rank name	LB JK	LB A	LT JK	LTA	LB T	LB T	LB CL	LT CL	UTA	UT JK	LB CR	LB D	UB A	UB JK	LT CR	UB T	LT D	UT JK	UB CL	UT CL	UB D	UT D	UT CR	UB CR	LT LM	LB LM	UT LM	UT B	LB B	LT B	UB LM	UB B	g	Q	D																									
Rank mean	0.216	0.252	0.295	0.294	0.340	0.363	0.383	0.414	0.426	0.437	0.441	0.465	0.471	0.472	0.480	0.504	0.513	0.528	0.532	0.538	0.575	0.583	0.608	0.613	0.636	0.651	0.672	0.741	0.769	0.777	0.845	0.888																												
Comparisons	0.652																																				32	6.162	0.3574																					
	0.629	0.616																																						31	5.458	0.3166																		
	0.561	0.563	0.613																																							30	5.434	0.3152																
	0.553	0.525	0.590	0.574																																							29	5.408	0.3137															
	0.525	0.517	0.522	0.551	0.528																																							28	5.382	0.3122														
	0.456	0.489	0.514	0.483	0.505	0.505																																							27	5.355	0.3106													
	0.435	0.420	0.488	0.475	0.437	0.482	0.485																																						26	5.327	0.309													
	0.420	0.399	0.417	0.447	0.429	0.414	0.462	0.454																																						25	5.3	0.3074												
	0.397	0.384	0.398	0.378	0.401	0.406	0.394	0.431	0.442																																					24	5.268	0.3054												
	0.392	0.391	0.391	0.357	0.332	0.378	0.386	0.383	0.419	0.431																																					23	5.233	0.3035											
	0.367	0.356	0.358	0.342	0.311																																											22	5.2	0.3016										
	0.358	0.331	0.353	0.319																																													21	5.163	0.2995									
	0.320	0.323	0.328	0.314																																													20	5.126	0.2973									
	0.316		0.320																																															19	5.086	0.295								
	0.310																																																			18	5.044	0.2926						
	0.297																																																					17	4.998	0.2899				
	0.298																																																									16	4.95	0.2871
																																																										15	4.898	0.2841
Standard error is $\sqrt{(1/m+1/nb)/MS \text{ residual}} = 0.058$																																																										14	4.842	0.2808
df = 4604																																																										13	4.781	0.2773
Q level at 0.05																																																										12	4.714	0.2734
																																																										11	4.641	0.2692