The mechanisms of intertidal fish coexistence: a model

Barrett, C.J. a, Johnson, M.L. b, Hull, S.L. b

a (Cefas, Pakefield Road, Lowestoft, Suffolk, U.K., NR33 0HT.

b CEMS, University of Hull, Filey Road, Scarborough, North Yorkshire, U.K., YO11 3AZ

ABSTRACT

Research into the ecology of intertidal fishes of the U.K. appears to be lacking, reportedly due to the mobility and cryptic nature of the more common species. However, some intertidal fishes contribute to the diets of commercially important species such as cod (Gadus morhua), haddock (Melanogrammus aeglefinus) and near-threatened European otter (Lutra lutra). The current study contains the first comprehensive research into the ecology of intertidal fishes from the English, Yorkshire coast and Welsh, Anglesey coast, identifying and addressing the mechanisms which allow for their coexistence. Seven mechanisms were identified which promote interspecific fish coexistence. It was found that coexistence can occur when: (I) fish diversity on a shore is low, thus minimising high degrees of co-occurrence within pools, (II) co-occurrence on shores (at tidal height level) is minimal and when fishes do co-occur, they are of similar sizes thus reducing size-dominated hierarchies, (III) the significant variables which predict fish presences differ, (IV) there is an abundance of shelter/protection readily available, which reduces the competition to access such features, (V) morphology is such, that for the majority of the year, it is more profitable for the piscivorous fishes to predate on food items other than fish, (VI) competition for prey items is reduced, when variability of resources is high, and (VII) there is a difference in the most targeted prey items between fish species, despite some overlap in targeted prey items.
INTRODUCTION

Perhaps due to their mobile and often cryptic nature, research into the ecology of intertidal fish of the U.K. appears to be lacking. However, some studies have found that intertidal fish species such as the common blenny/shanny (*Lipophrys pholis*) and long-spined sea scorpion (*Taurulus bubalis*) contribute to the diets of commercially valuable species, such as cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*), respectively (Pinnegar & Platts, 2011). Additionally, intertidal fishes are important prey items of the near-threatened European otter (*Lutra lutra*). Therefore, baseline information on their ecologies could be of ecological importance.

Between October 2009 and October 2012, the author conducted what could be considered the first comprehensive research into the ecology of intertidal (specifically, rock pool) fish from the English (Yorkshire) and Welsh (Anglesey) coasts, in order to identify the mechanisms which allow for their coexistence. This was achieved through seven topic areas of research: (i) the spatiotemporal distributions and abundances, (ii) the predictors of presence, (iii) the degrees of co-occurrences, (iv) the diets, (v) the conditions, (vi) the ecomorphologies, and (vii) the diel activities, of intertidal fish.

To summarise, it was found that *Lipophrys pholis* and *Taurulus bubalis* are ‘residents’ of all the sampled rocky shore sites, and on the east coast, *L. pholis* appear on-shore before *T. bubalis*. Also, on both a monthly and seasonal scale, *L. pholis* populations persisted on the shores for longer periods of time than other fish species. When *T. bubalis* appear, usually in the lower-shore pools, *L. pholis* tend to extend their spatial range, moving up-shore. *T. bubalis* were rarely found on the upper-shore (which may indicate less resilience to environmental stressors), except for at shores of high fish diversity. This resulted in high degrees of co-occurrence at the Thornwick site, although co-occurrence did not occur between *L. pholis* and *T. bubalis* at the Penhos site, indicating that here, although both species occurred at the same tidal height, they were occupying different pools. This may be because the smaller of the species were competitively excluded from pools of which the two
species initially shared, which may be why factors which predict the presence of these two species were dissimilar. Also, it was found that on the east coast that the presences of all fish were predicted by algal abundance, whereas this was less of an important feature on the west coast.

It was assumed that pools were being used for shelter, rather than for their food availability. In the case of *L. pholis*, at Thornwick Bay, they were found to consume large quantities of the acorn barnacle, *Semibalanus balanoides*, while none were found on the site itself, and so the algae which predicted the presence of the fish, may have been as a means of shelter/protection. However, previous studies (Utne et al., 2003; as described later) have found that primarily, fish will seek food and will only prioritise shelter if a predator is in the vicinity. As the Anglesey fish were not predicted by algal abundance (at least, not to the same degree that the English fish were), this may mean that they were in more favourable (food plentiful) pools, as predation risks were lower. While this was not necessarily demonstrated in the co-occurrence study, predation could also have been in the form of piscivorous fish other than *T. bubalis*, birds or large crab species, which may have been in greater numbers on the east coast, although this is uncertain. It could however, also mean that fish such as *L. pholis* and *T. bubalis* are quite flexible in their choices of habitat.

Additionally, the factors which predicted the presence of *L. pholis* and *T. bubalis* differed between coasts. Where they co-occurred, their total lengths were similar, which would minimise the risk of the piscivorous (as determined by the dietary studies) *T. bubalis* predating on *L. pholis*. Morphology, similar to predictors of fish presence, differed between coasts. This was possibly due to restricted gene flow between populations and local adaptation to different habitats, as also found in Eurasian perch (*Perca fluviatilis*) by Svanbäck & Eklöv (2006). Anglesey specimens of *L. pholis* appeared more efficient at predator detection (more laterodorsally positioned eyes) while the Yorkshire species seemed more efficient escaping a predator (larger pectoral fin sizes, for speed and manoeuvrability) and perhaps swimming in exposed conditions and for ‘anchoring’ in wave surges. If these assumptions are true, the Anglesey specimens may have the more optimal avoidance mechanism, as
their conditions were found to be ‘good’ throughout the year, while Yorkshire specimen condition lowered significantly during the winter. It may be that generating high speeds to escape predators are energetically taxing (hence the lower condition), while, like the Anglesey specimens, detecting a predator well in advance may not require the need for fast swimming (hence no change in their condition).

It was found that morphology helped to promote coexistence between the more common species. At shores where numbers of, and degrees of co-occurrence with, *T. bubalis* were high, their potential prey, *L. pholis* had developed deeper bodies and larger heads, which may create too long a handling time for a gape-limited predator such as *T. bubalis* to consider them energetically profitable. However, some small specimens of *L. pholis* were found to be prey items of *T. bubalis*, albeit in very small frequencies. This may have been as a result of high numbers of *L. pholis* recruits, which would be easy prey for larger specimens of *T. bubalis*. In general however, *L. pholis* and *T. bubalis* were found to have very broad diets (more so of *L. pholis*, though). While some prey item overlap did exist (the extent of which was small) *T. bubalis* and the rock goby (*Gobius paganellus*) shared a prey preference of the shore crab, *Carcinus maenas*. Found to be a specialist, this may be one reason why *G. paganellus* was in relatively low numbers when *T. bubalis* also occurred on the same shore, and in larger numbers, when *T. bubalis* did not.

Lastly, the diel activity research revealed that *L. pholis* did not differ in numbers or sizes between day and night samples. This may indicate that it was the same specimens being recorded throughout the sample period, which hints that (at least during the time of study), *L. pholis* did not migrate very far, if at all. As no predators (such as *T. bubalis*) were detected during this investigation, their lack of movement may suggest that specimens were in their ‘ideal’ surroundings and that food availability may have been plentiful (the primary preference of a fish, according to Utne et al., 2003) and should a predator have been present, shelter/protection opportunities may also have been sufficient.
MECHANISMS OF COEXISTENCE

Armstrong & McGehee, (1980) dictate (following a mathematical model by Volterra (1928) and Gause’s (1934) ‘Competitive Exclusion Principle’) that two species which use the same resources cannot permanently coexist (Hardin, 2005). This implies that interspecific competition cannot allow permanent coexistence. However, Hardin (2005) goes on to state that in stable conditions, “Complete competitors cannot coexist,” and does not state whether these competitors are, as Volterra (1928)/Gause (1934) suggested, of different species, or whether the competitors are/could be from the same species. The implication is that intraspecific (as well as interspecific) competition cannot allow permanent coexistence.

The studies directly recognised seven mechanisms of interspecific coexistence, which is promoted when one or more of the following is/are met:

1) Fish diversity on a shore is low, thus minimising high degrees of co-occurrence within pools. This compliments the findings of Wilson (1990), who considers niche diversification as a mechanism of coexistence, where species either inhabit different niches within a habitat, to demote co-occurrence, or utilise the niche at different times, which would also demote co-occurrence. The latter was proven true by Ranta et al., (1981) who found that Scandinavian flora of the same community had significantly different flowering times, which promoted coexistence, lowering competition for pollinators.

2) Co-occurrence on shores (at tidal height level) is minimal, and when fishes do co-occur, they are of similar sizes, thus reducing size-dominated hierarchies. Therefore, size variation
may promote coexistence if the different sized fishes target different prey taxa. This needs
to be further tested. Levin (1974) suggested that if species grow at a similar rate,
coexistence can be promoted, presumably because size dominance would not occur. This
was named ‘initial patch composition’ by Wilson (1990) and Wilson (2011), although it is
only theory based and has not been applied to actual species before.

3) The significant variables which predict fish presences differ. Where mechanism (2) is not
maintained, i.e. fishes are of different sizes, a size-dominance hierarchy often occurs
(Costello, 1992 and Wiederholm, 1987), but coexistence may still be maintained if the
smaller species shift to different microhabitats. Costello (1992) observed that the painted
goby (Pomatoschistus pictus), a small species, were found in open water, whilst the red-
mouthed goby (Gobius cruentatus), were found in areas of greater protection (holes, under
rocks). Widerholm (1987) made similar observations; the black goby, the largest of three
observed gobioids (Gobius niger) occupied well vegetated habitats, while the smallest
species, the common goby (Pomatoschistus microps) occupied open water and the middle
sized gobiod, the sand goby (Pomatoschistus minutus) occurred between the two habitat
types. As the variables which predict fish presence does not necessarily mean habitat
‘preference,’ such variables may change, depending on factors such as availability of shelter,
presence of predators, prey availability and presence of competitors. This may be why the
variables which predicted the presence of species such as L. pholis and T. bubalis on the east
shore were different to those variables which predicted the presence of the same species on
the west shore.

4) There is an abundance of shelter/protection readily available, which reduces the
competition to access such features. This supports the ‘pool load capability’ hypothesis of
Monteiro et al., (2005). This hypothesis assumes that a pool contains only a limited amount of shelter/protection, to a limited size and number of fish. Monteiro et al., (2005) believed that where these limits are not reached, intraspecific coexistence of L. pholis is promoted, as is interspecific coexistence of L. pholis and Coryphoblennius galerita, Montagu’s blenny. If these limitations are exceeded, in a pool which is low of, or lacks such characteristics, these fishes would then be more prone to predation or may become competitively excluded.

5) Morphology is such that for the majority of the year (excluding breeding times, when recruits will be targeted), it is more profitable for the piscivorous fishes (such as Taurulus bubalis) to predate on food items other than fish. This finding was very similar to the study of Webster et al., (2011) who found that in areas of high predator presence, the three-spined stickleback (Gasterosteus aculeatus) had deeper bodies, which would increase their handling time and also their time to escape, should they be targeted as prey. In the morphology study, L. pholis were found to have deeper bodies and larger heads where T. bubalis numbers were high (and also possibly other predators such as large crab species and sea birds, although this was not confirmed). Here, it would be less energy taxing for T. bubalis to consume a larger number of smaller, less mobile prey items, than a smaller number of larger, mobile prey items.

6) Competition for prey items is reduced, when variability of resources is high, as resources were found to be high on all shores. Coexistence may further be strengthened if the fish species consume different sizes of the same prey species, if a size range is available. Such a mechanism has also been found to promote the coexistence of two sympatric bat species, Rhinolophus affinis and Rhinolophus pearsoni (Jiang et al., 2008). Here, as prey resources were high and varied, Jiang et al., (2008) found that the coexistence of these Chinese bats were promoted, as interspecific competition was greatly reduced. Similarly, Scognamillo et
2003) found that an abundance of medium-sized prey items also allowed the jaguar
(Panthera onca) and puma (Puma concolor) to coexist, in Venezuela.

7) There is a difference in the most targeted prey items between fish species, despite some
overlap in targeted prey items. When Zaret & Rand (1971) looked at the diet of nine,
sympatric, Panama stream fishes, overlap was found to be reduced in the dry season by
fishes shifting to different microhabitats, reportedly due to increased competition, meaning
fishes had to target different prey items. However, the taxonomic resolution of prey items
applied in their (Zaret & Rand, 1971) study may be one reason why their study appeared to
(perhaps erroneously) validate competitive exclusion. The prey items within the fish
specimens were recorded at a relatively low taxonomic resolution (to order level), which
would provide a less accurate representation of dietary preference than species-level data,
as recorded where possible in the current study. For example, in the current study, Lipophrys
pholis and T. bubalis were found to consume Littorina littorea, Littorina obtusata and
Littorina saxatilis at Filey, during summer. However, L.pholis also consumed high frequencies
of Littorina neglecta, while T. bubalis did not consume any. A lower taxonomic resolution
(even to genus level) would therefore have shown a higher degree of dietary overlap
between the two fishes than the more accurate, higher (species level) taxonomic resolution.
Had Zaret & Rand (1971) conducted their dietary studies at such a resolution as the current
study, perhaps their findings may have differed.
OBSERVATIONS

Other mechanisms may also have been inadvertently recognised from findings of the research chapters. For example, species diversity and degrees of co-occurrence were noticeably less between the monthly sampling in 2010 and seasonal sampling in 2011, at Thornwick Bay. This may be evidence of the ‘intermediate timescale-disturbance’ coexistence mechanism, as described by Wilson (1990 & 2011), as it is likely that disturbances such as anthropogenic and environmental stresses occurred ‘intermediately’ between these years. At Abberfraw for example, weather may have influenced fish diversity, as at this shore in the winter of 2009, pools were frequently ice-covered, which was again observed at the Penrhos shore, in the winter of 2012. This was not observed, during the current study, for shores on the Yorkshire coast during winter sampling, which may be due to the more saline conditions on this coast (Dooley, 1974) than the west coast. Crisp (1964) described similar adverse conditions around Anglesey, during the winter of 1962-1963, calling it ‘severe.’ This implies that such conditions may not occur frequently (every year), but such conditions (Bayliss, 1958 and Wardle & Allen, 1983) may mean that fish diversity becomes high again, if the ‘intermediate-timescale disturbance’ concept is true here. This however, would need to be determined during further work.

When trapping the fish during the diel activity study, it was observed that L. pholis surrounded the bait at a set distance. It was then the larger specimens who sampled the bait first and the smaller specimens, last. It was observed that if a smaller specimen tried to sample the bait first, the larger specimens showed aggression, trying to attack them. This may imply that intraspecific coexistence is maintained via a size-related hierarchy, but was not possible to directly test during the field work.

If these observations are found to be valid, during further studies, in conjunction with the seven mechanisms of coexistence mentioned earlier, the model in Fig 1 may provide an example of how intertidal fishes are able to coexist. The model (Fig 1) includes ‘disturbance’ as a factor which will
alter the coexistence or exclusion of fishes, whether the disturbance be anthropogenic or
environmental. If disturbance(s) is/are ‘intermediate,’ coexistence should be promoted, as fish
numbers will be reduced and therefore, so will the levels of competition (Wilson, 1990 and Wilson,
2011). Disturbances are inevitable on a rocky shore, although their severities and periods may vary
greatly. It would be particularly difficult to determine whether a disturbance can be classified as
‘intermediate’ and because of this complication, if disturbance(s) is/are identified following such
studies as those conducted in this thesis, the research should be carried out again, as mechanisms
which allowed for coexistence of fishes before may no longer apply, or may have changed.
Fig 1: A conceptual model of the ways in which coexistence can be achieved for intertidal fish. Green lines indicate environmental factors. Assuming the ‘intermediate-timescale disturbance’ concept is valid, broken lines denote that coexistence (or competitive exclusion) is never permanent, as when disturbance occurs, the mechanisms which allow for coexistence may change. However, if disturbance is intermediate, coexistence can be promoted if numbers of competitors are reduced, but if the level of disturbance is too great, all fish may be removed from the shore. Where ‘NO,’ competition is increased. (Model created by author).
THE COSTS OF COEXISTENCE (TRADE-OFFS)

It has been documented (Kneitel & Chase, 2004; Chase & Leibold, 2003; Turnbull et al., 1999 and Levine & Rees, 2002) that in order for maintained coexistence, trade-offs must occur, and of the mechanisms identified in the current study, trade-offs have surely featured in maintaining such synchronicity.

If it is not due to intermediate disturbance, the mechanism of a low degree of species co-occurrence may be due to a trade-off between interspecific competition and availability of resources and/or shelter, similar to the findings of Utne et al., (1993) and Wiederholm (1987). Utne et al., (1993) describe a trade-off between food availability and predation risk in the two-spotted gobies (Gobiusculus flavescens), whereby (ex-situ) specimens tended to favour shelter availability over food availability in the presence of a predator (a cod, Gadus morhua). Before the presence of this predator, G. flavescens preferred locations where food availability was high, regardless of the level of shelter in these areas.

As previously mentioned, in-situ, on the Swedish coast, Wiederholm (1987) found a trade-off between predation risk and competition for prey and shelter, with the largest species being in the prime location and the smallest being in the least desirable location. This meant that P. microps (the smallest species) had prey and refuge less readily available, but was able to avoid competition with the larger fishes. Accepting the thesis research, if the same applies, it may mean that the factors which predicted fish presence did not necessarily reflect their ‘preferred’ habitat type, as the variables identified may have been as a compensation, to avoid competition or predation. For example, in Wiederholm’s (1987) study, P. microps was found in a micro-habitat of mud, with no vegetation present (used for shelter and prey availability). This however, was not the preferred habitat type of this species, but instead, was exhibiting a trade-off, as its existence in the lesser
preferred habitat type meant a much lower (perhaps even non-existent) degree of competition with the larger gobioid species.

The morphological mechanism of coexistence, as found in the thesis, appears similar to the threespine stickleback (*Gasterosteus aculeatus*) study of Webster *et al.* (2011). They found that where coexistence was occurring between the sticklebacks and piscivorous, gape-limited fish, the sticklebacks had developed deeper bodies, to reduce the likelihood of being eaten. If attack *did* occur, such morphology would also allow a higher chance of escape, as their handling time would be increased. However, a trade-off occurred (likely to also be the case in the current study) between morphology and energy loss, as the deeper body meant that predation was decreased, but hydrodynamic drag and associated energy expenditure increased. A deeper body may also mean that availability of hiding places is reduced. It could be expected that a similar trade-off would exist for the *L. pholis* in the thesis research. Where their bodies were deeper and heads were larger, in the presence of high numbers of potential predators, they would surely be subjected to the same increased drag and energy expenditure as the sticklebacks.

Similar to Velasco *et al.* (2009), diet was also found to be a mechanism of interspecific coexistence, although they (Velasco *et al.*, 2009) did report any considered trade-offs which allow for this mechanism. This finding *could* have been due to a difference in feeding-related morphology between species, although it was found in the current study that *Lipophrys pholis* and *Taurulus bubalis* were generalists and *could* eat the same prey items. If both then targeted the more easily accessible, less energetically taxing and more profitable (in terms of energy gain) prey items, competitive exclusion would eventually occur. However, this does not seem to be the case. Instead, a trade-off may be occurring between competition and prey selection. In the presence of other species with similar dietary preference, fish are targeting a wide range of abundant prey items (with a wide range being exhibited in the diet research), rather than a small range of more accessible,
profitable prey, thus reducing competition, but requiring greater energy expenditure to get the same energy gains.

REFERENCES


23.


