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Saltmarsh as habitat for fish and nektonic crustaceans: Challenges in sampling designs and methods

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Abstract This is a review of research into the ecological role of saltmarsh as habitat used directly by fish and nektonic crustaceans such as shrimp (prawns) and portunid crabs. The quality of information about direct use of saltmarshes by nekton is poor, with even the most influential works suffering from obvious limitations. Attempts to generalize about nekton use of saltmarshes are hampered by sampling difficulties, poor sampling design, and inconsistent reporting of flooding regime and landscape structure. The difficulty in sampling nekton from shallow, vegetated marsh flats while inundated contributes to the fragmentary results of nekton work. A range of sampling methods have been described that vary in portability, size, amount of above-ground structure, escape rates of nekton, and expense; none has yet become standard. Poor experimental design in studies of saltmarsh nekton includes lack of replication, limited spatial scale, and lack of baseline data before management changes are made. Attempts to determine effects on commercial fisheries of losses in area or quality of saltmarsh by correlations between catch data and marsh loss should use active adaptive management. A second type of study, aimed at understanding how the saltmarsh is important to fisheries, can be tackled usefully at a smaller scale. To assist in the comparison of results from different studies, flooding regime should be reported as a proportion of time the marsh is submerged, and landscape structure as proportions of the marsh that are covered by intertidal flats, pools and drainage creeks. Flooding regime and landscape structure at the sites and at the time of sampling should then be put in the context of the typical pattern for the marsh under study.

Key words: coastal wetland, fisheries, *Fundulus*, hydroperiod, *Spartina alterniflora.*

INTRODUCTION

Saltmarsh is one of the highest intertidal habitats in estuaries, often forming the buffer between land and sea. Depending on the amount of freshwater input and the extent to which marshes are inundated by seawater at high tide, saltmarshes range in salinity from brackish to hypersaline. Vegetation consists of grasses, herbs or low shrubs. Unvegetated pans of varying size often form part of the marsh. Saltmarshes are widespread on all inhabited continents. Despite early accounts of saltmarsh being predominantly distributed on temperate coasts (e.g. Chapman 1974), they also cover large tracts in tropical waters. In Australia, for example, 76% of all saltmarsh (including unvegetated pans) occurs in the tropical northern states of Queensland and Northern Territory (Bucher & Saenger 1994). Moreover, the area under saltmarsh is greater in those states than the area of mangrove forest (Bucher & Saenger 1994). Vascular plant species richness is, however, considerably higher away from the tropics (Adam 1990). In the temperate waters of North America, Europe (with major exceptions, see Dame & Allen 1996) and parts of South Africa, saltmarshes extend from the very top of the intertidal zone down to mean water level. In the warmer waters of North America, South Africa, Australia and Asia, mangroves dominate the mid-intertidal zone and saltmarshes are mostly restricted to the very highest part of the intertidal zone (Adam 1990). At some sites in South America, and in Australia where *Spartina* has been introduced, *Spartina* grows seaward of the mangrove forest (Adam 1990).

Saltmarsh areas have been reduced dramatically over the last century as human activities and coastal developments have reclaimed the habitat. Saltmarshes have aesthetic and educational values, evocatively described by Bertness (1992) in his account of a saltmarsh in New England, USA. Ecological work, however, aims to investigate the conservation value of saltmarsh mainly on the basis of its importance to one or more of five factors: (i) filtering of freshwater surface overflow; (ii) stabilization of substrate; (iii) biodiversity; (iv) export of energy and nutrients that sustain production elsewhere in the estuary; and (v) direct use by fauna. The first, second and third of these are not covered here, the fourth is mentioned briefly, and the fifth is the main topic of this review.

In this paper I review the ecological role of saltmarsh as habitat used directly by fish and nektonic crustaceans such as shrimps (prawns) and portunid crabs. Other invertebrate groups and birds also occur on

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saltmarshes but these are not mentioned further here. After first examining the geographical spread of nekton studies, I briefly outline general patterns of use of saltmarshes by nektonic fauna. The literature, however, is fragmentary and has competing claims about marsh use. This is partly because researchers of saltmarsh nekton face challenges that I group under three headings: sampling difficulties, sampling design, and reporting of flooding regime and landscape structure. Solutions to these challenges are then discussed.

Geographic spread of research

The wide distribution of saltmarshes around the world is not matched by the geographical spread of scientific studies. To demonstrate the extent of literature from different regions, I searched for any studies of fish or nektonic crustaceans related to saltmarsh habitat, using electronic databases covering the 19-year period from 1978 to the end of 1996 (Aquatic Sciences & Fisheries Abstracts 1978–Sept 1996; Current Contents 1996). Each of these articles was also examined for mention of other studies of nekton on saltmarshes. Only articles containing original field or laboratory data about nekton and published in refereed journals were included. Papers reporting studies in creeks alongside marshes were included where the authors used results to demonstrate aspects of saltmarsh ecology. Works based solely in freshwater marshes backing saltmarshes were excluded, as were review papers. The location of work in each article was recorded. In the case of laboratory studies the location in the field from which samples were taken was the location recorded. One hundred and thirteen articles were found using the above criteria (Table 1). The literature is overwhelmingly from North America (90%). Saltmarshes occur all along the coasts of North America but are especially extensive along the Atlantic and Gulf coast of USA. Most papers were from these regions (85%), with a large proportion of studies having been done in just a few states (Georgia, Louisiana, North Carolina, Virginia). Eleven percent of all papers report work from just one location, Sapelo Island in Georgia. Seven percent of papers reported work in Florida saltmarshes, and half of these were on marshes that were in close proximity to mangroves. There were surprisingly few papers from Europe (7%), given the large number of botanical studies published from there (Adam 1990). Only 3% of papers were from southern hemisphere marshes, all of these being from Australia. Although the estuarine ichthyofauna of South Africa is well studied, no references to works on the direct use of saltmarsh by nekton were found. Links are, however, beginning to be made between estuarine fish and saltmarsh in South Africa using stable isotope studies (Paterson & Whitfield 1997). It is perhaps not surprising that reviews such as those by Vernberg (1993) and Mitsch & Gosselink (1993) of saltmarsh work mention only studies done in the USA, without stating any intended geographical limit to their review.

Table 1. Geographic location of published studies of saltmarsh nekton

Location	No.	% of total
Georgia	14	12
Louisiana	13	12
North Carolina	12	11
Virginia	12	11
Texas	8	7
New Jersey	8	7
Florida	8	7
South Carolina	7	6
Other USA states	15	13
Total USA	97	86
Canada	5	4
Total North America	102	90
Europe	8	7
Australia	3	3
Total	113	100

DIRECT USE OF SALTMARSHES BY FISH AND CRUSTACEANS: GENERAL PATTERNS

Saltmarsh researchers have aimed to determine what nektonic animals use saltmarshes and when they use them. A generalization from studies of nekton is that fish and crustaceans using the marsh flat are mainly resident on or near the saltmarsh for their entire life cycle, while fish congregating around the edge of the saltmarsh are juveniles of species that spawn elsewhere in the estuary or in oceanic waters (Peterson & Turner 1994).

A more detailed classification by Peterson and Turner (1994) places nekton species into four distributional categories.

(1) On the marsh flat at all times [remaining in pools at low tide—in North America, dominated by Cyprinodontiformes such as killifish (*Fundulus*)].

(2) On the marsh flat at high tide, but retreating to subtidal fringing vegetation at low tide [killifish again, and also minnows (*Cyprinodon*), grass shrimp (*Palaemonetes*) and portunid crabs (*Callinectes*)].

(3) Onto the marsh edge at high tide, but penetrating only a few metres onto the flat, and into subtidal creeks at low tide [this type comprises mainly juveniles of commercially important species such as mullet (*Mugil cephalus*) and penaeid shrimps/prawns]

(4) Remaining subtidal, not really entering saltmarsh at all, but being in close proximity in creeks [e.g.

juvenile Atlantic menhaden (*Brevoortia tyrannus*), a major commercial fish species in USA].

A number of studies have recorded the movement of fish onto the marsh on the tidal front. The phenomenon of killifish (*Fundulus heteroclitus*) moving in over the marsh on the leading edge of the tidal front has been described by Rozas (1995) in southeastern USA. In subtropical Australian saltmarshes toadfish (Tetraodontidae) push in on this tidal front, going as far as 500 m onto the marsh (B. E. Thomas & R. M. Connolly unpubl. data). Kneib & Wagner (1994) found that larger fish, while waiting longer to move onto the marsh after flooding, then moved further onto the flat than smaller fish and retreated earlier, perhaps because of a greater risk of stranding. This does not follow from the estuary-based model that has shallow water as offering protection to small fish from larger predators (Ruiz *et al.* 1993), and predicts that small fish would go further onto saltmarsh where water is shallower.

There is a small body of evidence which points to the importance of vegetation in structuring fish assemblages on the marsh flat, although there have been far fewer surveys comparing vegetated and unvegetated patches than in other habitats (e.g. seagrass, Bell & Pollard 1989). It has been shown that different species predominate where vegetation is lacking. In Texas, for example, brown shrimp (*Penaeus aztecus*) and grass shrimp (*Palaemonetes pugio*) are more common in patches of *Spartina alterniflora* whereas white shrimp (*Penaeus setiferus*) are equally abundant in *S. alterniflora* and unvegetated patches, while still other nektonic species are more common in unvegetated patches (Zimmerman & Minello 1984; Minello & Zimmerman 1985; variations on this pattern in Louisiana by Rozas & Reed 1993). Research into how the size of an unvegetated patch or distance from vegetation affects nekton has not been done. In many places, including tropical northern Australia where large areas of saltmarsh are unvegetated, there are no records of sampling of nekton.

There is a paucity of experimental evidence that vegetation is involved in structuring nekton assemblages, directly or indirectly. The work showing most clearly that small fish have better foraging opportunities and a better chance of escaping predators in vegetated habitat has actually been done in freshwater marshes backing saltmarsh in Louisiana (Rozas & Odum 1988), although the main fish species are the same, including *Fundulus heteroclitus*, so results might be applicable to saltmarsh. The influence of vegetation on predation rates by saltmarsh fish on brown shrimp has also been demonstrated in the laboratory (Minello & Zimmerman 1983).

As the conservation value of saltmarshes becomes clearer, marshes are less likely to be reclaimed. Even where marshes are preserved, however, human impacts can affect the vegetation of the marsh. In tropical and subtropical Australia, for example, the vegetation of many saltmarshes is likely to be affected by grazing cattle and the alteration of drainage regimes to reduce abundances of insect pests (Connolly & Bass 1996). Further survey and experimental work is urgently needed to determine any effects that changes in vegetation type, height, or density might have on nekton.

Few generalizations can be made about the effects of predation on saltmarsh fish populations, and studies in this area have often failed to account for the natural behaviour of predators (Kneib 1995). Kneib's (1995) description of attempts to examine xanthid crab predation on *Fundulus heteroclitus* provides a lesson in ensuring experimental evidence relates to natural patterns. Despite young killifish being trapped at low tide in tiny pools (as small as a few centimetres in diameter) around xanthid crab burrows, and laboratory experiments showing that these crabs do eat young fish, the fish were rarely found in crab gut contents in the wild. This is explicable once it is known that the crabs feed only once the marsh is inundated, by which time the fish have dispersed from pools.

HOW CONVINCING ARE THE FINDINGS?

While being able to make the general statements above, the literature is actually highly fragmented, and full of competing claims and varied descriptions of nekton use of saltmarshes. Why is it difficult to generalize?

Sampling difficulties

Most nekton work has been done in creeks supplying and draining the flats, or in pools remaining on the flats at low tide. Many of the questions scientists want to answer require work on the saltmarsh flat that is inundated at high tide but emergent at low tide; this is the habitat that comprises the main area of most saltmarshes. It is not easy to sample the inundated flat, and no standard method has yet been adopted.

Usual methods for collecting estuarine fish such as trawling are impracticable on marsh flats because waters are too shallow for boat access. This has led to the development of a variety of devices for sampling nekton on marsh flats, as follows (with examples of studies using them): block nets (Hettler 1989) and flume nets (Peterson & Turner 1994) on saltmarsh edge; flume weir (Kneib 1991); lift net (Rozas 1992); pop net (Connolly *et al.* 1997); drop samplers (water pumped out, Zimmerman & Minello 1984; Rakocinski *et al.* 1992); traps (Smith & Able 1994); dip net (Morton *et al.* 1988; in glass pans set in mud to mimic tiny pools, Kneib 1984); and hand trawl (Gibbs 1986). The flume weir, flume nets, lift net, block net, and pop net use the ebb tide to help collect fish out of vegetation.

Poisoning has also been used to collect fish from pools on the marsh (Gibbs 1986). The methods offer a range in portability, size, amount of above-ground structure, escape rates of nekton, and expense (Rozas & Minello 1997).

Boat transportation of sampling equipment on marsh flats is also restricted by the shallowness of the water, and this increases the relative attractiveness of sampling in marsh creeks. Another attraction of working in tidal creeks draining marsh flats is that fish are concentrated into a small volume of water and are more easily caught, using a fyke net for example. When sampling in creeks in lieu of sampling on the marsh flat, it is necessary, for most questions, to adjust abundances for the area of marsh flat drained by a creek. The area of flat is the important variable for benthic-feeding animals such as portunid crabs, but for animals such as zooplanktivorous fish that use the entire water column, estimates of the volume over the marsh flat are probably more appropriate (Varnell & Havens 1995). In the absence of behavioural or ecological knowledge, assumptions must be made that the size of a saltmarsh makes no difference to the way that fish use the flat (Varnell & Havens 1995), and that in general fish use is homogeneous.

A test of how well samples from creeks might represent nekton on marsh flats is provided by Connolly *et al.* (1997), who make a quantitative comparison of fish densities on marsh flats with those in creeks draining the same flats in an Australian estuary. Pop nets were used to sample fish from the flats at high tide, and fyke nets to sample fish in creeks draining the same flats. The number of fish per pop net was small (about 1 fish/10 m^2), and initial discussions centred on the possibility that the pop nets might not be working, perhaps because of gear avoidance by fish. Yet when the average marsh-flat density was multiplied to account for the total area of marsh drained, more fish would have been expected to be caught in creeks than were actually caught (Connolly *et al.* 1997). Either fyke nets in creeks were not working and/or fish use of the flats was not homogeneous. A weakness of the study was that all pop nets were placed near creeks, where higher abundances might be expected than further from creeks.

The comparison by Connolly *et al.* (1997) of fish densities on a marsh flat with those in draining creeks was done on a marsh that had the creeks as the only entry/exit avenue for fish, even on the highest of tides. Many marsh areas have more than one possible entry/exit avenue for fish, including directly over the saltmarsh bank to and from the open water. The actual entry/exit points are usually not known (Rozas 1995), and it is not adequate to assume that sampling in creeks will represent assemblages on the marsh flat. Indeed, sampling in creeks alone cannot demonstrate whether fish visit adjacent marsh flats at all. It is therefore necessary in answering many questions to sample from the submerged flats themselves.

Poor sampling design

If the design of surveys describing patterns of fish use is poor, our confidence that results are repeatable is reduced. In the following section I highlight aspects of saltmarsh sampling design that need improving, using as examples key papers in nekton use of saltmarsh as habitat. All of the papers cited below contain useful information and insights into how fish use marshes.

The most instructive work to date bearing upon the question of how far different size classes of nekton move onto saltmarsh flats is by Kneib & Wagner (1994), using Kneib's (1991) flume weir to sample nekton. This sampling method is the largest yet used on inundated saltmarsh flats (100 m^2) and has been shown to catch a high proportion of most nekton species in the enclosed marsh area (Kneib 1991). The flume weir is a semipermanent structure, however, that is not easily transported from site to site. This led Kneib and Wagner to build one flume weir at a single site in the low marsh (25 m from a creek) and a single site in the high marsh (90 m from creek) on Sapelo Island, Georgia. Although each flume weir was sampled several times over two months, the design was spatially unreplicated, and made impossible any estimation of how catches would vary among sites within either the low or high marsh. Although this is the best work to date comparing assemblages from low and high marsh, it cannot be stated with any confidence that differences between the sites were representative of differences between strata.

Another issue reducing confidence in the general applicability of results from nekton studies is the limited spatial scale over which surveys are done, even where replicate samples are taken. For example, the well conceived study by Peterson and Turner (1994) demonstrating which fish move out of creeks onto saltmarsh flats was restricted to a straight stretch of creek bank 175 m long. McIvor and Odum (1988) found that fish assemblages (and *Fundulus heteroclitus* abundances) near flat, depositional stretches of creek bank differed from those near steep, eroding banks. The nature of the 175 m stretch in the survey by Peterson and Turner might therefore have a large bearing on their results, and until the same survey (including same netting type and mesh size) is repeated elsewhere, we cannot be confident of the wider applicability of their results.

Other surveys are overly restricted temporally. Nekton abundance on marshes can vary markedly from day to day (Varnell *et al.* 1995) and, where marshes or marsh creeks are inundated twice daily, between night and day [e.g. Rountree & Able (1993), who demonstrated that nekton abundances differed in saltmarsh creeks from night to day, and that the differences changed with season, and Kneib & Wagner (1994), who found differences between night and day catches on marsh flats regardless of tidal state].

The designs of surveys comparing nekton from altered (impounded or Open Marsh Water Management, which uses altered drainage regimes to increase flushing to reduce insect densities) and unaltered saltmarshes are especially poor, even though management manipulations of marshes are done on a relatively large scale. The weaknesses in design are acknowledged by authors in some cases. Comparisons suffer from having little or no spatial replication (e.g. Herke 1995; Harrington & Harrington 1982; Hoese & Konikoff 1995; on nekton generally; Fitz & Wiegert 1991 on blue crabs) or a lack of baseline ('before') data (e.g. Talbot & Able 1984).

Studies that attempt to determine the importance of saltmarsh to fisheries production (which might involve direct use of the marsh by juveniles of commercial species and/or a contribution from marshes to food resources for fish in other places) also suffer from problematic designs. The relationship between fisheries and saltmarsh has been examined by correlating fisheries catches with reductions in saltmarsh area in estuaries used by the fish species (Boesch & Turner 1984). This correlative evidence is confounded by other changes in estuaries, including changes to the quality and quantity of other potential habitats, and by changes to fishing effort. It is well known, for example, that some oceanic fisheries with no obvious link to nearshore habitats have declined because of overfishing (Houde & Rutherford 1993). The challenge is to demonstrate that loss or degradation of saltmarsh actually affects fisheries production. A case is made by Herke (1995) for the importance of Louisiana saltmarshes to commercial and recreational fish stocks derived from juveniles using the saltmarsh. It is worth noting, however, that Herke's (1995) logic is convincing because his effective definition of saltmarsh includes the open water surrounding the marsh. The dependence of the fishery on marsh habitat can therefore be argued on the basis of absence of alternative habitats for juveniles of the key commercial species. The Louisiana marshes are submerging as a result of human activities, and areas are becoming unvegetated as they sink lower in the intertidal. The proportion of open water to marsh flat is increasing. The consequences of losing vegetated marsh habitat without a reduction in total estuarine area are not clear.

Reporting of flooding regimes and landscape structure

The importance of different flooding regimes ['hydroperiods' in Rozas's (1995) terminology)] has already been mentioned with respect to sampling difficulties. The lack of consistency in reporting flooding regimes also acts as an impediment to the transfer of results of nekton research from study to study. There are marked differences in hydroperiod between coastal regions. Hydroperiods in marshes of the Atlantic coast of USA, for example, are predominantly influenced by astronomical tides, whereas those of marshes on the Gulf Coast of USA are characterized by only slight regular tidal influence and are strongly influenced by meteorological/atmospheric events (Rozas 1995). But even marshes within the same region differ in important ways, such as the capacity of creeks to supply and drain water, and height in the intertidal zone. The importance of recording and reporting the flooding regime of marshes has been explained by Rozas (1995). The flooding regime presumably affects the likelihood that fish enter a marsh, the distance fish move onto a marsh, the period over which fish remain on a marsh, and the frequency with which fish are able to enter the marsh (Kneib 1997).

Variable flooding regimes are also an important consideration, I believe, when considering the conflicting claims made about energy and nutrient transfer between saltmarshes and elsewhere in estuaries. Differences in height of the marsh in the intertidal zone result not only in different levels of production but also in different levels of export (Taylor & Allanson 1995). Even on the same marsh during a single tidal period there are marked fluctuations caused by wind and waves. More turbulent water results in increasing export of particulate nitrogen and phosphorus, but not of dissolved nitrogen and phosphorus (Childers *et al.* 1993). The type of tidal time–velocity asymmetry is also likely to be important. Marshes in eastern USA have a tide characterized by faster flow rates near the ebb point, both on flooding and ebbing tides (ebb-dominated). These marshes tend to export energy and sediment (Dame & Allen 1996). Conversely, European marshes are characterized by faster flows near the high tide (flood-dominated), and tend to import carbon and sediment (Dame & Allen 1996). Energy and nutrient exchange is also influenced by other factors such as the position of the marsh within an estuary, its age (stage of evolution), and plant species composition (Adam 1990). Kneib (1997) describes how energy and nutrient transfer in living biota through 'trophic relay' has been largely overlooked. Energy and nutrients in small, resident nekton on intertidal marsh flats might be transferred to deeper parts of an estuary or offshore waters by a series of predator–prey interactions (Kneib 1997).

The most important influences on nekton use of saltmarshes other than flooding regime are geomorphic features, or landscape structure (Kneib 1997). The reporting of such figures as the proportions of marsh covered by intertidal flats and semipermanent pools is rare. Where authors refer to drainage density it is often reported as being of low or high density, without definition of those categories. The inconsistency in reporting of landscape structure impedes comparison of results of marsh nekton studies within regions and especially across regions.

SOLUTIONS

Sampling difficulties

Saltmarsh studies are common enough that it should be possible to look for general patterns of nekton use. Any difference in results between locations is usually confounded by the use of different techniques, net sizes or mesh sizes. Where these can be standardized with those used by previous workers, the degree of confounding is minimized, and the quality of the information coming from the study is maximized. Where creeks are to be sampled as an indication of nekton use of marshes, an attempt to demonstrate how representative the creek catch is of the marsh flat fauna is worthwhile.

It is preferable to use sampling methods that are easily transported on the marsh flat, as these encourage properly replicated survey designs. Lift nets (Rozas 1992) and pop nets (Connolly 1994) fall into this class, but these have mostly been small in area. The work of Kushlan (1981) showing how the size of sampling devices affects sampling reliability is useful, but needs to be expanded to include larger nets. Techniques such as flume weirs (Kneib 1991) and flume nets (Peterson & Turner 1994) are able to sample larger areas, and for these methods the task is to make them more portable. Kneib (1997) has argued that assemblages of fish on the saltmarsh are mobile, and that sampling devices do not therefore need to be moved. The aim of sampling is to obtain a representative sample of the assemblage over the area of interest, and this is usually best done by randomly selecting sampling locations. Non-random sampling will only suffice in a limited number of situations where enough is already known about patterns of fish use that we can be sure that more limited sampling is representative. Even in these situations, however, replicate samples are still required. Moving sampling devices between sampling times can also help to avoid the problem encountered by Loftus & Eklund (1994) of long-term effects of permanent devices on habitat, which in turn affect fish abundances.

Poor sampling design

Sampling designs in saltmarsh studies have been and will continue to be hampered by the difficulty in sampling. Notwithstanding this difficulty, improved designs will greatly increase our confidence in results. The value of fundamental features such as replication and interspersion of treatments (Hurlbert 1984; Andrew & Mapstone 1987) and statistical power analysis to determine sample sizes necessary to demonstrate important ecological events (Peterman 1990; Fairweather 1991) is as great in saltmarsh work as in other marine ecological studies.

Survey results are most convincing where the pattern that they describe is found repeatedly and in more than one location. Every effort should be made to increase the spatial scale of surveys (an example is the 25 km long transects through Louisiana saltmarshes used by Baltz *et al.* (1993) for sampling fish at marsh edges). Where increasing the scale is not feasible because of resource limitations, the benefits of other workers repeating surveys in other locations but using the same methods is clear. Small-scale manipulative experiments examining the links between nekton and saltmarsh can be very informative. The sites of manipulation, while themselves being small, should nevertheless be spread over an area large enough to confirm that results can be generalized to the area or type of marsh being represented.

Opportunistic monitoring of biological variables after management changes such as the alteration of drainage regimes is really a type of impact assessment. There is a large literature on this topic, and best practice has moved a long way in recent years (Schmitt & Osenberg 1996). The need for replication is not diminished in these types of 'experiments'. Where an activity having a potential impact is not replicated, multiple control locations can still be used, and analyzed using asymmetric statistical models (Underwood 1993). The importance of collecting data prior to management changes is also well established (Green 1979).

Large-scale experiments can usually only be done as part of management plans having the power to control other activities in estuaries. This is known as adaptive management (Walters 1993). The most efficient experimentation for demonstrating any link between saltmarsh loss and reduced fisheries production is active adaptive management (Walters 1993). Under this scenario, changes to saltmarshes (increase or reduction in area or quality of saltmarsh) would be made in some estuaries or, more likely, in parts of estuaries, to actively seek the relationship between saltmarsh and fisheries production. For this to be successful there needs to be a will, for the duration of the experiment, not to vary other factors likely to confound results (e.g. changes to other aspects of estuaries such as major drainage patterns, or to fishing effort).

An alternative method of tackling the question of importance of saltmarsh to fisheries production is to demonstrate for a particular species of fish the necessary use of saltmarsh habitat or products (e.g.

Table 2. An example of information that should be routinely included in reporting results of studies of saltmarsh nekton, from a study of marsh nekton in subtropical Queensland, Australia by Thomas and Connolly (unpubl. data)

	Flooding regime (proportion of time submerged)	Landscape structure
Marsh-general	Average = 0.01, ranging from a high of 0.03 in summer and winter months to zero in spring and autumn.	Intertidal = 0.98 (vegetated = 0.79, unvegetated = 0.19). Pools absent Channels/creeks = 0.02
Study-specific	Winter (July 1997) 0.03 Summer (February 1998) 0.02	Sites spread over vegetated and unvegetated intertidal flats, at varying distances from channels/creeks.

Proportion of time submerged for the marsh in general is calculated as the total time inundated over a year, averaged over two years. Landscape structure is reported as a proportion of total marsh surface area, calculated from aerial photographs.

detritus). Analysis of one or more naturally occurring stable isotopes has been employed to separate the importance of different sources of primary production to invertebrate and fish production (Haines 1976; Fry & Sherr 1984; Peterson *et al.* 1986; Kwak & Zedler 1997). While the method has been shown to accurately portray food webs in some cases, even the use of multiple elements cannot resolve the relative importance of food sources having the same isotope signatures (e.g. edaphic and planktonic microalgae). The experimental addition of artificially enriched isotopic material has recently been used to manipulate isotopic signatures of primary producers and resolve such ambiguous situations in freshwater systems (Hall 1995) and aquaculture settings (Preston *et al.* 1996). Artificially enriched isotopic material has not yet been used to assist the tracing of food sources in saltmarshes, but offers an exciting possibility. Once enrichment has been used to separate isotope signatures, animals need to remain in the area until their signatures reflect that of their food source. This could easily be achieved in semi-permanent pools on the marsh or in subtidal creeks, but will need innovation to put into practice on the intertidal marsh flats themselves. A more direct approach to demonstrating the importance of saltmarsh habitat to fish production has been taken by Weisberg and Lotrich (1982). They demonstrated experimentally that the calorific requirements of a *Fundulus heteroclitus* population could be met only if most individuals fed upon the marsh flat, where they had better foraging opportunities. Smaller-scale experiments such as this can provide an understanding of how saltmarshes might be important to fisheries.

Manipulative experiments are also needed to differentiate between the effects on nekton assemblages of vegetation type (including unvegetated habitat) *vs* those of hydroperiod, which is often closely associated with vegetation type. Field experiments such as those done in freshwater marshes (Rozas & Odum 1988) attempting to tease apart the importance of vegetation in terms of providing food or protection from predators would be very useful in saltmarshes.

Reporting of flooding regimes and landscape structure

Comparisons among results of studies into nekton use of saltmarshes will be made more useful if reporting of flooding regimes and landscape structure is more consistent, because it will allow researchers to better understand the context of the sampling. Flooding regime can most easily be reported as a proportion of time that marsh sites are submerged. This incorporates several tidal factors such as amplitude and frequency of tides as well as height of the marsh within the intertidal zone. Kneib's (1997) graph of submergence time as monthly averages is highly informative, but would use too much space to be acceptable within every paper. I recommend that the average for the year should be stated, along with comments about any seasonality. Where meteorological influences on tides are pronounced, and inundation is unpredictable seasonally, this should be mentioned.

Landscape structure could most efficiently be reported as the proportion of marsh area under the categories listed as being salient to marsh nekton by Kneib (1997), viz. intertidal flats (vegetated or unvegetated) and embedded features—pools and creeks/channels.

Both the average proportion of time submerged and landscape structure should be reported for the marsh as a whole, before going on to describe submergence times and landscape features of the particular sites sampled, during the period sampled. It is especially important to describe any unusual events that differed from the long-run averages in flooding period already described. An example of how to report flooding regime and landscape structure is given in Table 2 for a recent study by B. E. Thomas and R. M. Connolly (unpubl. data) in Australia. Reporting would not normally be expected to be in table format.

CONCLUSIONS

Some of the challenges facing ecologists studying saltmarsh nekton are the same as those for ecologists generally. It is not only in saltmarsh work, for example, that the lack of standardization of sampling techniques across studies with similar aims limits our ability to generalize. Likewise, the call made here to adopt sound principles of sampling design in saltmarsh studies, even when monitoring the effects of relatively large-scale management changes, has been made for ecology more generally (Green 1979; Hurlbert 1984; Andrew & Mapstone 1987; Hurlbert & White 1993). The need for experimentation through management (active adaptive management) has also been explained for other marine systems (Walters 1993).

Other challenges faced by saltmarsh workers are engendered by the nature of the habitat. Sampling difficulties are particularly acute because of the difficulty in traversing marsh flats either by boat or terrestrial vehicle, and the difficulty in using nets to sample nekton in the shallow, vegetated habitat. Fortunately the ebb tide can be used to assist in the retrieval of nekton from nets, and the main challenge now is to design sampling devices large enough to avoid small-scale patchiness, but with a degree of portability, to encourage spatially replicated experimental designs.

The use of saltmarsh by nekton seems likely to be strongly affected by the flooding regime and landscape features of the marsh under study. Reporting of these should be standardized to assist in comparisons amongst results of different studies. Characteristics of the marsh in general as well as for the specific sampling sites and times used in the study should be reported.

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REFERENCES

Adam P. (1990) *Saltmarsh Ecology*. Cambridge University Press, Cambridge.

Andrew N. L. & Mapstone B. D. (1987) Sampling and the description of spatial pattern in marine ecology. *Oceanogr. Mar. Biol. Ann. Rev.* **25,** 39–90.

Baltz D. M., Rakocinski C. & Fleeger J. W. (1993) Microhabitat use by marsh-edge fishes in a Louisiana estuary. *Environ. Biol. Fish.* **36,** 109–26.

Bell J. D. & Pollard D. A. (1989) Ecology of fish assemblages and fisheries associated with seagrasses. In: *Biology of Seagrasses* (eds A. W. D. Larkum, A. J. McComb & S. A. Shepherd), pp. 565–609. Elsevier, Amsterdam.

Bertness M. D. (1992) The ecology of a New England salt marsh. *Am. Scientist* **80,** 261–8.

Boesch D. E. & Turner R. E. (1984) Dependence of fishery species on saltmarsh: the role of food and refuge. *Estuaries* **7,** 460–8.

Bucher D. & Saenger P. (1994) A classification of tropical and subtropical Australian estuaries. *Aquat. Conserv. Mar. Freshwat. Ecosyst.* **4,** 1–19.

Chapman V. J. (1974*) Salt Marshes and Salt Deserts of the World*. Verlag von Cramer, Germany.

Childers D. L., Cofer-Shabica S. & Nakashima L. (1993) Spatial and temporal variability in marsh–water column interactions in a southeastern USA salt marsh estuary. *Mar. Ecol. Prog. Ser.* **95,** 25–38.

Connolly R. M. (1994) Comparison of fish catches from a buoyant pop net and a beach seine net in a shallow seagrass habitat. *Mar. Ecol. Prog. Ser.* **109,** 305–9.

Connolly R. M. & Bass D. A. (1996) Do fish actually use saltmarsh flats? Ecology and management of Australian saltmarshes. In: *Proceedings of the Australian Coastal Management Conference, Glenelg, South Australia, April* 1996 (ed. N. Harvey), pp. 273–76. University of Adelaide, Adelaide.

Connolly R. M., Dalton A. & Bass D. A. (1997) Fish use of an inundated saltmarsh flat in a temperate Australian estuary. *Aust. J. Ecol.* **22,** 222–6.

Dame R. F. & Allen D. M. (1996) Between estuaries and the sea. *J. Exp. Mar. Biol. Ecol.* **200,** 169–85.

Fairweather P. G. (1991) Statistical power and design requirements for environmental monitoring. *Aust. J. Mar. Freshwat. Res.* **42,** 555–67.

Fitz H. C. & Wiegert R. G. (1991) Utilization of the intertidal zone of a salt marsh by the blue crab *Callinectes sapidus*: density, return frequency, and feeding habits. *Mar. Ecol. Prog. Ser.* **76,** 249–60.

Fry B. & Sherr E. B. (1984) $\delta^{13}C$ measurements as indicators of carbon flow in marine and freshwater ecosystems. *Contrib. Mar. Sci.* **27,** 15–47.

Gibbs P. J. (1986) The fauna and fishery of Wallis Lake. In: *Wallis Lake: Present and Future* (eds), pp. 1–7. Australian Marine Science Association, Sydney.

Green R. H. (1979) *Sampling Design and Statistical Methods for Environmental Biologists*. Wiley, New York.

Haines E. B. (1976) Stable carbon isotope ratios in the biota, soils and tidal water of a Georgia salt marsh. *Estuar. Cstl Mar. Sci.* **4,** 609–16.

Hall R. O. (1995). Use of a stable carbon isotope additions to trace bacteria carbon through a stream food web. *J. Nth Am. Benthol. Soc.* **14,** 269–77.

Harrington R. W. & Harrington E. S. (1982) Effects on fishes and their forage organisms of impounding a Florida salt marsh to prevent breeding by salt marsh mosquitoes. *Bull. Mar. Sci.* **32,** 523–31.

Herke W. H. (1995) Natural fisheries, marsh management, and mariculture: complexity and conflict in Louisiana. *Estuaries* **18,** 10–7.

Hettler W. F. (1989) Nekton use of regularly-flooded saltmarsh cordgrass habitat in North Carolina, USA. *Mar. Ecol. Prog. Ser.* **56,** 111–8.

Hoese H. D. & Konikoff M. (1995) Effects of marsh management on fisheries organisms: the compensatory adjustment hypothesis. *Estuaries* **18,** 180–97.

Houde E. D. & Rutherford E. S. (1993) Recent trends in estuarine fisheries: Predictions of fish production and yield. *Estuaries* **16,** 161–76.

Hurlbert S. H. (1984) Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* **54,** 187–211.

Hurlbert S. H. & White M. D. (1993) Experiments with freshwater invertebrate zooplanktivores: quality of statistical analyses. *Bull. Mar. Sci.* **53,** 128–53.

Kneib R. T. (1984) Patterns in the utilization of the intertidal salt marsh by larvae and juveniles of *Fundulus heteroclitus* (Linnaeus) and *Fundulus luciae* (Baird). *J. Exp. Mar. Biol. Ecol.* **83,** 41–51.

Kneib R. T. (1991) Flume weir for quantitative collection of nekton from vegetated intertidal habitats. *Mar. Ecol. Prog. Ser.* **75,** 29–38.

Kneib R. T. (1995) Behaviour separates potential and realized effects of decapod crustaceans in salt marsh communities. *J. Exp. Mar. Biol. Ecol.* **193,** 239–56.

Kneib R. T. (1997) The role of tidal marshes in the ecology of estuarine nekton. *Oceanog. Mar. Biol. Ann. Rev.* **35,** 163–220.

Kneib R. T. & Wagner S. L. (1994) Nekton use of vegetated marsh habitats at different stages of tidal inundation. *Mar. Ecol. Prog. Ser.* **106,** 227–38.

Kushlan J. A. (1981) Sampling characteristics of enclosure fish traps. *Trans. Am. Fish. Soc.* **110,** 557–62.

Kwak T. J. & Zedler J. B. (1997) Food web analysis of southern California coastal wetlands using multiple stable isotopes. *Oecologia* **110,** 262–77.

Loftus W. F. & Eklund A. (1994) Long-term dynamics of an Everglades small-fish assemblage. In: *Everglades: the ecosystem and its restoration* (eds S. M. Davis & J. C. Ogden), pp. 461–83. St Lucie Press, Delray Beach, Florida, CA.

McIvor C. C. & Odum W. E. (1988) Food, predation risk, and microhabitat selection in a marsh fish assemblage. *Ecology* **69,** 1341–51.

Minello T. J. & Zimmerman R. J. (1983) Fish predation on juvenile brown shrimp, *Penaeus aztecus* Ives: the effect of simulated *Spartina* structure on predation rates. *J. Exp. Mar. Biol. Ecol.* **72,** 211–31.

Minello T. J. & Zimmerman R. J. (1985) Differential selection for vegetative structure between juvenile brown shrimp (*Penaeus aztecus*) and white shrimp (*P. setiferus*), and implications in predator-prey relationships. *Estuar. Cstl Shelf Sci.* **20,** 707–16.

Mitsch W. J. & Gosselink J. G. (1993) *Wetlands*. Van Nostrand Reinhold, New York.

Morton R. M., Beumer J. P. & Pollock B. R. (1988) Fishes of a subtropical Australian saltmarsh and their predation upon mosquitoes. *Environ. Biol. Fish.* **21,** 185–94.

Paterson A. W. & Whitfield A. K. (1997) A stable carbon isotope study of the food-web in a freshwater-deprived South African estuary, with particular emphasis on the ichthyofauna. *Estuar. Cstl Shelf Sci.* **45,** 705–15.

Peterman R. M. (1990) Statistical power analysis can improve fisheries research and management. *Can. J. Fish. Aquat. Sci.* **47,** 2–15.

Peterson B. J., Howarth R. W. & Garritt R. H. (1986) Sulfur and carbon isotopes as tracers of salt-marsh organic matter flow. *Ecology* **67,** 865–74.

Peterson G. W. & Turner R. E. (1994) The value of salt marsh edge *vs* interior as a habitat for fish and decapod crustaceans in a Louisiana tidal marsh. *Estuaries* **17,** 235–62.

Preston N. P., Smith D. M., Kellaway D. & Bunn S. E. (1996) The use of enriched ^{15}N as an indicator of the assimilation of individual protein sources from compound diets for juvenile *Penaeus monodon. Aquaculture* **147,** 249–59.

Rakocinski C. F., Baltz D. M. & Fleeger J. W. (1992) Correspondence between environmental gradients and the community structure of marsh-edge fishes in a Louisiana estuary. *Mar. Ecol. Prog. Ser.* **80,** 135–48.

Rountree R. A. & Able K. W. (1993) Diel variation in decapod crustacean and fish assemblages in New Jersey polyhaline marsh creeks. *Estuar. Coast. Shelf Sci.* **37,** 181–201.

Rozas L. P. (1992) Bottomless lift net for quantitatively sampling nekton on intertidal marshes. *Mar. Ecol. Prog. Ser.* **89,** 287–92.

Rozas L. P. (1995) Hydroperiod and its influence on nekton use of the salt marsh: a pulsing ecosystem. *Estuaries* **18,** 579–90.

Rozas L. P. & Minello T. J. (1997) Estimating densities of small fishes and decapod crustaceans in shallow estuarine habitats: a review of sampling design with focus on gear selection. *Estuaries* **20,** 199–213.

Rozas L. P. & Odum W. E. (1988) Occupation of submerged aquatic vegetation by fishes: testing the role of food and refuge. *Oecologia* **77,** 101–6.

Rozas L. P. & Reed D. J. (1993) Nekton use of marsh-surface habitats in Louisiana (USA) deltaic salt marshes undergoing submergence. *Mar. Ecol. Prog. Ser.* **96,** 147–57.

Ruiz G. M., Hines A. H. & Posey M. H. (1993) Shallow water as a refuge habitat for fish and crustaceans in nonvegetated estuaries—an example from Chesapeake Bay. *Mar. Ecol. Prog. Ser.* **99,** 1–16.

Schmitt R. J. & Osenberg C. W. (1996) *Detecting Ecological Impacts: Concepts and Applications in Coastal Habitats.* Academic Press, San Diego.

Smith K. J. & Able K. W. (1994) Salt-marsh tide pools as winter refuges for the mummichog, *Fundulus heteroclitus*, in New Jersey. *Estuaries* **17,** 226–34.

Talbot C. W. & Able K. W. (1984) Composition and distribution of larval fishes in New Jersey high marshes. *Estuaries* **7,** 434–43.

Taylor D. I. & Allanson B. R. (1995) Organic carbon fluxes between a high marsh and estuary, and the inapplicability of the Outwelling Hypothesis. *Mar. Ecol. Prog. Ser.* **120,** 263–70.

Underwood A. J. (1993) The mechanics of spatially replicated sampling programmes to detect environmental impacts in a variable world. *Aust. J. Ecol.* **18,** 99–116.

Varnell L. M. & Havens K. J. (1995) A comparison of dimension-adjusted catch data methods for assessment of fish and crab abundance in intertidal salt marshes. *Estuaries* **18,** 319–25.

Varnell L. M., Havens K. J. & Hershner C. (1995) Daily variability in abundance and population characteristics of tidal salt-marsh fauna. *Estuaries* **18,** 326–34.

Vernberg F. J. (1993) Salt-marsh processes—a review. *Environ. Toxicol. Chem.* **12,** 2167–95.

Walters C. J. (1993) Dynamic models and large scale field experiments in environmental impact assessment and management. *Aust. J. Ecol.* **18,** 53–61.

Weisberg S. B. & Lotrich V. A. (1982) The importance of an infrequently flooded intertidal marsh surface as an energy source for the mummichog *Fundulus heteroclitus*: an experimental approach. *Mar. Biol.* **66,** 307–10.

Zimmerman R. J. & Minello T. J. (1984) Densities of *Penaeus aztecus, Penaeus setiferus*, and other natant macrofauna in a Texas salt marsh. *Estuaries* **7,** 421–33.