Fate of fish production in a seasonally flooded saltmarsh

Philip W. Stevens[1,2,3,*], Clay L. Montague[1], Kenneth J. Sulak[2]

[1]Department of Environmental Engineering Sciences, University of Florida, PO Box 116450, Gainesville, Florida 32611-6450, USA

[2]Center for Aquatic Resource Studies, US Geological Survey, 7920 NW 71 St, Gainesville, Florida 32653, USA

[3]*Present address:* Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, 1481 Market Circle, Port Charlotte, Florida 33953, USA

ABSTRACT: Although saltmarshes are thought to enhance the productivity of open estuarine waters, the mechanism by which energy transfer occurs has been debated for decades. One possible mechanism is the transfer of saltmarsh production to estuarine waters by vagile fishes and invertebrates. Monthly estimates of fish standing stock, net fish ingress, and predation were used to develop a biomass budget to estimate annual production of fishes and the relative yield to predatory fish, birds, and direct migration to the estuary. Annual production of saltmarsh fishes was estimated to be 31.0 g m^{-2} saltmarsh, which falls within the range of previously reported values for estuarine fish communities. The relative yields were 12 to 20 % to piscivorous fishes, 8 to 13 % to piscivorous birds, and 18 to 29 % to export. Annual export of fish biomass was 5.6 g fish m^{-2} saltmarsh, representing about 1 to 2 % of saltmarsh primary production. Saltmarsh fishes convert marsh production to high-quality vagile biomass (fishes concentrate energy, protein, and nutrients as body mass) and move this readily useable production to the estuary, providing an efficient link between saltmarshes and estuarine predators.

KEY WORDS: Saltmarsh impoundment · Outwelling hypothesis · Trophic relay · Wading birds

INTRODUCTION

Saltmarshes are among the most productive ecosystems in the world (Day et al. 1989, Montague & Wiegert 1990, Mitsch & Gosselink 1993, Montague & Odum 1997), and, although they are thought to enhance the productivity of open estuarine waters, the mechanism by which energy transfer occurs has been debated for decades (Haines 1979, Nixon 1980, Dame 1994). Historically, saltmarshes were thought to contribute to estuarine productivity by exporting large quantities of detritus, which then formed the base of the estuarine food web (Teal 1962, Odum & de la Cruz 1967, Wiegert et al. 1975). However, detrital and dissolved organic export from saltmarshes is variable among locations and is often only a minor contribution to estuarine productivity (Heinle & Flemer 1976, Marinucci 1982, Borey et al. 1983, Montague et al. 1987,

Dame et al. 1991, Williams et al. 1992, Taylor & Allanson 1995). Saltmarshes were also thought to supply nutrients to estuarine waters, thereby enhancing estuarine primary production (i.e. phytoplankton production). However, the majority of nutrients contained within saltmarsh plant tissues are recycled within the marsh and little is directly exchanged with the estuary relative to demand in estuarine waters (Haines et al. 1977, Valiela & Teal 1979, Nixon 1980, Hopkinson & Schubauer 1984).

Marsh sediments and their associated microbial communities can be sources or sinks for nutrients depending on the nutrient supply from other sources such as river discharge, upland runoff, and sewage effluent (Haines et al. 1977, Kaplan et al. 1979, Valiela & Teal 1979). For example, marshes with high input of nitrogen (the limiting nutrient in many estuaries) are likely to be sites of net denitrification, whereas

marshes with low input of nitrogen are likely to be sites of net nitrogen fixation (Haines et al. 1977, Kaplan et al. 1979, Valiela & Teal 1979, Montague et al. 1987). Although the historical paradigm of saltmarshes supplying detritus and nutrients directly to open estuarine waters remains equivocal, an alternative paradigm has been emerging that emphasizes the role of saltmarshes in providing food and refuge to young estuarine nekton and the role of nekton in transferring saltmarsh production to estuarine waters (Haines 1979, Haines & Montague 1979, Montague et al. 1981, 1987, Werme 1981, Boesch & Turner 1984, Knieb 1997).

Kneib (1997) described the movement of energy across the marsh landscape to the estuary via predator–prey relationships as 'the trophic relay' and developed a detailed conceptual model of these interactions. Resident nekton (those species that complete their life history within marshes) convert saltmarsh production into vagile biomass, which then may move across the marsh landscape as smaller residents are consumed by larger residents. The larger residents are more likely to move to subtidal creeks or seagrass beds during low water to escape desiccation or thermal stress on the marsh surface, which makes them susceptible to predation by young transient nekton (those species that use marshes periodically for food and refuge). The latter may move to deeper estuarine waters as they mature, or may be eaten by larger adult transients that occasionally foray into marsh creeks seeking prey. Non-predatory transient nekton (e.g. herrings, silversides, and mullets) also convert marsh foods into vagile biomass when present in the marsh as juveniles. They may be consumed by larger predatory transients during their residence within the marsh, or eventually emigrate to the open estuary as they reach maturity, moving the incorporated marsh resources with them.

The migrations involved in the 'trophic relay' occur at different spatial and temporal scales (Kneib 1997). For example, daily intertidal migrations occur as resident nekton move between marsh surface and creek habitats, or transient nekton move in and out of marsh creeks. In addition, seasonal migrations occur as larval and early juvenile stages move into marshes and later emigrate to the open estuary, and, in some cases, the open ocean. The interspecific interactions between resident marsh fishes and transient predators that occur within the marsh may be important mechanisms for moving the marsh resources that have been incorporated into resident nekton to the adjacent estuary.

Despite the potential importance of nekton in energy transfer from the marsh to the estuary, few studies have estimated saltmarsh nekton production (Welsh 1975, Valiela et al. 1977, Meredith & Lotrich 1979, Schooley 1980, Weinstein 1983) or emigration (Herke et al. 1992, Deegan 1993), and none have measured these components simultaneously. The boundaries of saltmarsh systems are open and ill defined, and the conduits of transport (i.e. creeks) are broad and complex. Thus, estimating the boundaries within which production has occurred and measuring the exchange of nekton between saltmarshes and the estuary create difficult challenges with respect to sampling.

In east-central Florida, saltmarsh impoundments that have been reconnected to the estuary by culverts provide unique research opportunities that enable the estimation of both saltmarsh fish production and exchange rates of nekton with the estuary (for a history of impoundment construction, management strategies, and recent reconnection efforts see Brockmeyer et al. 1997). The boundaries between saltmarshes and the estuary are clearly defined by a system of dikes, thereby confining nekton into a known area, and the exchange of aquatic organisms is restricted to culverts. Open culverts allow sampling of nekton as they move between saltmarshes and the adjacent estuary. Where culverts are left open year-round, these nekton movements are driven by a strong seasonal component reflective of the hydrology of the northern Indian River Lagoon (Stevens et al. 2006). Thus, marsh to estuary fish movements occur on the order of months, not hours as in tidal marshes, and may therefore be easier to track over the course of a year. Although impoundments differ morphologically from natural systems, understanding the function of reconnected impoundments should provide a general model of saltmarsh ecology and linkages to the adjacent estuary by movement of aquatic organisms.

The artificial boundaries, creeks, and connections to the estuary, together with the seasonal hydrology associated with reconnected saltmarsh impoundments in the northern Indian River Lagoon, permit a biomass budget of saltmarsh fishes to be constructed (Fig. 1). Outputs from the standing stock of fish within the impoundment are the result of emigration and predation/death. Inputs to the standing stock of fish within the impoundment are the result of immigration and production. Monthly estimates of standing stock, immigration, emigration, and predation can be used to estimate annual production of fishes in the saltmarsh (Fig. 1). This estimate of saltmarsh fish production can be compared to estimates from other locations and other estuarine habitats, such as seagrass beds and open estuarine waters. More importantly, the yield to predatory fish, birds, and emigration can be quantified. The objective of the present study was to estimate the annual production of fishes in a seasonally flooded saltmarsh in the Indian River Lagoon, Florida (i.e. reconnected impoundment) and to quantify the relative yield to predatory fish, birds, and direct migration to the estuary.
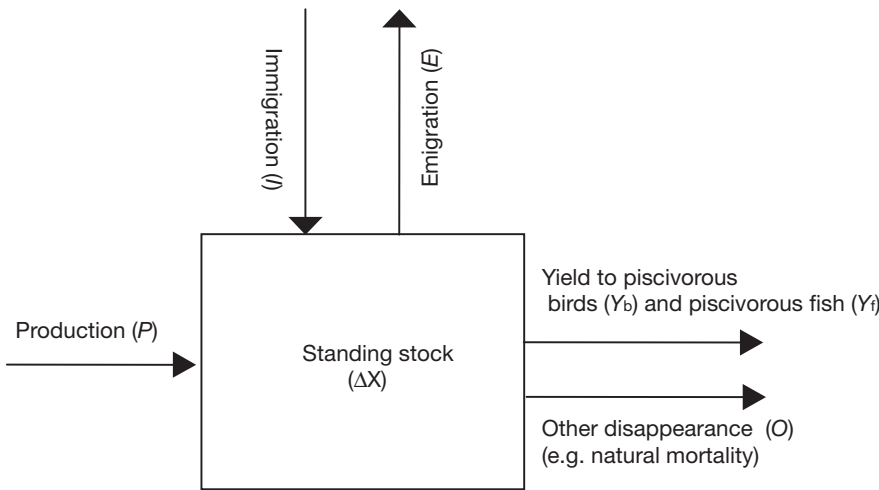
Fig. 1. Nekton biomass budget in a saltmarsh impoundment. Let net fish ingress $(M) = I - E$, and $P = \Delta X/\Delta\text{time} + Y_b + Y_f + O - M$

MATERIALS AND METHODS

Fish production estimates from Ricker's equations. Numerous studies have estimated fish production from equations based on Ricker (1946) as modified by Allen (1950) (a list of such studies is given in Day et al. 1989 and Chapman 1978). The only data needed for these equations are changes (usually monthly) in fish standing stock (number and biomass). The basic equations are: $P = G \times B$, where $G = (\ln w_2 - \ln w_1)/\Delta t$ is the instantaneous coefficient of growth; $B = B_1(e^{G-Z} - 1)/(G - Z)$ is the average biomass; $Z = -(\ln N_1 - \ln N_2)/\Delta t$ is the instantaneous coefficient of population change attributable to mortality and migration; w_1 and w_2 are the mean weights of individuals at time t_1 and t_2, respectively; and N_1 and N_2 are the number of fish present at time t_1 and t_2, respectively.

The model assumes that correction for immigration and emigration of fishes is not needed provided that fish density and size-class-specific growth are estimated often enough to assess abundance and growth of fishes in the sampling area during each sampling period (Chapman 1978). Monthly fish densities from Stevens et al. (2006) were used as basis data to estimate fish production in a reconnected saltmarsh impoundment (dominated by *Distichlis spicata* and *Paspalum vaginatum*) in Banana Creek, east-central Florida (Table 1). Detailed descriptions of the study site and sampling methods can be found in Stevens et al.

(2006), and are summarized in the following subsection. Monthly impoundment fish densities were substituted into the above equations to estimate annual fish production. This fish production estimate can be compared to that developed in a biomass budget (see following subsection) in the same study impoundment, and to other studies that used Ricker's method.

Fish production estimate from biomass budget. The fish production estimate derived from Ricker's equations lumps population changes due to migration and mortality into a single variable (Z). The unique research opportunities provided by impoundments (dikes confine fishes into a known area and exchange of fishes are restricted to culverts), however, have made it possible to estimate rates of immigration, emigration, and potential consumption by piscivorous birds and fishes. These estimates, together with a production estimate, allow the relative yield to fishes, birds, and migration to be quantified.

A biomass budget (Fig. 1) was developed from field data collected in a reconnected saltmarsh impoundment in Banana Creek (Stevens et al. 2006). Fish standing stock, fish immigration, fish emigration, and piscivore abundance (large fish and birds) were measured monthly for 1 yr beginning July 2000 and ending July 2001. For detailed descriptions of the study site (Impoundment C20C) and sampling methods see Stevens et

Table 1. Estimates of monthly fish standing stock (July 2000 to July 2001), net fish ingress, and piscivorous fish abundance within Impoundment C20C. Data are from Stevens et al. (2006). Fish standing stock was measured by cast net, net fish ingress was measured by culvert traps, and piscivorous fish abundance was measured by gill nets

| | Standing stock | | | | Ingress | Abundance |
| | Creek | Ditch | Creek | Ditch | (g fish per | (g piscivorous fish |
	(no. of fish m^{-2})		(g fish m^{-2})		culvert h^{-1})	per 10 m net h^{-1})
Jul	0.1	0.2	0.6	2.2	15.6	1173
Aug	0.5	1.5	3.4	3.5	−3.1	1204
Sep	0.0	0.2	0.0	0.2	0.3	9552
Oct	0.1	0.2	0.5	2.7	−8.1	2121
Nov	0.3	0.5	0.1	1.8	0.0	1278
Dec	3.8	23.0	5.6	16.9	−6.0	3166
Jan	12.6	57.8	11.6	38.5	−25.3	2262
Feb	11.4	9.1	16.0	16.2	−11.5	736
Mar	1.3	6.3	2.0	6.5	−6.3	1367
Apr	5.4	3.7	9.2	6.6	−3.2	6962
May	18.2	1.3	20.0	2.6	−0.8	635
Jun	2.7	3.0	8.4	9.6	−13.2	14225
Jul	19.4	2.5	32.8	6.7		

al. (2006). In summary, fish density (comprising mostly resident saltmarsh fishes such as *Cyprinodon variegatus* and *Poecilia latipinna*) was measured by cast net, both in a marsh creek and in a ditch (borrow ditch for impoundment dikes) that surrounds the perimeter of the marsh. Fourteen sites for cast-net deployment were randomly selected, in both the impoundment ditch and the creek for each monthly sampling. Immigration and emigration through impoundment culverts was measured for 4 days and 4 nights consecutively with culvert traps. A culvert trap was placed at each of 4 culvert locations connecting the impoundment to the estuary. Each culvert location consists of 1 flapgated culvert and 1 with slots for riserboards. Thus, 1 culvert was fished with a culvert trap and 1 remained unfished at each location. Piscivorous fish abundance (e.g. *Lepisosteus platyrhincus*, *Sciaenops ocellatus*, *Elops saurus*, and *Cynoscion nebulosus*) was determined with gill nets placed in the impoundment creek and ditch and deployed for 2 to 3 h between 17:00 and 21:00 h Eastern Standard Time. Piscivorous bird abundance (e.g. *Egretta thula* and *Hydranassa tricolor*) was determined from bird counts conducted throughout the entire impoundment between 07:00 and 10:00 h Eastern Standard Time. Basic assumptions of the biomass budget were: (1) estimated densities of fish and rates of migration and predation resulting from monthly sampling were representative of the entire month and (2) other disappearance (*O*) includes mortality aside from predation by fish and birds. Note that data are available only for production as $P - O$, an underestimate of total production (*P*) because the amount of *O* is unknown.

Estimates of biomass budget parameters. Monthly fish population biomass was estimated from cast-net sampling (Table 1). Population biomass for the ditch and creek was estimated by multiplying fish densities within respective habitats by the area of each habitat. The area of the creek was determined from aerial photography by dividing the creek into small grids of known areas and counting the number of grids within the creek (area = 26 195 m^2). The area of the perimeter ditch was determined by multiplying the length of the ditch by its average width (area = 3633 m length × 10 m width = 36 330 m^2). Impoundment standing stock for the biomass budget was the sum of creek and ditch population biomass. Estimated population biomass was multiplied by 5 (100/20) to correct for cast-net efficiency, which was estimated to be within a range of from 10 to 28 % in gear-testing studies conducted in the study impoundment (Stevens 2006).

Monthly estimates for net fish ingress were calculated by multiplying hourly culvert averages (Table 1) by hours in the month, and by the number of open culverts. Because fished and unfished culverts did not significantly differ in catch (Stevens et al. 2006), average

catch in the 4 fished culverts was assumed to represent the remaining unfished culverts. Net fish ingress values were multiplied by 6.7 (100/15) to account for culvert-trap catch efficiency, which was estimated to be within a range of 15 to 20 % in gear-testing studies conducted in a nearby impoundment (Stevens 2006).

To determine the daily consumption of marsh fishes by piscivorous fish, an estimate of impoundment fish abundance was needed. Good water clarity during April 2001 allowed for a count of Florida gar *Lepisosteus platyrhincus*, which remain close to the surface and are conspicuous. Counts of *L. platyrhincus* in a given area were extrapolated to the entire impoundment. A total of 28 Florida gar were counted along a stretch of perimeter ditch (4150 m^2), resulting in a density of 6.7×10^{-3} fish m^{-2}. Multiplying this density by area of ditch and creek within the impoundment accessible to Florida gar results in an estimate of 332 Florida gar in the impoundment. The gill net catch immediately following the observation was 10.3 Florida gar per 10 m net h^{-1}. The result of gill net catch per unit effort divided by total Florida gar abundance is 0.03. Thus, the gill net catch per unit effort represents 3 % of the impoundment population of Florida gar. Catch per unit effort data from gill nets (Table 1) were converted to impoundment fish population by multiplying by 30. Using a conversion factor from this method, however, assumes that all other piscivorous fish species are caught similarly to *L. platyrhincus* in gill nets.

Daily prey consumption by piscivorous fishes was based upon published values for estuarine fishes (Table 2). Hunt (1960) and McGoogan & Gatlin (1998) estimated prey consumption from feeding experiments. Buckel et al. (1999) estimated prey consumption from diet analyses, and Hartman & Brandt (1995) and Hartman (2000) estimated prey consumption from both diet and observed growth rates. An estimate of 0.04 g wet prey d^{-1} g^{-1} predator body weight (intermediate among literature estimates) was used in the biomass budget. For each month, the estimated population biomass of piscivorous fishes (g piscivorous fish per marsh) was multiplied by estimated consumption by piscivorous fishes and multiplied by the number of days in each month.

Bird consumption estimates used in the biomass budget were taken from published values (Table 3). Junor (1972) hand-reared piscivorous birds (darters, cormorants, and herons) and estimated daily prey consumption (g wet weight) by birds to be 16 % of the bird's wet body weight. Kushlan (1978) summarized the relationship between bird size and prey consumption for wading birds, Walsberg (1983) summarized daily energy expenditure of free-living birds, and Birt-Friesen et al. (1989) estimated field metabolism of free-living seabirds using doubly labeled water and activity

budgets. Average bird consumption per day was generated for each piscivorous species by substituting the weight of a typical adult bird into each of 4 equations (Table 3). These average bird consumption estimates were multiplied by average monthly bird abundance within the impoundment (Table 4) and multiplied by the number of days in each month.

Sensitivity analysis of biomass budget. An analysis was performed on all biomass-budget parameter estimates to determine the sensitivity of these parameters to the overall fish production estimate (total g fish per impoundment yr^{-1}). Each parameter estimate was individually increased by 30% and also decreased by 30%, and the production calculation was recomputed. The

changed budget parameters included: creek fish density, ditch fish density, creek area, ditch area, cast-net gear efficiency, net fish ingress catch per unit effort, culvert-trap gear efficiency, gill net catch per unit effort, conversion from gill net catch per unit effort to population estimate, daily consumption by piscivorous fish, bird abundance, and daily consumption by birds.

RESULTS AND DISCUSSION

The results of the production calculation using the biomass budget are given in Table 5, which includes monthly estimates for standing stock, consumption by

Table 2. Daily prey consumption estimates (g wet prey consumed g^{-1} predator wet body weight d^{-1}) reported for selected estuarine fishes

Species	Common name	Age class	Prey consumption	Source
Lepisosteus platyrhincus	Florida gar	Juvenile	0.0281	Hunt (1960)
Cynoscion regalis	Weakfish	1	0.051	Hartman & Brandt (1995)[a]
Cynoscion regalis	Weakfish	2	0.036	Hartman & Brandt (1995)[a]
Pomatomus saltatrix	Bluefish	0	0.048	Hartman & Brandt (1995)[a]
Pomatomus saltatrix	Bluefish	1	0.043	Hartman & Brandt (1995)[a]
Pomatomus saltatrix	Bluefish	2	0.037	Hartman & Brandt (1995)[a]
Sciaenops ocellatus	Red drum	Juvenile	0.014–0.023	McGoogan & Gatlin (1998)[b]
Pomatomus saltatrix	Bluefish	0	0.04–0.12	Buckel et al. (1999)
Morone saxatilis	Striped bass	0	0.0326–0.0559	Hartman (2000)
Average			0.037–0.049	

[a]After accounting for estuarine residency of each species and maximum weight of each size class
[b]Conversions: assimilation efficiency = 0.80 (for kJ digestible energy to kJ prey intake), 1 kJ = 0.23892 kcal, 1 kcal = 0.833 g wet biomass

Table 3. Daily prey consumption estimates reported for piscivorous birds taken from published values. Conversions: assimilation efficiency = 0.80 (for kJ energy expenditure to kJ prey intake), 1 kJ = 0.23892 kcal, 1 kcal = 0.833 g wet biomass

Species	Common name	Weight[a] (g)	Junor (1972)[b]	Kushlan (1978)[c]	Walsberg (1983)[d]	Birt-Friesen et al. (1989)[e]	Average
			Prey consumption (g wet weight prey d^{-1})				
Pelecanus occidentalis	Brown pelican	3723	596	614	385	632	557
Mycteria americana	Wood stork	2724	436	455	318	504	428
Ardea herodias	Great blue heron	2588	414	433	309	485	410
Phalacrocorax auritus	Double-crested cormorant	1816	291	308	249	375	306
Anhinga anhinga	American anhinga	1226	196	211	196	282	221
Casmerodius albus	Great egret	908	145	158	163	227	173
Nycticorax nycticorax	Black-crowned night heron	863	138	151	158	218	166
Dichromanassa rufescens	Reddish egret	454	73	81	107	137	99
Hydranassa tricolor	Louisiana heron	409	65	74	100	127	92
Egretta thula	Snowy egret	363	58	66	93	116	83
Florida caerulea	Little blue heron	363	58	66	93	116	83
Butorides striatus	Green heron	227	36	42	70	83	58
Megaceryle alcyon	Belted kingfisher	136	22	26	51	57	39

[a]Wet weight of adult birds (Terres 1980)
[b]y = 16% weight of bird d^{-1}, where y = g wet weight prey d^{-1}
[c]$\log y = 0.96\log x - 0.64$, where y = g wet weight prey d^{-1}, and x = weight of bird (g)
[d]$\ln y = \ln 12.84 + 0.61\ln M$, where y = kJ prey d^{-1}, and M = weight of bird (g)
[e]$\log y = 2.99 + 0.727\log x$, where y = kJ energy expenditure d^{-1}, and x = weight of bird (kg)

Table 4. Estimates of monthly piscivorous bird abundance (no. birds per impoundment) in Impoundment C20C. Data are from Stevens et al. (2006). Bird abundance was estimated by averaging bird counts within the impoundment (n = 2 bird counts mo^{-1})

Species	Common name	2000						2001					
		Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun
Pelecanus occidentalis	Brown pelican								0.5				
Mycteria americana	Wood stork	3			8	1.5		1.5					
Ardea herodias	Great blue heron	1.5	1	0.5	2.5	1.5		0.5	1	0.5			1.5
Phalacrocorax auritus	Double-crested cormorant	0.5			0.5	0.5							
Anhinga anhinga	American anhinga	0.5	0.5	2			1	0.5	1		0.5	0.5	
Casmerodius albus	Great egret	3	20	2.5	3.5	0.5	1	6	2			0.5	
Nycticorax nycticorax	Black-crowned night heron					2							
Dichromanassa rufescens	Reddish egret	0.5	4.5										
Hydranassa tricolor	Louisiana heron	4	24	1	1.5		5.5	5	1.5	2	0.5	1.5	1.5
Egretta thula	Snowy egret	0.5	94.5	1	3.5			16	1				
Florida caerulea	Little blue heron						0.5				0.5		
Butorides striatus	Green heron	2	3	1		0.5	0.5				1	1.5	2
Megaceryle alcyon	Belted kingfisher		1		0.5	1.5	1	1.5	1		0.5		

piscivorous fishes and birds, and net fish ingress. Over the study period, 1.6 metric tons of saltmarsh fishes were consumed by piscivorous fishes, 1.1 metric tons were consumed by birds, and 2.4 metric tons were exported directly from the saltmarsh to the estuary. On the basis of saltmarsh area (entire impoundment), direct export was about 5.6 g fish m^{-2} marsh yr^{-1} (2390 kg fish yr^{-1}/4.27 × 10^{5} m^{-2} marsh).

Table 5. Fish production (kg fish per impoundment mo^{-1}) in Impoundment C20C, estimated from biomass budget: $P - O = \Delta X + Y_f + Y_b - M$, where P: production; O: other disappearance; X: standing stock; Y_f: yield to piscivorous fish; Y_b: yield to piscivorous birds and M: net fish ingress

	ΔX	Y_f	Y_b	M	$P - O$
Jul	587	44	101	622	109
Aug	−1040	45	456	−124	−415
Sep	534	344	39	013	904
Oct	−223	79	175	−325	356
Nov	3458	46	58	1	3561
Dec	4711	118	31	−240	5100
Jan	−3475	84	119	−1010	−2263
Feb	−3605	25	42	−413	−3124
Mar	976	51	12	−249	1288
Apr	684	251	8	−124	1067
May	−257	24	13	−33	−188
Jun	2674	512	26	−508	3720
Total[a]	5025	1620	1080	−2390	10117
% production[b]	38	12	8		18

[a]Over the course of the study, the effects of marsh surface migrations cancel out (see 'Discussion'). Assuming negative production during February (−3124 kg fish per impoundment yr^{-1}) is attributable to O and O is negligible aside from February, impoundment fish production is ~13 241 kg yr^{-1}
[b]% production for O is 24 %

The sensitivity analysis of the biomass budget showed that the model is relatively robust. Biomass budget output (production estimate $P - O$) did not change by >15 % when changes to input parameters were varied by 30 %. Manipulation of cast-net gear efficiency resulted in the greatest changes to output. For example, if cast-net gear efficiency was 15 or 29 % instead of the estimated 20 %, then estimated fish production ($P - O$) would change from 10 117 to 8609 or 11 625 kg fish per impoundment yr^{-1} (output changes of 15 %). Changes to creek fish density or creek area resulted in output changes of 13 %, and changes to ditch fish density or ditch area resulted in output changes of 2 %. Manipulation of culvert-trap catch per unit effort or efficiency parameters resulted in changes to output of 7 %. For example, if culvert-trap efficiency was 11 or 21 % instead of the estimated 15 %, then estimated fish production ($P - O$) from the biomass budget would change by 7 %. Manipulation of parameters associated with fish and bird consumption resulted in changes to output of 3 to 5 %. For example, if the conversion from gill-net catch per unit effort to impoundment piscivore population was 21 or 39 rather than the estimated 30 (gill net catch per unit effort represents 2.6 or 4.8 % of the impoundment piscivore population rather than 3 %), then estimated fish production would change by 5 %.

Assuming that standing stock, consumption, and migration estimates (based on direct sampling) used in the fish biomass budget were accurate, then negative values resulting from the biomass budget were attributable to mortality (other than predation) and marsh surface migrations. Negative production ($P - O$) values in July and May were probably the result of fish migrating from the ditch and creek (where standing stock is measured) to the marsh surface, because water
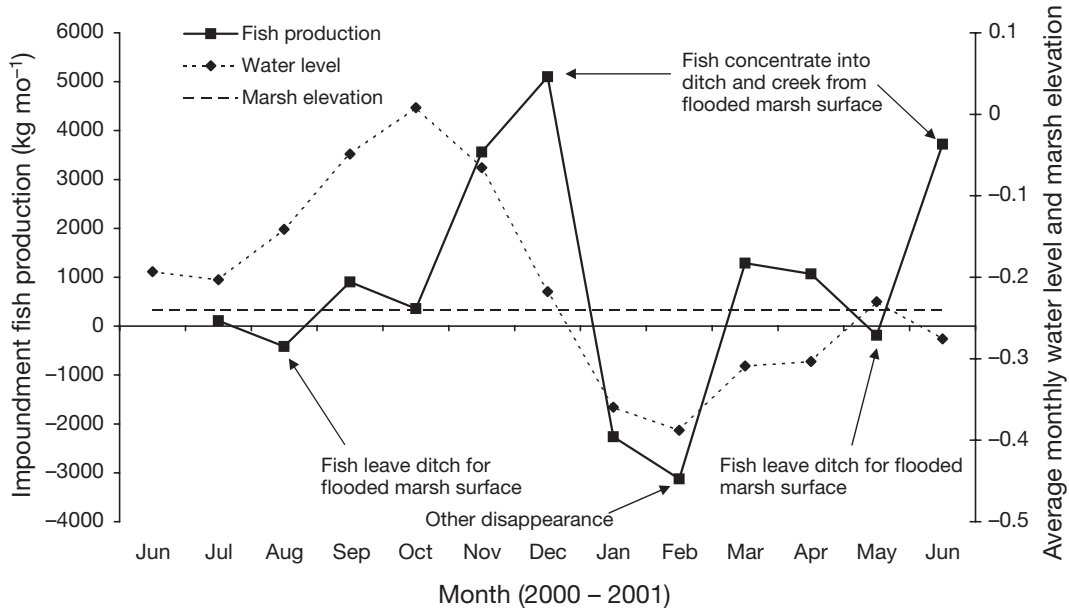
Fig. 2. Estimated fish production (kg mo^{-1}), average monthly water level (m), and marsh elevation (m) in Impoundment C20C. Water level and marsh elevation were surveyed with respect to the 1988 North American Vertical Datum (NAVD 88) (Stevens et al. 2006)

levels exceeded the threshold of marsh flooding (Fig. 2). High production ($P - O$) values in December and June probably resulted from fish migrating from the marsh surface back to the ditch and creek as water drained the marsh (Fig. 2). Over the long run, marsh surface migrations should cancel. For example, fish leaving the ditch and creek to the marsh surface in July may result in negative production values, but when the fish return to the ditch and creek in December, this production is added back in addition to the fish production (and bird consumption) that occurred on the marsh surface. Thus, correcting for marsh surface migrations is not necessary to estimate total production during the study.

Negative production also occurs in February, which cannot be explained by marsh surface migrations because water levels remained low through the following month. This negative production occurred following a month where fish densities were the highest (~35 fish m^{-2}) and freezes occurred (Stevens et al. 2006). If the negative fish production is attributable to mortality caused by freezes or density-dependent effects, then this other disappearance (O) should be added to production. Assuming O is negligible aside from the February mortality, total fish production in the study impoundment was estimated at 13 241 kg fish per impoundment yr^{-1} (Table 5). On the basis of saltmarsh area (combining impoundment fish habitats: ditches, creeks, and marsh surface), production for the study impoundment was 31.0 g fish m^{-2} yr^{-1} (13.241×10^6 g fish per impoundment yr^{-1}/4.27×10^5 m^2 per impoundment).

Fish production estimated from the biomass budget is within the range of published estimates of estuarine fish communities (Table 6). Estimates range from 2.6 g fish m^{-2} yr^{-1} for seagrass fish communities in Mosquito Lagoon, Florida, to well over 30 g fish m^{-2} yr^{-1} for coastal and estuarine fish communities in Mexico, Louisiana, and California. Fish production calculated from Ricker's equations for the study impoundment (22.6 g fish m^{-2} yr^{-1}) is shown in Table 6, and agrees relatively well with the estimate from the biomass budget.

Closed saltmarsh impoundments (no estuarine connectivity), located only 8 and 28 km to the north of the study impoundment, were as much as 17 g fish m^{-2} yr^{-1} more productive than the study impoundment (Schooley 1980, our Table 6). Studies comparing open and closed impoundments in the Indian River Lagoon, Florida, have shown that resident fish densities are much higher in closed impoundments (Rey et al. 1990, Taylor et al. 1998). Greater standing stock of resident fishes in closed systems may result from prevention of resident fish migration to the estuary and reduction in transient estuarine predators. Another explanation for greater standing stock of resident fishes is higher fish production rates due to greater food resources (e.g. microalgae or mosquito larvae), greater food quality, or greater access to food as a result of longer flooding. Although fish production may be higher in closed impoundments, the biomass is trapped within the closed system, except for transfer by bird predation. The trapping of fish biomass and manipulation of

Table 6. Estimates of fish production (g m^{-2} yr^{-1}) among estuarine communities. References are from Table 10.3 in Day et al. (1989), except Schooley (1980), Adams (1976), and Allen (1982)

Fish community	Location	Fish production	Source
Seagrass	Mosquito Lagoon, Florida	2.6[a]	Schooley (1980)
Estuarine	Laguna Madre, Texas	12.1–57.6[a]	Hellier (1962), Jones et al. (1963)
Seagrass	North Carolina	18.4[a]	Adams (1976)
Saltmarsh	Banana Creek, Florida	22.6[b], 31.0[c]	Present study
Lagoon	Terminos Lagoon, Mexico	20.0[a]	Yáñez-Arancibia & Lara Domínguez (1983)
Coastal lagoon	Cuba	22.0–27.6[a]	Holcik (1970)
Coastal lagoon	Mexico, Pacific coast	24.6–66.7[a]	Yáñez-Arancibia (1978)
Coastal	Mexico, Pacific coast	34.5[a]	Warburton (1979)
Estuarine	Barataria Bay, Louisiana	35.0–72.8[a]	Day et al. (1973), Wagner (1973)
Littoral zone of tidal marsh	California	37.4[a]	Allen (1982)
Saltmarsh impoundments	Mosquito Lagoon, Florida	38.8–59.2[a] 31.5–40.0[b]	Schooley (1980)

[a]Based on summation of production estimates for component species
[b]Based on production equations in Ricker (1946) modified by Allen (1950) and Chapman (1978), but substituting monthly biomass of whole community rather than summation of species
[c]Based on fish biomass budget: annual fish production/area of saltmarsh

water levels to provide optimal foraging depths to wading birds may explain why managed impoundments are successful at providing feeding opportunities to avian wildlife (e.g. Smith & Breininger 1995).

The fate of fish production within the study impoundment is shown in Fig. 3 (results derived from Table 5). Overall mortality by biomass (combining other disappearance and consumption by fishes and birds) was 44% yr^{-1}. For comparison, mortality rates were estimated at 0.023 to 0.041% d^{-1} (~8.4 to 15.0% yr^{-1}) for *Leiostomus xanthurus* (e.g. Currin et al. 1984), 23 to 61% (2 wk mortality) for *Penaeus aztecus*
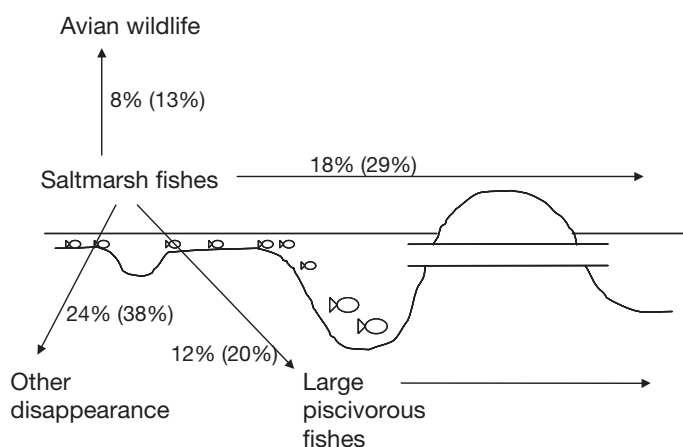

Fig. 3. Fate of fish production in Impoundment C20C. The remaining 38% of fish production was attributable to changes in standing stock (i.e. biomass accumulated during the study period). This surplus standing stock may later enter one or several of the above pathways. Numbers in parentheses show percentage of production if the accumulated biomass is prorated among the pathways

(Minello et al. 1989), and as high as 50% yr^{-1} for mummichog *Fundulus heteroclitus* (Meredith & Lotrich 1979). Note that 38% of fish production was attributable to changes in standing stock (Fig. 3). This means that fish standing stock accumulated during the study period. This fish production may enter one of the pathways shown in Fig. 3 (emigration, consumption, or other disappearance) sometime in the future. If the fish production accumulated as standing stock is prorated among the pathways, then an additional 8% of fish production will be consumed by piscivorous fish, another 5% will be consumed by piscivorous birds, an additional 14% will be lost to other disappearance, and another 11% will emigrate to the estuary.

The pathway of consumption by piscivorous fishes shown in Fig. 3 represents the trophic relay. Assuming a 10% energy transfer for each increase in trophic level, piscivorous fishes potentially move 1.2 to 2.0% of fish production to the adjacent estuary after consuming 12 to 20% of saltmarsh fish production. Consumption by piscivorous fish within the impoundment was greatest during August through October, when large juvenile *Sciaenops ocellatus* and *Cynoscion nebulosus* were abundant within the impoundment, and during April and June when *Lepisosteus platyrhincus* were abundant, coincident with low-salinity pulses (Stevens et al. 2006). Thus, the movement of marsh production to the estuary by trophic relay was greatest during high water level, when water conditions were most favorable for large piscivorous fish (i.e. cool temperatures and high dissolved oxygen), and during late spring and early summer, when low salinity allowed opportunistic *L. platyrhincus* to take advantage of favorable water conditions and abundant food within the impoundment.

Direct export of fish biomass was estimated to be 18 to 29 % (Fig. 3). The greatest export occurred as the water level receded during winter, concentrating resident fishes in ditches and creeks (Stevens et al. 2006). The high value associated with direct fish biomass export may be unique to seasonally flooded marshes, because a long period of low water level may prompt fishes to migrate from the impoundment in response to overcrowding (Stevens et al. 2006). Interestingly, piscivorous fish abundance was low during low winter water level and temperature, allowing resident fishes to leave the impoundment with minimum predation by large fishes.

The combined export of fish biomass from impoundment to estuary (combining direct export and movement by piscivorous fish consumption) was 19 to 31 %. In closed impoundments in Mosquito Lagoon, the transfer of net primary marsh production to fish production (fish production/net marsh production) was estimated at 6.5 % (Schooley 1980). Multiplying this transfer ratio (6.5 %) by exported fish production (19 to 31 %), the saltmarsh primary production that moved to the estuary in the tissues of fish was about 1 to 2 %. For comparison, the quantity of marsh primary production exported as detritus in a similar high-elevation marsh in Texas (dominated by *Distichlis spicata*) was 3 to 5 % (Borey et al. 1983). Thus, the movement of saltmarsh production by fishes may be similar to that exported as detritus.

This study is, to our knowledge, the first to quantify the yield of estuarine fishes to predators and direct export to the estuary and to estimate movement of saltmarsh primary production to the estuary by fishes. Of equal importance in evaluating the significance of saltmarsh export to the estuary is the quality of exported products. Qualitative factors include energetic content, protein content, and nutrient content of food sources. Small juvenile transient fishes incorporate marsh foods into their tissues as they consume detritus and algae from saltmarsh creeks. Residents are able to cover the shallow marsh surface, thereby consuming marsh foods that would otherwise be difficult for transient fishes to access (Werme 1981). The quality of these marsh foods is concentrated as they are incorporated into the tissues of fish. For example, detritus contains about 1 to 2 % nitrogen (Day et al. 1989), whereas fish tissue contains >10 % nitrogen (Deegan 1993). In addition, fish tissue has concentrated levels of protein and lipids relative to detritus, and higher energetic content. From the perspective of large estuarine fishes and mammals, the quality of resident and small transient fish tissues is readily useable. Thus, marsh fishes not only move saltmarsh production to the estuary, but also convert low-quality saltmarsh foods to higher quality vagile biomass, providing an efficient link between saltmarshes and higher trophic carnivores in the adjacent estuary.

The movement of saltmarsh production to the estuary by fishes quantified in this study illustrates the value of saltmarsh–estuarine connectivity, because the export of resident marsh fishes may represent a substantial food source for estuarine predators. For example, when almost all Indian River Lagoon saltmarshes were impounded (with no connection) during the 1970s, marsh fish production was trapped behind a system of dikes, and was unavailable for consumption by estuarine predators. At >16 200 ha of saltmarshes impounded (Brockmeyer et al. 1997), lost fish biomass to the estuary may have totaled >840 metric tons yr^{-1} (if pre-impoundment saltmarshes exported fish biomass at the magnitude of the study impoundment, 5.2 g fish m^{-2} marsh). If resident fish export from other reconnected saltmarsh impoundments in the vicinity is similar to that of the study impoundment, then resource managers can expect an export of 5.2 metric tons of small marsh fish annually for every 100 ha of impounded marsh reconnected. Although the numbers associated with the export of fish biomass from these seasonally flooded saltmarshes seem colossal, it is not known whether the exported biomass can actually enhance the diets of estuarine predators and represent an ecologically significant source of food compared to what is already present in the estuary. The next logical step in expanding upon the knowledge obtained during this study is to use stable isotope analysis, or other analytical research tools, to directly test the value of saltmarsh fishes to the diet of estuarine predators in areas where saltmarshes have been reconnected.

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