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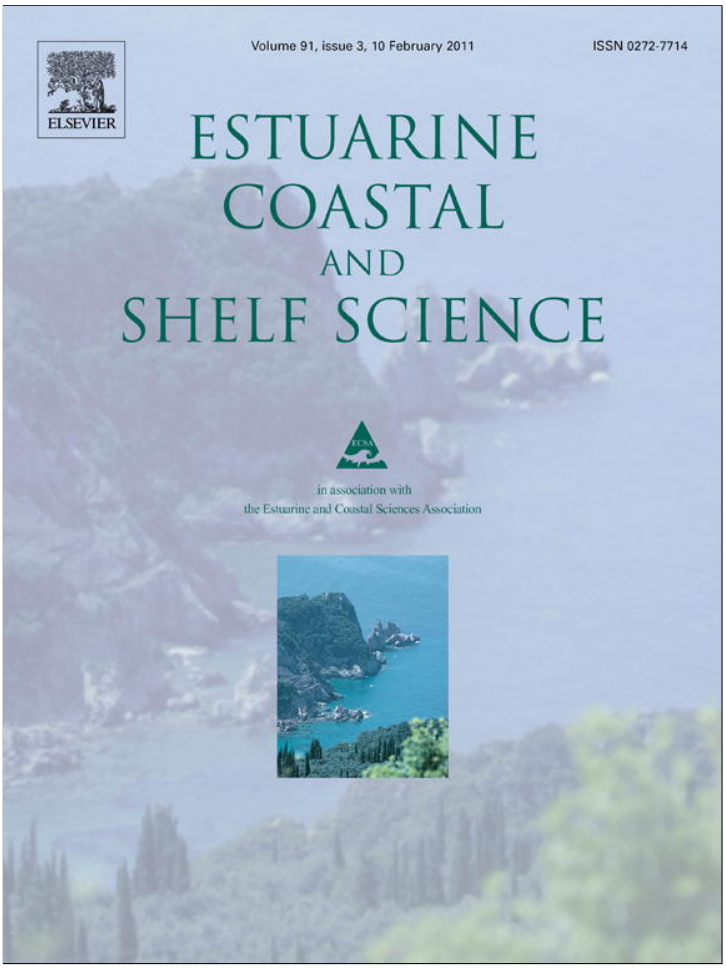

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Nekton community response to a large-scale Mississippi River discharge: Examining spatial and temporal response to river management

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ABSTRACT

Freshwater flow is generally held to be one of the most influential factors affecting community structure and production in estuaries. In coastal Louisiana, the Caernarvon Freshwater Diversion (CFD) is managed to control freshwater discharge from the Mississippi River into Breton Sound basin. Operational since 1991, CFD has undergone several changes in management strategy including pulsed spring flooding, which was introduced in 2001. We used a 20-yr time series of fisheries-independent data to investigate how variation in freshwater inflow (i.e., pre- and post-CFD, and pre and post spring pulsing management) influences the downstream nekton community (abundance, diversity, and assemblage). Analyses of long-term data demonstrated that while there were effects from the CFD, they largely involved subtle changes in community structure. Spatially, effects were largely limited to the sites immediately downstream of the diversion and extended only occasionally to more down-estuary sites. Temporally, effects were 1) immediate (detected during spring diversion events) or 2) delayed (detected several months post-diversion). Analysis of river management found that pulsed spring-time inflow resulted in more significant changes in nekton assemblages, likely due to higher discharge rates that 1) increased marsh flooding, thus increasing marsh habitat accessibility for small resident marsh species, and 2) reduced salinity, possibly causing displacement of marine pelagic species down estuary.

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1. Introduction

Coastal restoration and marsh creation are important management tools to offset the loss of coastal wetland habitats. In coastal Louisiana, with an estimated marsh loss of 61.3 km^2 yr^{-1} (Barras et al., 2003), there is an enormous push to restore and enhance estuarine ecosystems to slow or reverse habitat loss and provide support for fisheries production. One of the primary techniques identified for restoration and protection of coastal marshes in Louisiana involves the use of siphons and water control structures to regulate freshwater flow into marsh areas (LCPRA, 2007). The goals of these freshwater diversions are manifold and include controlling salinity, improving water quality, restoring vegetated marshes and increasing the quality and quantity of fisheries habitat.

For estuarine nekton communities, freshwater flow is generally held to be one of the most influential factors affecting biotic community structure and production (Montague and Ley, 1993; Lonegeran and Bunn, 1999; Alber, 2002; Kimmerer, 2002). Specifically, riverine flows deliver large quantities of allochthonous resources to estuaries (Lane et al., 2004), and those resources may be readily assimilated by secondary consumers (Rozas et al., 2005; Wissell and Fry, 2005). While little direct information exists regarding the value of resource subsidies made available by freshwater flow, numerous studies document how biological populations, such as phytoplankton (Riley, 1937; Sin et al., 1999), invertebrates (Montagna and Kalke, 1992; Wilber, 1992, 1994; La Peyre et al., 2009) and fishes (Rose and Summers, 1992; Houde and Rutherford, 1993; Piazza and La Peyre, 2007; Kimmerer et al., 2009) vary with flow. However, as riverine flow can vary in timing and quantity, generalizations regarding the positive or negative effects of freshwater flow on biological productivity, and the explicit effects of various mechanisms that may control biological responses, remain elusive. With the re-engineering of many of the world's large rivers altering cycles of flow (Postel and Richter, 2003; Poff et al., 2007; Palmer et al., 2008), understanding

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the effects of changes in riverine inflow on biological resources becomes of utmost importance.

Past studies indicate that both the timing and quantity of riverine flow appear to be critical in determining the direction of effects. For example, the timing and quantity of freshwater inflow are held to be particularly important for recruitment in resident nekton consumers that key into flood events for spawning and rapid growth (Kneib, 1997). Similarly, it has been suggested that riverine flows, specifically water quantity and timing, affect species growth or abundance (Piazza and La Peyre, 2007; La Peyre et al., 2009; Piazza and La Peyre, 2010); the management of flow quantity and timing may also influence the availability of optimal nekton habitat in estuaries (Kimmerer, 2002; Piazza and La Peyre, 2007, but see Kimmerer et al., 2009). A number of studies suggest that diversion effects on physicochemical attributes such as salinity are key to their influence on species (Wilber, 1992; Livingston et al., 2000; La Peyre et al., 2009).

Caernarvon Freshwater Diversion (CFD) is one of the largest freshwater control structures in coastal Louisiana, discharging freshwater from the Mississippi River into the Breton Sound Basin. Since the diversion became operational in 1991, discharge at the structure (quantity and timing of freshwater flow into the downstream estuary) has been manipulated. Changes in management operation, combined with the availability of long-term fishery-independent data (1988–2007) collected at downstream stations in Breton Sound, provided a unique opportunity to examine the effects of freshwater flow and variation in timing and quantity of flow on nekton community response.

The main objective of this study was to investigate how freshwater inflow influences the downstream nekton community structure (abundance, diversity, assemblage) and to examine how alternative management tactics (i.e., spring continuous flow versus spring pulsed flow) affect the downstream nekton community. Specifically, we tested the hypotheses that (1) increased freshwater input from a diversion would alter downstream nekton assemblages, (2) pulsed spring flow from a diversion would differentially impact nekton communities as compared to continuous spring flow; and (3) impacts to nekton communities would vary by distance from the diversion (up-estuary versus down-estuary), and over time (during diversion versus 3 months post-diversion).

2. Study area

Breton Sound is a 271,000 ha estuary in the Mississippi River deltaic plain in southeast Louisiana (Fig. 1). It is microtidal and consists of bays, lakes, bayous, canals, and fresh, intermediate, brackish, and saline marshes. The CFD is located at the head of Breton Sound and is capable of delivering substantial amounts of freshwater (227 m^3 s^{-1}) and allochthonous organic matter and sediments (4.5×10^8 kg yr^{-1}) to the basin (Snedden et al., 2007a). From 1991 to 2000, the structure was managed for maximum flow, as allowed by Mississippi River water levels and

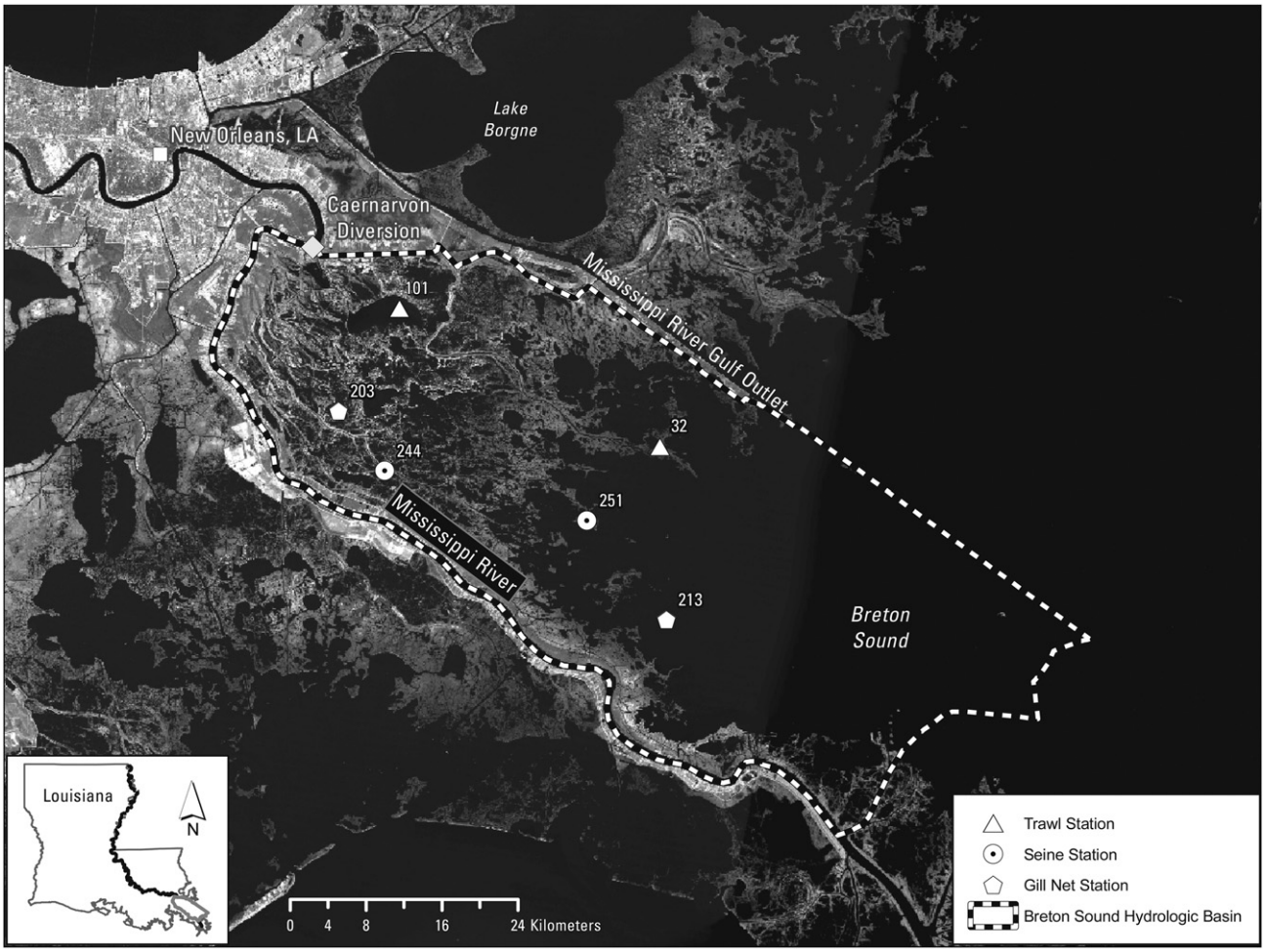

Fig. 1. Map of study area and station locations in Breton Sound, Louisiana, USA. Station locations refer to Louisiana Department of Wildlife and Fisheries long-term fishery-independent stations (LDWF 2002) sampled monthly with seine (Sta. 244, 251), gill net (Sta. 203, 213) and otter trawl (Sta. 101, 32) gear types.

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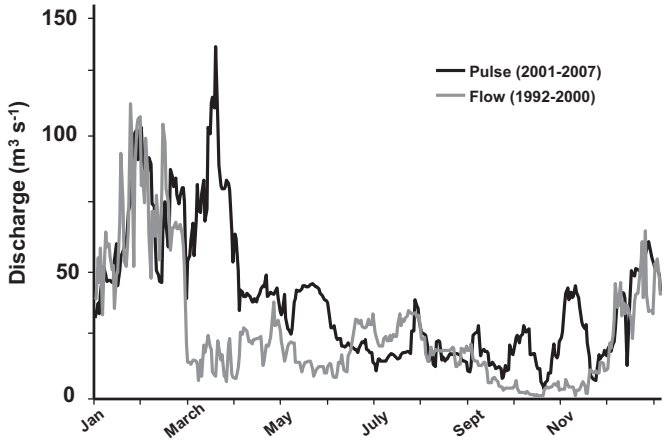

Fig. 2. Mean daily discharge by flow years (1992–2000) and pulse years (2001–2007) ($m^3\ s^{-1}$) from the Caernarvon Freshwater Discharge structure. Dark line represents the mean discharge from pulse management years; grey line represents the mean discharge from flow management years.

political constraints associated with the commercial fishing industry. Beginning in 2001, winter/spring high-flow freshwater pulsing through the diversion structure was implemented to simulate seasonal flood-pulse events (Fig. 2). Pulses are periodic large fluxes of river water into the basin and are capable of inundating upper basin marshes (~5700 ha) for several days (Piazza and La Peyre, 2007; Snedden et al., 2007a,b). Without the riverine pulse, inundation of the upper basin marshes is dominated by meteorological forcing, similar to those marshes occurring east of Bayou Terre Aux Boeufs that are hydrologically separated from diversion flow (Rozas et al., 2005).

3. Methods

3.1. Nekton communities

3.1.1. Environmental and nekton community data

Discrete water temperature (°C), salinity, and water clarity (m) measurements were collected at each station in Breton Sound in conjunction with biological sampling throughout the entire period of record (1988–2007; LDWF 2002). Water temperature and salinity were measured with a Beckman RS 5 portable salinometer or equivalent. Water temperature and salinity measurements were collected at two depths, 0.3 m beneath the surface and 0.3 m above the bottom, and averaged. Water clarity was measured with a 30-cm, white Secchi disk. Nekton community data were compiled from fishery-independent seine (15-m nylon bag seine; 6-mm mesh), gill net (4-panel: 1, 1.25, 1.5, 2-inch mesh), and otter trawl (6 ft) stations in Breton Sound monitored by the Louisiana Department of Wildlife and Fisheries (LDWF; for complete sampling protocols see LDWF 2002). For each gear type, one upper basin station and one lower basin station were chosen for analyses. Upper basin stations were defined as 'high impact' (HI), because of their close proximity to the Caernarvon diversion, while lower basin stations were defined as 'low impact' (LI) (Station Id (HI, LI): seine (244, 251), gill net (203, 213), trawl (101, 32); Fig. 1). Stations were sampled approximately biweekly without replication between 1988 and 2007 by LDWF. For this study, we investigated only the effects of the freshwater inflow on nekton communities during the spring (April, May, June) and summer (July, August, September) time periods, because the largest abundances of nekton occur during these months in this region (Zimmerman et al., 2000).

All nekton metrics were calculated separately by gear type, station and season. Gill net samples for each sampling day were pooled across mesh panel sizes to form an overall gill net variable. Alpha (α) diversity for each sample was calculated with both Shannon diversity (H') and evenness (E). Each nekton species was classified according to life history, ubiquity, threatened status, and environmental tolerance based on the literature (i.e., Hoese and Moore, 1998; Froese and Pauly, 2009). Resident species were defined as those that spend their entire life cycle within the estuary (e.g., *Lepomis macrochirus*, *Poecilia latipinna*), and members of this group spawn in the estuary. Estuarine-dependent species were defined as those that spend at least a portion of their life cycle in the estuary. Members of this group spawn on the continental shelf and migrate into the estuary for the juvenile portion of their life cycle. Species were classified as ubiquitous if they were consistently found throughout the estuary. Species were classified as species of concern, based on their state and federal status, as listed in Lester et al. (2005). We also investigated how the abundance of killifish (*Fundulus* spp.) responded to management, based on earlier work that proposed killifish as indicator species, because they can withstand poor conditions and have been predicted to increase as other species decline (Deegan et al., 1997).

3.1.2. Data analyses

For spring and summer months, biweekly nekton abundances were pooled into monthly sums, and environmental samples were pooled into monthly means. To test the effect of the CFD, samples from each station collected prior to 1991 were categorized as pre-Caernarvon samples (PRE-CFD), and samples collected 1991–2007 were classified as post-Caernarvon samples (POST-CFD). Likewise, to test the effect of riverine management technique, samples collected 1991–2000 were classified as continuous flow samples (FLOW), and samples collected 2000–2007 were classified as pulsed samples (PULSE).For ANOVA analyses listed below, data were tested for normality with the Shapiro–Wilks test. In the event that the residuals were not normally distributed, the data were log-transformed. Data are reported as mean ± SE, and significance level used was $\alpha = 0.05$ unless indicated otherwise. All data were analyzed separately by gear type.

3.1.2.1. Environmental variables. To test the effects of CFD (PRE vs POST) and CFD management (FLOW, PULSE), for each station and season, means of environmental variables (water temperature, salinity, water clarity) were compared using ANOVA (SAS, 1989). Least-squared means was used to investigate post-hoc differences among treatments when ANOVA results were significant.

3.1.2.2. Species abundance, diversity, biomass. Analysis of variance (ANOVA) was used to test for differences in means of nekton abundance, species richness, species diversity, and each grouped metric (resident, estuarine-dependent, species of concern, killifish) that occurred in response to CFD (PRE vs POST) and CFD management (FLOW vs PULSE) (SAS, 1989). Analyses were run separately by station in order to compare effects at high and low impact stations. Analyses were run for spring and summer data separately in order to test effects during the diversion (spring), and immediately post-diversion (summer). Least-squared means was used to investigate post-hoc differences among treatments when ANOVA results were significant.

3.1.2.3. Nekton assemblage structure. Multivariate analyses of nekton communities were performed for each gear type, by station and season (spring and, summer), on a full species abundance matrix. PRIMER software (Clarke and Gorley, 2006) was used to test the effect of both CFD (PRE vs POST) and river management (PULSE vs FLOW) separately on species assemblages. First, by gear type, a one-way analysis of similarity (ANOSIM) was performed on

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stations and season separately to test for differences in species compositions due to both CFD and CFD management. These analyses were performed on both high and low impact stations, for spring and summer seasons separately to compare species assemblage changes as a function of location (up versus down estuary) and timing (during, immediately post-diversion event). ANOSIM was performed on a Bray–Curtis dissimilarity matrix computed on the fourth-root transformed abundances, using non-transformed abundance data.When differences were detected between treatments ($p < 0.1$), we interpreted differences in species compositions for each station and season with the one-way SIMPER test on standardized fourth-root transformed abundances.This transformation was used to downweight the contribution of common species so that the presence of rare species could also play a role in determining community structure (Clarke and Warwick, 2001). SIMPER identifies the percent role of individual species in accounting for assemblage differences (Clarke and Gorley, 2006).

4. Results

4.1. Environmental variables

For all gear types, water temperature was significantly cooler during the spring months as compared to summer months ($p < 0.001$), and salinity was significantly lower at high impact stations ($p < 0.0001$). Significant effects of CFD operation and management were found with significant decreases in salinity at most gear type and station combinations (Table 1). While water clarity increased at high impact and low impact stations for gill net samples after the Caernarvon opening, it did not change across other gear types and station combinations. In contrast, pulsing resulted in statistically significant decreases in water clarity across most gear type and station combinations (Table 1). CFD did not significantly affect water temperature.

4.2. Species abundance, diversity, biomass

For seine samples, 119,620 individuals representing 83 species were caught during spring and summer at stations 244 (HI) and 251 (LI). Species richness was higher at the LI station (Sta. 244 = 52 sp.; Sta. 251 = 72 sp.). Abundance in seine samples was dominated by *Anchoa mitchilli* and *Palaemonetes* spp., which composed 28% and 30% of the total abundance, respectively.

Spring and summer gill net samples at stations 203 (HI) and 213 (LI) captured 15,769 individuals representing 58 species. Species richness was evenly split (Sta. 203 = 37 sp.; Sta. 213 = 44 sp.); however, the downstream station (Sta. 213) accounted for 70% of the total abundance. Six species, *Leiostomus xanthurus* (spot; 21%), *Brevoortia patronus* (gulf menhaden; 20%), *Dorosoma cepedianum* (gizzard shad; 12%), *Ariopsis felis* (sea catfish; 11%), *Micropogonias undulatus* (atlantic croaker; 9%), and *Cynoscion nebulosus* (spotted seatrout; 9%) dominated the abundance.

Overall spring and summer nekton abundance in samples taken at otter trawl stations 101 (HI) and 32 (LI) was 22,314 individuals, with the majority of individuals (76%) captured at the downstream station. Captured individuals represented 64 species, which were dominated by *Anchoa mitchilli* (36%) and *Farfantepenaeus aztecus* (35%). Species richness in otter-trawl samples was evenly distributed between stations (Sta. 101 = 43 sp.; Sta. 32 = 47 sp.).

4.2.1. CFD effects

Post-Caernarvon opening, there were a few significant changes in some of the nekton parameters measured (Table 2). These changes varied however by gear type and location (up- versus down-estuary), but no significant differences were noted due to timing (spring versus summer). At the HI seine station, there was a significant increase in mean species richness and a decrease in number of individual killifish, post-CFD. The LI seine station had a significant increase only in the number of ubiquitous species sampled. In contrast, the HI gill net results showed an increase in estuarine residents (individuals and species), and the LI gill net station showed increased overall abundance but decreased diversity and number of ubiquitous individuals. Few changes were noted in the trawl samples with only species richness declining slightly post-CFD.

4.2.2. Inflow management effects (PULSE vs FLOW)

Inflow management had significant effects on trawl and seine catches in particular, and few significant effects on gill net samples (Table 3). Again, there were no significant seasonal effects, but rather changes varied by location and gear type. The seine LI station indicated decreased nekton abundance, richness, and number of estuarine residents and ubiquitous species in pulsed versus flow management. In contrast, both the HI and LI otter-trawl samples

Table 1
Overall mean ± SE, and range in parentheses of environmental variables collected at seine, gill net, and trawl stations in Breton Sound, Louisiana during spring and summer 1988–2007. ANOVA was used to test for differences in these environmental variables, by gear type, due to Caernarvon (C: PRE vs POST) and inflow management (P: FLOW vs PULSE).

	Seine		Gill net		Trawl	
	Sta. 244	Sta. 251	Sta. 203	Sta. 213	Sta. 101	Sta. 32
Salinity (psu)	3.8 ± 0.2	10.4 ± 0.3	1.8 ± 0.1	13.4 ± 0.2	2.0 ± 0.1	12.8 ± 0.2
	(0.2–11.0)	(1.5–21.8)	(0.3–13.3)	(0.5–31.8)	(0.0–26.0)	(3.4–27.0)
	$N = 135$	$N = 135$	$N = 822$	$N = 841$	$N = 481$	$N = 499$
	$C = -3.9^{**}$	$C = -2.4$	$C = -3.9^{***}$	$C = -2.9^{***}$	$C = -6.1^{***}$	$C = -0.8^{*}$
	$P = +0.3$	$P = +0.8$	$P = -0.4^{***}$	$P = -0.6^{***}$	$P = -0.9^{**}$	$P = -0.3$
Water clarity (m)	0.7 ± 0.0	0.6 ± 0.0	0.8 ± 0.0	0.8 ± 0.0	0.7 ± 0.0	0.5 ± 0.0
	(0.2–2.4)	(0.1–0.9)	(0.2–3.7)	(0.2–2.1)	(0.1–2.3)	(0.1–2.2)
	$N = 138$	$N = 135$	$N = 832$	$N = 846$	$N = 469$	$N = 496$
	$C = 0.0$	$C = +0.1$	$C = +0.2^{***}$	$C = +0.2^{***}$	$C = 0.0$	$C = 0.0$
	$P = -0.2^{***}$	$P = -0.2^{***}$	$P = -0.3^{***}$	$P = -0.3^{***}$	$P = -0.2^{***}$	$P = -0.1$
Water temperature (°C)	27.8 ± 0.3	27.9 ± 0.3	28.2 ± 0.1	27.3 ± 0.1	27.8 ± 0.2	27.8 ± 0.2
	(17.8–33.7)	(9.4–34.1)	(16.8–32.7)	(16.4–32.2)	(14.1–34.8)	(13.0–33.7)
	$N = 136$	$N = 135$	$N = 827$	$N = 841$	$N = 478$	$N = 498$
	$C = -0.6$	$C = -1.0$	$C = +0.3$	$C = -0.8$	$C = -0.2$	$C = -0.3$
	$P = -0.4$	$P = -0.3$	$P = -0.3$	$P = -0.2$	$P = -0.3$	$P = -0.4$

* 0.05; ** 0.01, *** 0.001.

Table 2
The effects of Caernarvon on nekton communities. Reported are mean (SE) for spring and summer samples combined. Significant differences are in bold ($p < 0.05$).

	Seine				Gill net				Otter trawl			
	Sta. 244		Sta. 251		Sta. 203		Sta. 213		Sta. 101		Sta. 32	
	PRE	POST	PRE	POST	PRE	POST	PRE	POST	PRE	POST	PRE	POST
N	26	112	24	112	35	193	34	196	61	295	71	413
Nekton abundance	318.7 (63.6)	341.5 (45.8)	563.2 (298.3)	531.9 (85.9)	11.7 (1.3)	22.3 (2.1)	**32.0 (3.9)**	**50.8 (5.0)**	17.8 (3.6)	14.4 (1.0)	45.1 (7.8)	33.3 (2.4)
Nekton diversity												
Species richness	**10.5 (0.7)**	**12.7 (0.3)**	12.3 (0.8)	12.0 (0.4)	4.4 (0.3)	4.6 (0.1)	6.0 (0.3)	5.6 (0.2)	2.5 (0.2)	2.6 (0.1)	**4.0 (0.2)**	**3.3 (0.1)**
Shannon diversity (H′)	1.6 (0.1)	1.6 (0.04)	1.5 (0.1)	1.3 (0.1)	1.1 (0.1)	1.1 (0.03)	**1.4 (0.1)**	**1.1 (0.03)**	0.5 (0.1)	0.6 (0.02)	0.8 (0.1)	0.7 (0.02)
Shannon Evenness (E)	0.7 (0.03)	0.6 (0.02)	0.6 (0.04)	0.5 (0.02)	0.8 (0.02)	0.8 (0.01)	0.8 (0.02)	0.7 (0.01)	0.7 (0.04)	0.7 (0.01)	0.7 (0.03)	0.7 (0.01)
Estuarine residents												
Number of individuals	298.2 (63.8)	241.7 (25.7)	409.6 (292.9)	431.0 (82.3)	**3.2 (0.6)**	**12.3 (1.8)**	4.6 (0.8)	7.7 (0.7)	10.6 (2.9)	6.2 (0.5)	15.1 (4.4)	10.9 (1.0)
Number of species	7.7 (0.4)	8.3 (0.3)	4.5 (0.4)	5.6 (0.2)	**1.4 (0.2)**	**2.3 (0.1)**	1.1 (0.1)	1.1 (0.04)	1.2 (0.1)	1.0 (0.05)	0.9 (0.1)	0.8 (0.02)
Ubiquitous species												
Number of individuals	287.3 (63.0)	226.5 (25.0)	404.4 (292.1)	425.1 (83.0)	0.6 (0.2)	0.9 (0.2)	**4.3 (1.7)**	**2.5 (0.6)**	10.2 (2.9)	5.9 (0.5)	15.6 (4.4)	10.7 (1.0)
Number of species	6.1 (0.3)	6.0 (0.2)	**3.3 (0.3)**	**4.3 (0.2)**	0.4 (0.1)	0.4 (0.04)	0.7 (0.1)	0.5 (0.04)	1.0 (0.1)	0.9 (0.04)	0.9 (0.1)	0.9 (0.03)
Species of concern												
Number of individuals	7.4 (4.6)	3.7 (1.1)	0.04 (0.04)	0.8 (0.3)	0	0	0	0	0.1 (0.03)	0.2 (0.03)	0	0.03 (0.009)
Number of species	0.6 (0.1)	0.7 (0.1)	0.04 (0.04)	0.3 (0.1)	0	0	0	0	0.1 (0.03)	0.1 (0.01)	0	0.03 (0.008)
Killifish												
Number of individuals	**86.4 (22.7)**	**37.6 (5.0)**	4.2 (2.9)	9.3 (3.1)	0	0	0	0	0.1 (0.04)	0.6 (0.1)	0	0
Number of species	2.0 (0.2)	1.3 (0.1)	0.3 (0.1)	0.7 (0.1)	0	0	0	0	0.1 (0.04)	0.1 (0.01)	0	0

Table 3
The effects of management regime (FLOW PULSE) on nekton communities. Reported are mean (SE) for spring and summer samples combined. Significant differences are in bold ($p < 0.05$).

	Seine				Gill net				Otter trawl			
	Sta. 244		Sta. 251		Sta. 203		Sta. 213		Sta. 101		Sta. 32	
	FLOW	PULSE	FLOW	PULSE	FLOW	PULSE	FLOW	PULSE	FLOW	PULSE	FLOW	PULSE
N	60	52	60	52	104	90	104	92	109	186	213	200
Nekton abundance	321.7 (71.0)	364.3 (55.7)	**696.8 (134.87)**	**341.7 (94.8)**	22.1 (2.6)	22.5 (3.4)	55.4 (8.0)	45.6 (5.5)	**10.3 (1.2)**	**16.8 (1.5)**	**25.7 (2.6)**	**41.4 (4.1)**
Nekton diversity												
Species richness	13.0 (0.4)	12.3 (0.6)	**13.9 (0.6)**	**9.8 (0.5)**	4.7 (0.2)	4.4 (0.2)	5.7 (0.2)	5.5 (0.3)	**2.2 (0.1)**	**2.8 (0.1)**	**2.9 (0.1)**	**3.7 (0.1)**
Shannon diversity (H′)	1.6 (0.1)	1.6 (0.1)	1.4 (0.1)	1.2 (0.1)	1.1 (0.05)	1.0 (0.05)	1.2 (0.04)	1.1 (0.05)	**0.5 (0.04)**	**0.6 (0.03)**	**0.6 (0.03)**	**0.8 (0.03)**
Shannon evenness (E)	0.6 (0.02)	0.7 (0.02)	0.5 (0.03)	0.5 (0.03)	0.8 (0.02)	0.8 (0.02)	0.7 (0.02)	0.7 (0.02)	0.7 (0.03)	0.7 (0.02)	0.7 (0.02)	0.7 (0.02)
Estuarine residents												
Number of individuals	225.3 (25.9)	296.9 (47.0)	**517.5 (123.7)**	**281.4 (93.7)**	9.7 (1.5)	12.8 (3.2)	8.1 (1.0)	5.9 (0.6)	**5.2 (0.8)**	**8.9 (0.7)**	11.5 (1.5)	11.3 (1.3)
Number of species	8.2 (0.2)	8.3 (0.5)	**5.9 (0.3)**	**4.7 (0.2)**	2.2 (0.1)	2.1 (0.1)	1.2 (0.1)	1.0 (0.05)	**0.7 (0.05)**	**1.5 (0.1)**	0.8 (0.03)	0.9 (0.04)
Ubiquitous species												
Number of Individuals	215.0 (25.5)	275.9 (45.8)	**510.6 (124.3)**	**277.7 (94.0)**	0.7 (0.2)	1.1 (0.2)	**3.6 (1.0)**	**1.7 (0.5)**	**5.1 (0.8)**	**8.5 (0.7)**	11.4 (1.5)	11.3 (1.3)
Number of species	6.2 (0.2)	5.7 (0.3)	4.2 (0.2)	3.9 (0.2)	0.3 (0.04)	0.5 (0.1)	0.5 (0.05)	0.4 (0.1)	**0.7 (0.05)**	**1.2 (0.1)**	0.9 (0.03)	0.9 (0.04)
Species of concern												
Number of individuals	4.0 (1.5)	5.0 (2.2)	1.0 (0.4)	0.3 (0.1)	0	0	0	0	**0.1 (0.02)**	**0.3 (0.1)**	0.03 (0.01)	0.02 (0.01)
Number of species	0.6 (0.1)	0.7 (0.1)	0.3 (0.1)	0.2 (0.1)	0	0	0	0	0.1 (0.01)	0.1 (0.02)	0.03 (0.01)	0.01 (0.008)
Killifish												
Number of individuals	**52.6 (8.6)**	**37.1 (7.5)**	12.3 (4.2)	2.0 (0.7)	0	0	0	0	0.3 (0.1)	0.9 (0.2)	0	0
Number of species	1.5 (0.1)	1.2 (0.1)	0.8 (0.1)	0.5 (0.1)	0	0	0	0	0.05 (0.01)	0.2 (0.03)	0	0

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indicated increased nekton abundance, richness and diversity during pulse management versus flow management. The gill net low impact station indicated only a significant decrease in the number of ubiquitous species during pulse management as compared to flow management.

4.3. Nekton community assemblages

4.3.1. CFD effects (PRE vs POST)

The ANOSIM results demonstrated significant changes in species composition at only up-estuary stations for seine (244) and gill net (203), and no apparent changes in species composition with otter trawl catch, or at any down estuary, low impact stations (Table 4). In particular, species composition of seine catches at the up-estuary station (244) were significantly affected by opening of the CFD in both spring (during) and summer (post-opening) with increased *A. mitchilli*, *M. undulatus* and *Palaemonetes* spp. abundance, and decreased *Cyprinodon variegatus* and *P. latipinna* abundance as indicated by SIMPER. Furthermore, ANOSIM indicated a significant change in species composition of gill net catch during the summer at the high impact station (203).The SIMPER analysis identified that these changes were generally driven by a decrease in brackish species, such as *Litopenaeus setiferus*, and an increase in fresher species, such as *Micropterus salmoides* (largemouth bass). No Caernarvon opening effects were identified from the otter-trawl data.

Table 4
ANOSIM and SIMPER results for pre- and post-CFD comparison of total abundance, by gear type, station and season. All reported results were significant at $p < 0.1$. Presented are the Global R for significant ANOSIM tests, along with top five dominant species and the SIMPER results for percentage distribution of dominant species showing dissimilarity in species composition pre- and post-CFD. Percentage numbers in bold indicate an increase in that species post-CFD. Normal font indicates a decrease in percent of that species post-CFD.

Season	Spring	Summer	Summer
Gear	Seine	Seine	Gill net
Station	244	244	203
Global R	0.543	0.552	0.396
A. felis			7.23
A. mitchilli	**5.54**	**4.58**	
C. variegatus	7.58	5.17	
D. cepedianum			**9.9**
F. grandis	6.06		
L. xanthurus			9.89
M. beryllina		3.55	
M. undulatus	**5.23**		7.01
M. salmoides			**7.29**
P. latipinna	6.84	4.47	
Palaemonetes spp		**4.47**	
Cumulative percentage	31.25	22.24	34.19

4.3.2. Inflow management effects (PULSE vs FLOW)

The ANOSIM results demonstrated that species composition was affected by river management with significant differences for all gear types varying by location and timing. Pulsing effects on nekton species composition for the seine gear were immediate (spring) at the HI seine station and lagged (summer) at the LI station (Table 5). At the HI station, changes in nekton community in the spring were driven by increased abundances of A. *mitchilli* and *Palaemonetes* spp., and decreased abundances of *B. patronus*, *M. beryllina* and *M. undulatus* (SIMPER; $p < 0.1$). In general, differences at the LI station were driven by decreased abundance of brackish species: species contributing most to the change in nekton assemblage were *A. mitchilli* and *M. beryllina,* which increased relative to the community composition, while *Palaemonetes* spp., *L. setiferus* and *C. nebulosus* all decreased as a percentage of the nekton assemblage.For the gill net data, only the down estuary (LI) station was found to have a significant change in nekton composition with a decrease in abundance of some estuarine-dependent species such as *Mugil cephalus* and *Bairdiella chrysoura* and an increase in an important fishery species, gulf menhaden (*B. patronus*) (ANOSIM/SIMPER $p < 0.1$). ANOSIM indicated significant effects on the otter trawl catch composition in spring and summer, and at both up and down estuary stations. In particular, ANOSIM determined that effects on community composition at the up estuary, high impact station occurred immediately (spring), and these effects lasted into the summer, while impacts at the down estuary, low impact station were only noted for the summer. In all cases, SIMPER identified the driver of these changes as increases in many estuarine-dependent species (i.e., high impact station: *A. mitchilli*, *L. parva*; low impact station *Sphoeroides parvus*, *Cynoscion arenarius*).

Table 5
ANOSIM and SIMPER results for pulsing management (FLOW vs PULSE) comparison of total abundance, by gear type, station and season. All reported results were significant at $p < 0.1$. Presented are the Global R for significant ANOSIM tests, along with top five dominant species and the SIMPER results for percentage distribution of dominant species showing dissimilarity in species composition during FLOW and PULSE. Percentage numbers in bold indicate an increase in that species during PULSE management. Normal font indicates a decrease in the percent of that species during PULSE management.

Season	Spring	Summer	Spring	Spring	Summer	Summer
Gear	Seine	Seine	Gill net	Trawl	Trawl	Trawl
Station	244	251	213	101	101	32
Global R	0.165	0.186	0.124	0.136	0.175	0.17
A. felis						**5.33**
A. mitchilli	**6**	**4.02**		**12.19**	**17.69**	
B. chrysoura			10.35			
B. patronus	8.79		**13.35**	**8.79**		
C. arenarius						**5.39**
C. nebulosus		3.01	9.11			
C. sapidus					**8.22**	
F. aztecus				**7.86**		**5.19**
G. bosc					**9.56**	
L. parva				**7.42**	**8.15**	
L. setiferus		2.82			**6.91**	**6.79**
L. xanthurus			11.11			
M. beryllina	6.1	**3.13**				
M. cephalus			8.65			
M. undulatus	5.33			**11.06**		
Palaemonetes spp	**6.6**	5.21				
S. parvus						**5.23**
Cumulative percentage	32.82	18.19	52.57	47.32	50.53	17.37

5. Discussion

While both CFD and river management had significant impacts on salinity and water clarity at most of the sample stations, these changes in water parameters were not consistently linked with significant changes in nekton measures, or nekton assemblage. This finding suggests that differences we detected in nekton assemblages, and the mechanisms that may have contributed to these differences, represent a complex combination of effects from changing hydrodynamic patterns and physical habitat availability. Work in this and other estuaries where inflow is managed have documented numerous environmental attributes that may covary with freshwater flow; a combination of many of these parameters may be necessary to explain and predict the response of nekton populations at the community or at the species level (e.g., Livingston et al., 1997, 2000; Kimmerer et al., 2009). Clearly though, both the addition of managed freshwater inflow, and the management regime used (timing, quantity), had impacts on nekton assemblages and distribution within the receiving estuary.

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Extensive work downstream of the CFD during pulse management has documented significant changes in flow patterns, such as changes in water level variation and circulation (Snedden et al., 2007a,b), sediment deposition (Wheelock, 2003), sediment discharge rates (Snedden et al., 2007a) and nutrient concentrations and hydrographic patterns (Lane et al., 1999, 2004, 2007; Snedden et al., 2007a; Hyfield et al., 2008). While many of these impacts decreased with distance from the diversion (see Day et al., 2009 and references within, de Mutsert, 2010), impacts were still often evident down estuary, but were highly variable and likely influenced by proximity to the Gulf, the openness of Breton Sound estuary, and estuarine and climatic variability.

The low impact stations examined in this study were highly exposed to the Gulf of Mexico and located 30 km downstream from CFD itself. Consequently, we detected few differences in nekton assemblages at these stations, and changes that we did see were lagged. Direct effects of CFD on nekton at these downstream stations are likely limited by the decreasing level of hydrographic and sediment impacts with distance from CFD (see review by Day et al. (2009)). For example, Lane et al. (1999) found that CFD under FLOW management had very limited impacts on water quality, with sediments trapped within a few kilometers, rapid assimilation of nutrients immediately downstream of the structure, and short-term impacts on salinity.

In our study, differences in nekton abundance, diversity and assemblages at down estuary stations were only found in the summer (seine and trawl samples), indicating a lagged effect. It is possible that some of these lagged changes were due to displacement of populations with the isohaline (i.e., increases in some common species such as *C. arenarius*, *A. felis*, *F. aztecus*, *L. setiferus*). In a review of several studies downstream from Caernarvon, Day et al. (2009) indicated a temporal lag between discharge and minimum salinity in the lower estuary during 2001 pulsing. While it is not clear if this effect is the norm, this relationship may help explain the fact that most low impact station changes were detected during summer months. Similarly, Rozas et al. (2005) found a difference in nekton assemblage between sites located down estuary from Caernarvon and sites located east of Bayou Terre Aux Boeufs in marshes separated from Caernarvon input months after Caernarvon winter/spring pulse events. They attributed these subtle community changes to lingering salinity effects from the pulsed inputs.

In contrast to the low impact stations, there were clearly changes in nekton abundance, diversity and assemblage at the high impact (upper estuary) stations. Significant changes in nekton assemblages were detected in response to Caernarvon (pre- and post-CFD) with respect to both season and gear types with differences at high-impact gill net (summer only) and seine stations (spring and summer). Additionally, we detected pronounced changes in nekton assemblage between FLOW and PULSE management across all three gear types. While CFD impacts were largely documented in the summer months, assemblage differences detected between FLOW and PULSE management were evident immediately in spring samples, suggesting that differences in the hydrodynamics or flow through the basin, under low and high-flow regimes, may have driven some of the nekton distributions. Variation in the management of freshwater inflow could influence the extent and timing of salinity, water level and marsh flooding impacts at points downstream of CFD (Snedden et al., 2007a).

During high-flow pulses, Caernarvon is capable of freshening the entire estuary for periods up to 1 month; however, during lower flows, freshwater distribution and, consequently, salinity effects are highly variable (Lane et al., 2007; Snedden et al., 2007b). Additionally, during high-flow pulses, the volume of water in upper Breton Sound estuary is replaced over two times, resulting in over half of the annual water turnover (Swenson et al., 2006) and extensive marsh surface flooding (>20 cm) in the upper estuary that extends throughout the pulsed events (Piazza and La Peyre, 2007, Snedden et al., 2007b).Therefore, direct effects of freshening on fisheries may have been confounded with large-scale differences in habitat availability, as well as changes in the capture efficiency of different gear types as physical habitats change. For example, when discharge is less than 100 m^3 s^{-1}, the majority of the diversion output flows down estuary as channelized flow. In contrast, when diversion discharges exceed 100 m^3 s^{-1}, more diverted river water sheet flows over the marsh, raising water levels on the marsh surface (Snedden et al., 2007a). During FLOW management, mean discharge through CFD during spring rarely exceeded 100 m^3 s^{-1}, but during PULSE management discharge consistently exceeded 100 m^3 s^{-1} driving large-scale habitat flooding in the estuary (Table 6). Therefore, some of the nekton assemblage differences we detected may be partially explained by understanding differences in habitat availability that occur between pulsing and non-pulsing management regimes, although, unfortunately, few data exist on marsh flooding during non-pulsed river management.

Two specific habitat effects that have been documented as resulting from high inflow events – increased SAV coverage up estuary, and increased marsh flooding – may improve access for small marsh residents and nursery species to shallow foraging, spawning or rearing habitat (Kimmerer, 2002; Rozas et al., 2005; Piazza and La Peyre, 2007). These habitat changes may not only impact nekton distributions and populations, but they may also affect gear efficiency. For example, nekton effects documented at seine stations during PULSE management involved both increased abundance in ubiquitous species (i.e., *A. mitchilli*) and decreased abundance in marsh residents (i.e., *C. variegatus* and *P. latipinna*). The observed decrease in marsh residents may have been due to the fact that changes in physical habitat availability made marsh habitat available to residents, displacing their populations to an area where they were not captured by the seine nets. Using a drop sampler on the marsh surface immediately downstream from Caernarvon during spring pulses, Piazza and La Peyre (2007) found that greatest densities of marsh residents, including *C. variegatus*, were captured on the marsh surface when water depth was between 11 and 20 cm. If seine sampling occurred during this level of flooding, it is possible that the apparent reduction in *C. variegatus*

Table 6
Number of days of mean daily discharge (m^3 s^{-1}) from the Caernarvon Freshwater Discharge structure into Breton Sound, LA during spring (March–June). When flow is less than 100 m^3 s^{-1}, 99% of diverted river water flows through channelized flow routes and does not traverse vegetated marsh as sheet flow (Snedden et al., 2007a,b).

	Year	Mean daily discharge (m^3 s^{-1})		
		50–99	100–149	>150
FLOW	1993	0	0	0
	1994	1	0	0
	1995	0	0	0
	1996	19	6	0
	1997	0	0	0
	1998	8	6	0
	1999	1	6	0
	2000	7	49	0
PULSE	2001	27	1	13
	2002	2	0	12
	2003	0	1	3
	2004	2	2	15
	2005	4	2	20
	2006	53	48	0
	2007	6	74	8

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may have been reflecting a population displacement of this species to more optimal habitat. Therefore, it is likely that nekton are not simply responding to changed salinity, as one might predict but are also keying into other factors such as changes in habitat availability, water depth or flow (Kneib, 1997; Kimmerer, 2002; Rozas et al., 2005; Piazza and La Peyre, 2007; Day et al., 2009).

Pelagic species may also respond to changes in physical habitat, although what looks like a significant change in abundance and assemblage at a static station, may simply reflect displacement seaward (Laprise and Dodson, 1993; Kimmerer, 2002). For example, the gill net data showed decreases in some important species including *C. nebulosus*, and *M. cephalus*; changes in abundance of these species may be due to displacement of their population centers down estuary with the isohaline. In the San Francisco Estuary, Kimmerer (2002) suggested that abundance of marine species may respond negatively to flow due simply to seaward displacement of their habitat, but it is less clear as to the overall impact on population size (Day et al., 2009).

There are a number of other factors that complicate efforts to precisely link inflow and its management to estuarine conditions and processes. For example, climate patterns, river stages, and estuarine variability have been found to both enhance and moderate the effects of riverine inflow (i.e., Twine et al., 2005; Snedden et al., 2007a; Piazza et al., 2010,). Variability in meteorological factors associated with the El Niño Southern Oscillation (ENSO) have been shown to affect the surface water balance and streamflow within the Mississippi River basin in different ways, making climatic effects on Mississippi River flow highly complex and often difficult to identify (Twine et al., 2005). Although our study spans a 20-yr time period, we did not specifically consider climate variability in these analyses, except insofar as water temperature and salinity may have been affected. However, recent work has shown many estuarine communities may be affected by large-scale climate forcing that affects their abundance and distribution (i.e., Zimmerman et al., 2000; Garcia et al., 2004; Meynecke et al., 2006; Piazza et al., 2010). In fact, studies in Louisiana have demonstrated that climatological forcing can affect nekton abundances and distribution through its effect on precipitation, regional wind patterns, river discharge, and associated environmental variables (Childers et al., 1990; O'Connell et al., 2004; La Peyre et al., 2009; Piazza and La Peyre, 2009; Soniat et al., 2009; Piazza et al., 2010).For example, Piazza et al. (2010) documented a teleconnection between winter ENSO conditions and juvenile brown shrimp (*Farfantepenaeus aztecus*) abundance in Breton Sound following the spring, and this relationship was forced by a combination of the quantity of freshwater and remote alongshore wind forcing. In this study, our analyses simply divided the data by flow and by pulsing management, but failed to account for variability in Mississippi River discharge during the different years and event or differences in larger-scale conditions in the Mississippi River that could influence the discharge and environmental conditions of the water.

While conditions that affect discharge are often difficult to identify or to use in predictive models, river discharge has been identified as a driver of nekton community dynamics (Montagna and Kalke, 1992; Loneragan and Bunn, 1999; Alber, 2002; Livingston et al., 1997; Kimmerer, 2002; Rozas et al., 2005; Piazza and La Peyre, 2007; Day et al., 2009). Management of the freshwater inflow at Caernarvon had subtle effects on the nekton community downstream based on management regime (flow versus pulse), geographic location (up versus down estuary), and time frame (spring/immediate, summer/delayed). While impacts were largely limited to stations close to CFD, temporal effects from the diversion were evident in both spring and summer, suggesting that, in the short-term, the diversion had both immediate and lagged (3 months) effects on the nekton community. The fact that we did not detect stronger impacts of CFD or river management regimes may be due to the effects of large-scale modifiers (i.e., climate) that may mask or enhance the effects of the managed flow regimes. Depending on the objectives of the CFD for any given year, river management (i.e., discharge amount and pattern) could be altered on an annual basis, depending on climate patterns and other short-term goals, to promote ecosystem health and productivity.

While conditions that affect discharge are often difficult to identify or to use in predictive models, river discharge has been widely identified as a driver of nekton community dynamics (Montagna and Kalke, 1992; Loneragan and Bunn, 1999; Alber, 2002; Livingston, Kimmerer, 2002; Rozas et al., 2005; Piazza and La Peyre, 2007; Day et al., 2009). Understanding the mechanisms which drive the nekton responses are key to better understanding the dynamics of these systems, and their sensitivity to management changes. This study, using both long-term records of river discharge and nekton community composition, was able to explicitly link changes in nekton community distribution with discharge timing and flow rate and demonstrate how these variations in discharge can alter impacts downstream. Our findings indicate that these impacts may result from a combination of salinity effects, similar to de Mutsert's (2010) findings, but that these impacts may also be largely driven by variation in physical habitat availability as has been suggested by Rozas et al. (2005) for this same basin, and for select species in the northern San Francisco Estuary (Kimmerer, 2002; Kimmerer et al., 2009; Feyrer et al., 2006). In particular, our comparison of the two types of river management (flow and pulsed), indicates that higher pulsed flows may result in greater short-term changes to habitat availability and physicochemical characteristics in the receiving basin, as compared to smaller, lower flow diversion events, thus impacting nekton assemblages differently. Knowing the dominant mechanisms that explain estuarine response, and linking the timing and flow rates of freshwater input to those dominant mechanisms, is the key to building predictive models which can inform and guide river management; what remains is to better understand how changing discharge timing and flow may interact with these subtle changes in community composition and ultimately alter energy flow or food web interactions (Kimmerer, 2002; Rozas et al., 2005; Day et al., 2009; Piazza, 2009; de Mutsert, 2010).

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