

Early marine distribution and trophic interactions of juvenile salmon in
Puget Sound

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Abstract

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Some species of Pacific salmon (*Oncorhynchus* spp.) in Puget Sound have been experiencing widespread declines. Of particular concern are the wild fall-run chinook salmon (*O. tshawytscha*), which are believed to have the longest residence in and dependence on the estuarine environment. There is mounting evidence that growth during the early marine residence of most ocean-type species of anadromous Pacific salmon determines overall marine survival trends. I studied juvenile salmon at delta, nearshore, and neritic sites in a northern (NPS) and a southern (SPS) Puget Sound sampling region from April through September 2001 and 2002 to evaluate spatial and temporal differences in distribution, size structure, and diet among species (chum, pink, coho, and chinook) of salmon and between hatchery and unmarked (coho and chinook) salmon. With this basic life history information, I used the Wisconsin bioenergetics model to compare spatially and seasonally relevant quantitative estimates of consumption demand and growth performance between species of juvenile salmon, and between hatchery and unmarked chinook salmon emigrating through nearshore environments in Puget Sound. I found that foraging conditions for juvenile salmon were dynamic, varying spatially, annually, and seasonally. Ultimately, spatial and temporal differences in environmental conditions and the forage base may significantly influence the potential for growth and survival of juvenile salmon entering different areas of Puget Sound.

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INTRODUCTION

Need/Rationale

Many Pacific salmon stocks in Puget Sound are experiencing widespread declines. All Puget Sound chinook salmon (*O. tshawytscha*) and Hood Canal summer-run chum salmon (*O. keta*) are listed as threatened, while Puget Sound coho salmon (*O. kisutch*) are candidates for listing under the Endangered Species Act (ESA). These species employ different (and often multiple) life history strategies, however all use Puget Sound for feeding and migration on their journey to the Pacific Ocean. While there is valuable background information on juvenile salmon in Puget Sound and Hood Canal from the 1970's and 1980's, little is known about the ecology of juvenile salmon in current times during their residence in Puget Sound. Puget Sound may serve as an important rearing environment during a potentially critical transition from freshwater to the open ocean for these juvenile salmon.

The highest mortality during the period between seaward migration and adult return of Pacific salmon is believed to occur in the estuarine and early marine stages (Parker 1962; Royal 1962; Furnell and Brett 1986). Estimates for this early “coastal” mortality rate ranged between 55 and 75% for juvenile pink salmon (*O. gorbuscha*) in British Columbia (Parker 1968). A modeling study on factors affecting declines in Snake River spring/summer chinook salmon concluded that, while much-advocated mitigation to dam-induced mortality, including dam breaching, may reduce mortality on chinook salmon, reductions in estuarine/early ocean mortality must be reduced by 5-10% to stabilize these salmon stocks (Kareiva et al. 2000). There is mounting evidence that estuarine/early marine residence is a “critical period” (Hjort 1914) for most species of anadromous Pacific salmon and that growth during this period determines overall marine survival trends (Holtby et al. 1990; Hargreaves 1997; Murphy et al. 1998; Tovey 1999).

Most explanations for early marine mortality have focused on either food limitation or predation. Beamish and Mahnken (1998) incorporated both of these explanations into a cohesive and more explicit “critical size – critical period” hypothesis. In their hypothesis, regulation of salmon abundance through ocean mortality occurs in

two stages. The first stage occurs soon after juvenile salmon enter the estuarine or nearshore marine environment. Mortality in this phase is hypothesized to be mainly due to predation. Size at this stage is critical because it partially determines the amount of predation risk. According to size-spectrum theory, larger, fast-growing individuals spend less time vulnerable to the many gape-limited predators than their smaller and slower-growing conspecifics (Sogard 1997). The densities of the predators and juvenile salmon also affect predation risk. The second big peak in mortality comes in the late fall and winter of their first year in the ocean and is a function of the condition of the juvenile. It is the growth preceding this stage, mainly during the summer, which is critical in ensuring the juvenile reaches a size and condition that will reduce its chances of being “culled” during its critical first winter. The final size of salmon populations are mainly set after this first winter, and shifting ocean-climate conditions will cause the stock level to fluctuate around a mean carrying capacity (Beamish and Mahnken 1998).

Smolt size at ocean entry is considered important for the survival of some salmon stocks (Parker 1971; Healey 1982; Ward et al. 1989; Henderson and Cass 1991). Dietary overlaps among juvenile salmon, and between hatchery and wild salmon, may result in inter- and intra-specific competition that would negatively affect growth rates and overall smolt size (Fisher and Pearcy 1996; Sturdevant 1999). In addition, seasonal shifts in prey resources and water temperature may affect the potential growth rates of juvenile salmon. Poor quality feeding areas, which may vary over short and longer time frames, may result in increased susceptibility to predation due to poorer condition and smaller sizes of fish (Brodeur et al. 1992; Perry et al. 1996). The quality of feeding areas can also affect migration rates and residence times, since salmon are believed to leave areas of poor food quality faster than when food sources are abundant (Healey 1982; Simenstad and Salo 1982; Orsi et al. 2001). The carrying capacity of localized areas may be exceeded when episodically high densities of salmon are produced by coincident releases of large numbers of hatchery salmon during peak wild salmon emigrations, leading to competition for a limited food supply if diets are similar.

Background

Estuarine and coastal marine environments play an important role in the life history of salmon, although the relative importance differs among species due to differences in residence times and utilization of these environments (Simenstad et al. 1982; Aitken 1998). Salinity gradients in estuaries provide a physiological transition zone for migrating juveniles as they undergo smoltification (Simenstad et al. 1982; Thorpe 1994). Physical characteristics, including structure provided by shallow water habitat and emergent aquatic vegetation or woody debris, and high turbidity regions, may facilitate predator avoidance (Simenstad et al. 1982; McMahon and Holtby 1992; Gregory and Levings 1996, 1998). The higher productivity of prey communities in estuarine and marine waters (relative to freshwater) provides favorable foraging conditions and valuable rearing and nursery habitat for juvenile salmon (Simenstad et al. 1982; Thorpe 1994; Aitken 1998). Rapid growth rates of up to 5-10% body weight/day (which is among the highest for all life history stages) have been recorded in coastal and estuarine waters (Table 1).

Estuarine and nearshore marine environments may be particularly important to chinook salmon, which reside much longer in estuarine environments than the other species of Pacific salmon (Stober et al. 1973; Shepard 1981; Simenstad et al. 1982). The diverse life history strategies of chinook salmon result in migrations of juveniles into estuaries throughout much of the year (Reimers 1973; Iwamoto and Salo 1977). Fall-run chinook salmon subyearlings and spring-run yearlings enter Puget Sound as early as March, and populations peak in nearshore areas in the summer months, although some may persist through the fall. Juvenile chinook salmon are known to spend 6-16+ weeks in Puget Sound and Hood Canal with individuals remaining for 1-7 weeks (Simenstad et al. 1982). There are also resident chinook salmon that remain in Puget Sound until maturity (Simenstad et al. 1982). Rapid growth rates, 0.37-0.87mm/day, have been recorded for juvenile chinook salmon in Puget Sound (Salo 1969). The relatively high usage of (and potential dependence on) Puget Sound estuaries by ESA-listed fall-run chinook salmon suggests that juvenile outmigration through Puget Sound may be a critical period in their life history.

Salmon, while often described as opportunistic feeders (Healey 1982), do show some diet preferences in estuaries by species, size, season and habitat (Table 2; Kaczynski et al. 1973; Conley 1977; Harris and Hart 1977; Fresh et al. 1978; Simenstad et al. 1980; Fresh et al. 1981; Godin 1981; Healey 1982; Pearce et al. 1982; Parametrix 1985; S. Bollens, San Francisco State University, unpublished data; J. Cordell, University of Washington, unpublished data; J. Cordell and C. Simenstad University of Washington, unpublished data; C. Simenstad and J. Cordell, University of Washington, unpublished data). Chinook and coho salmon, which are larger in size during their seaward migration, tend to be increasingly piscivorous as they grow, whereas pink and chum salmon feed mainly on invertebrates (Kaczynski et al. 1973; Healey 1982; Simenstad et al. 1982). Epibenthic and planktonic crustaceans are dominant prey items in the diets of all salmon species. In general, as fish grow and move from shallow nearshore environments to offshore waters, diets shift from epibenthic and neustonic prey items to more planktonic and nektonic prey. Early in their estuarine residence, and at the smaller sizes, pink and chum salmon feed mainly on epibenthic harpacticoid copepods and other epibenthic crustaceans. Chinook salmon, which tend to have the most diverse usage and dependence on estuarine environments, have the most diverse diets, feeding largely on neustonic and drift insects. Coho salmon also have diverse diets but tend to focus more on larger planktonic crustaceans (euphausiids, amphipods, and crab larvae) and fish.

Diet information for juvenile salmonids in nearshore (Kaczynski et al. 1973; Conley 1977; Fresh et al. 1978; Fresh et al. 1981; Pearce et al. 1982; Parametrix 1985; S. Bollens, San Francisco State University, unpublished data; J. Cordell, University of Washington, unpublished data; J. Cordell and C. Simenstad University of Washington, unpublished data; C. Simenstad and J. Cordell, University of Washington, unpublished data) and neritic (Fresh et al. 1981; Beamish et al. 1998) Puget Sound waters is relatively limited and dates mainly to the 1970's (Table 3). Major diet items for all species included euphausiids, crab larvae, insects, amphipods and copepods (epibenthic and planktonic), as well as larval and juvenile fishes for chinook and coho salmon. The greatest potential for dietary overlap appeared to exist between comparably sized chinook and coho salmon (Conley 1977; Parametrix 1985), and between chum and pink salmon

(Kaczynski et al. 1973; Conley 1977; Simenstad et al. 1980; Parametrix 1985) at nearshore sites, and between coho and chum salmon in neritic waters (Beamish et al. 1998). In addition, there may be substantial dietary overlap and potential for competition between and among hatchery and wild salmon, especially during large hatchery releases which tend to coincide with peak outmigration of wild salmon. In Puget Sound, hatchery production constitutes 70-75% of the salmon (mainly chinook and coho salmon) population in Puget Sound (HSRG 2002).

In the estuarine and marine environment, juvenile salmon face many potential predators including larger salmon and trout, Pacific cod (*Gadus macrocephalus*), walleye pollock (*Theragra chalcogramma*), spiny dogfish (*Squalus acanthias*; Table 4), birds and marine mammals (Emmett 1997). Few studies in estuaries have quantified juvenile salmonid mortality due to piscivores. In Puget Sound, there is concern that releases of yearling hatchery chinook salmon and juvenile coho salmon may result in intrageneric predation and cannibalism that may negatively impact natural populations (Buckley 1999). A few studies have reported low levels (≤ 1 fish/stomach) of salmonid predation based on estimates from limited diet analysis (Mathews and Buckley 1976; Cardwell and Fresh 1979; Fresh et al. 1981; Simenstad et al. 1982), however most studies were not designed to investigate predation. In order to infer an overall potential predation impact, diet data must be collected at the appropriate spatial and temporal scales and used in conjunction with predator abundances (Beauchamp et al. 1995). Even low apparent rates of predation could produce significant impacts if the predator abundance is high.

It is essential to take a food web perspective in order to understand the complicated array of potential processes and interactions affecting aquatic communities (Paine 1980, 1988). Determining which processes regulate populations in a food web, and the strength of interactions between populations, gives us insight into the underlying mechanisms and conditions that may mediate them (Paine 1980; Brandt and Hartman 1993). Quantifying consumption rates of a predator on specific prey populations is one way to estimate interaction strengths. There are various methods for estimating consumption (Ney 1990). Direct measurements are the most labor and time-intensive, involving field (and laboratory) measurement of gut contents, fullness, and gastric

evacuation rate. Results are subject to sampling bias, but this method produces realistic data for individual fish over discrete time intervals. Production-based approaches take a broad and simplified view of the food web, relating the biomass of a consumer population to the biomass of its prey base. This approach can be used with minimal labor and data to rapidly calculate consumption for populations on an annual basis, however individual and intra-annual consumption estimates are not possible and results are limited by the accuracy of the inputs.

Bioenergetically-based food web models, used in conjunction with directed field sampling, provide an effective method for quantifying trophic interactions in a temporal, spatial, and ontogenetic framework (Ney 1990; Hansen et al. 1993). The requisite field sampling is less labor-intensive than for direct measurement methods, and much of the physiology of feeding and metabolism is built in as model parameters. The widely used Wisconsin bioenergetics model (Hanson et al. 1997) uses an energy-balance approach in which total energy consumption (C), over a particular time frame, equals the sum of growth (G, positive or negative), metabolic costs (M), and waste losses (W). The Wisconsin model is very adaptable and operates on a daily time step, which allows for a fine-grained analysis of trophic interactions over short time scales. This sensitivity is particularly appropriate for dynamic conditions, like those experienced by emigrating juvenile salmon, where residence times are variable and short-term, and environmental factors (i.e., water temperature), diets, and sizes are rapidly changing. Bioenergetic models are, however, limited by the accuracy of their assumptions and input parameters, and expanding individual consumption estimates to a population level may magnify the individual error. The model is most useful for making relative comparisons of fish consumption rate estimates, more so than for making precise quantitative predictions or estimates of growth (Kitchell et al. 1977; Bartell et al. 1986; Ney 1993).

The Wisconsin bioenergetics model has been used successfully to identify carrying capacity of systems, seasonal bottlenecks in food supply, and impacts of predation primarily in freshwater systems (Kitchell et al. 1977; Stewart et al. 1981; Stewart and Ibarra 1991; Beauchamp et al. 1995; Rand et al. 1995; Cartwright et al. 1998; Baldwin et al. 2000). The model has also been used to estimate temporal consumption

demand and growth in estuarine and marine waters (Brandt et al. 1992; Brodeur et al. 1992; Ciannelli et al. 1998; Davis et al. 1998). In coastal marine waters, the bioenergetics model has yielded consumption estimates within 5-10% of independently generated field estimates for juvenile chinook and coho salmon (Brodeur et al. 1992). Other applications of the model include estimating mortality due to predation and evaluating and comparing growth performance under differing conditions like water temperature, prey quality and availability, and consumer density.

In the following chapters, I examine the feeding conditions and growth performance of juvenile salmon in Puget Sound by using bioenergetics modeling to synthesize information on their early marine trophic dynamics obtained from two years of sampling and from supporting literature. During two seasons of field sampling in a northern and a southern Puget Sound area, I obtained information on timing, size structure and diet of juvenile salmon at nearshore and neritic locations. Focusing on ESA listed chinook salmon, I used the Wisconsin bioenergetics model to determine and compare spatially and seasonally relevant quantitative estimates of consumption demand and growth performance between hatchery and wild (unmarked) chinook salmon and between different salmon species. I also investigated how seasonal, annual, and regional shifts in diet, temperature, and structure and sizes of the salmon community affect consumption of key prey taxa and salmon growth performance. A better understanding of the temporal distribution, trophic interactions, and survival of Puget Sound salmon stocks is necessary to identify and potentially remedy factors contributing to their decline.

NULL HYPOTHESES

Overarching hypothesis: Early marine residence represents a critical period for growth and survival of juvenile salmon in Puget Sound.

Primary question: *What is the role of nearshore and neritic Puget Sound habitat in the life history of juvenile salmon?*

1. There are no differences in the timing and relative abundance (as measured by catch rates) among sizes and species of salmon, between hatchery and unmarked juvenile salmon, rearing in or migrating through northern and southern Puget Sound sites.
2. There is no difference in catch timing, relative abundances, sizes, and temporal diet composition patterns of salmon between 2001 and 2002, between northern and southern Puget Sound sites and between nearshore and neritic sites.
3. There is no significant diet overlap among salmon species or between hatchery and unmarked salmon conspecifics.
4. There is no predation among juvenile salmon species or between hatchery and unmarked salmon in nearshore Puget Sound waters.

Secondary question: *Do feeding conditions (thermal experience, prey composition and energetic quality) or growth performance of juvenile salmon change during their residence in Puget Sound?*

1. There are no differences in the estimated growth and modeled consumption demand among sizes and species of salmon, or between hatchery and unmarked juvenile salmon, rearing in or migrating through northern and southern Puget Sound sites.
2. There are no differences in the estimated growth and modeled consumption demand for salmon within the outmigration “season”, between sampling years, between northern and southern Puget Sound sites, and between nearshore and neritic sites.
3. There is no difference in growth efficiency for salmon within the outmigration “season,” between sampling years, between northern and southern Puget Sound sites, and between nearshore and neritic sites.

OBJECTIVES

1. Measure and compare temporal and spatial distributions of juvenile salmon by species, size, age, and by hatchery or wild (unmarked) origins for chinook and coho salmon, in delta, nearshore and neritic waters of northern and southern Puget Sound during April through September, 2001 and 2002.
2. Describe and compare the temporal diet composition of juvenile salmon by capture zone (delta, nearshore or neritic), species, size, age, and by hatchery or wild (unmarked) origin for chinook and coho salmon, in the northern and southern regions of Puget Sound.
3. Using the bioenergetics model, estimate spatially and seasonally relevant temporal consumption demand and compare growth performance metrics for pulses of outmigrating juvenile salmon.
4. Determine the potential role of predation by juvenile salmon on the mortality of other juvenile salmon during their overlapping residence in Puget Sound.

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Table 1. Estuarine/early marine growth rates for outmigrating juvenile salmon.

Salmon Species	Growth Rate (mm/d or % wt/d)	Sample Area	Reference
Chinook (<i>O. tshawytscha</i>)	0.37mm/d	(Duwamish estuary) Puget Sound, WA	Salo 1969
Chinook (<i>O. tshawytscha</i>)	0.81-0.87mm/d	Nanaimo estuary, B.C.	Sibert 1975
Chinook (<i>O. tshawytscha</i>)	5.5%	Nanaimo estuary, B.C.	Healey 1982
Chinook (<i>O. tshawytscha</i>)	3.5%	Nitinat estuary, B.C.	Healey 1982
Chum (<i>O. keta</i>)	5.7%	Nanaimo estuary, B.C.	Healey 1979
Chum (<i>O. keta</i>)	5.7-8.6%	Hood Canal, WA	Salo et al. 1980
Chum (<i>O. keta</i>)	2.3-4.1%	Gulf of Alaska ("straits")	Orsi et al. 2001
Pink (<i>O. gorbuscha</i>)	3.1-7.1%	Auke Bay, Gulf of Alaska	Mortensen et al. 2000
Pink (<i>O. gorbuscha</i>)	1.5-7.6%	British Columbia	LeBrasseur and Parker 1964; Healey 1980
Pink (<i>O. gorbuscha</i>)	3.5-5.2%	Prince William Sound, AK	Willette 1996
Coho (<i>O. kisutch</i>)	1.5%	Nanaimo estuary, B.C.	Healey 1982
Coho (<i>O. kisutch</i>)	1.9%	Strait of Georgia, B.C.	Healey 1982

Table 2. Prey items, and their associated habitat, for juvenile Pacific salmon in estuarine and nearshore marine waters.

Habitats are ranked in order of importance to dietary contribution.

HABITAT	PREY	CHINOOK	COHO	CHUM	PINK
<i>Benthos/Epibenthos</i>		3	3	1	2
	Cumacean				
	Fish/invertebrate eggs				
	Gammarid amphipod	*		*	
	Harpacticoid copepod			*	*
	Isopod				
	Mysid		*		
	Ostracod				
	Polychaete	*	*		
	Shrimp		*		
<i>Plankton</i>		4	1	2	1
	Barnacle larvae/slough				
	Calanoid copepod			*	*
	Cladoceran				
	Crab larvae	*	*	*	*
	Euphausiid	*	*		
	Gammarid amphipod				
	Hyperiid amphipod				
	Larvacean			*	*
<i>Nekton</i>	Fish (larval, juvenile)	2	2	4	4
	<i>Herring</i>	*			
	<i>Sand lance</i>	*	*		
	<i>Salmon</i>		*		
<i>Neuston</i>	“Insects” - terrestrial and aquatic	1	4	3	3
	<i>Arachnidae</i>				
	<i>Coleoptera</i>				
	<i>Diptera</i>	*		*	
	<i>Homoptera</i>				
	<i>Hymenoptera</i>	*		*	
	<i>Lepidoptera</i>				
	<i>Trichoptera</i>				

* Dominant prey types

Table 3. Studies detailing dietary information on juvenile salmon in nearshore and neritic Puget Sound and Hood Canal waters.

REFERENCE	AREA*	ZONE**	DATE	JUVENILE SALMON DIETS
<i>Bax et al. 1978</i>	Hood Canal	nearshore, neritic	Jan-Jul 1977	chum, coho, chinook, cutthroat
<i>Beamish et al. 1998</i>	CPS	neritic, offshore pelagic	Apr-Sep 1997	chinook, chum, coho
<i>S. Bollens, San Francisco State University, CA, unpublished data</i>	Hood Canal	nearshore, offshore	Apr-Oct 1985-1987	chinook, chum
<i>Conley 1977</i>	Everett Bay, NPS	nearshore, neritic	Apr-May 1975	chinook, chum, coho
<i>J. Cordell, University of Washington (UW), Seattle, WA, unpublished data</i>	Shilshole Bay, CPS	nearshore	Jun-Aug 1999	chinook
<i>J. Cordell and C. Simenstad, UW, unpublished data</i>	Commencement Bay, CPS	nearshore	Mar-Jun 1983-1985	chinook, chum, coho
<i>Fresh et al. 1978</i>	Nisqually Reach, SPS	nearshore, neritic	Mar-Aug 1977-1978	chinook, chum, coho, pink
<i>Fresh et al. 1981</i>	CPS, SPS	nearshore, neritic, offshore pelagic	Aug 1978-Sep 1979	chinook, chum, coho
<i>K. Fresh, NOAA-Fisheries, Seattle, WA, unpublished data.</i>	SPS	nearshore, neritic	Mar 1974-Feb 1975; Feb-Jul 1978	chinook, chum, coho; chinook
<i>Kaczynski et al. 1973</i>	Port Susan - NPS, Anderson Island - SPS, Hood Canal	nearshore	Apr-Jun 1970-1971	chum, pink
<i>Parametrix 1985</i>	Everett Bay, NPS	nearshore, neritic	Apr-May 1984	chinook, chum, coho, pink
<i>Pearce et al. 1982</i>	Nisqually Reach, SPS	nearshore	Apr-Sep 1979-1980	chinook, chum, coho
<i>Simenstad et al. 1980</i>	Hood Canal	nearshore, neritic	Jan - Jul 1977-1979	chum, coho, chinook, cutthroat
<i>C. Simenstad and J. Cordell, UW, unpublished data</i>	Duwamish Head, CPS	nearshore	June 1980	chinook

*central Puget Sound (CPS), northern Puget Sound (NPS), southern Puget Sound (SPS)

**nearshore = intertidal and shallow subtidal (beach seine); neritic = shallow surface waters (tow net);

offshore pelagic = top 30-45m of surface waters over deep bottom (purse seine, trawl)

Table 4. Potential piscivorous juvenile salmon predators in the estuary/early marine environment.

Predator Species	Salmon prey	Sample Area	Reference
Juvenile coho salmon	pink and chum salmon	British Columbia, Gulf of Alaska, Puget Sound	Parker 1971, Kaczynski et al. 1973, Mortensen et al. 2000
Subadult coho salmon	chinook salmon	Puget Sound, WA	Fresh et al. 1981
Adult coho salmon	juvenile salmon	Gulf of Alaska	Wing 1985, Orsi et al. 2000
Subadult chinook salmon	chinook salmon	Pacific Ocean (near mouth of Columbia River)	Fresh et al. 1981
Coastal cutthroat trout	juvenile salmon	Puget Sound and Hood Canal, WA	Salo et al. 1980; Fresh et al. 1981; Jauquet 2002
Steelhead	chinook salmon	Pacific Ocean (near mouth of Columbia River)	Fresh et al. 1981
Dolly varden	pink, juvenile salmon	Gulf of Alaska, B.C. and AK	Lagler and Wright 1962, Mortensen et al. 2000
Sculpins	pink salmon	Gulf of Alaska	Mortensen et al. 2000
Pacific staghorn sculpin	juvenile salmon	Hood Canal, WA	Salo et al. 1980
Pacific cod	juvenile salmon	Hood Canal, WA	Salo et al. 1980
Spiny dogfish	chinook and coho salmon	Straits of Georgia, Gulf of Alaska	Beamish et al. 1992, Orsi et al. 2000
Walleye pollock	juvenile salmon	Prince William Sound, AK	Willette 1996